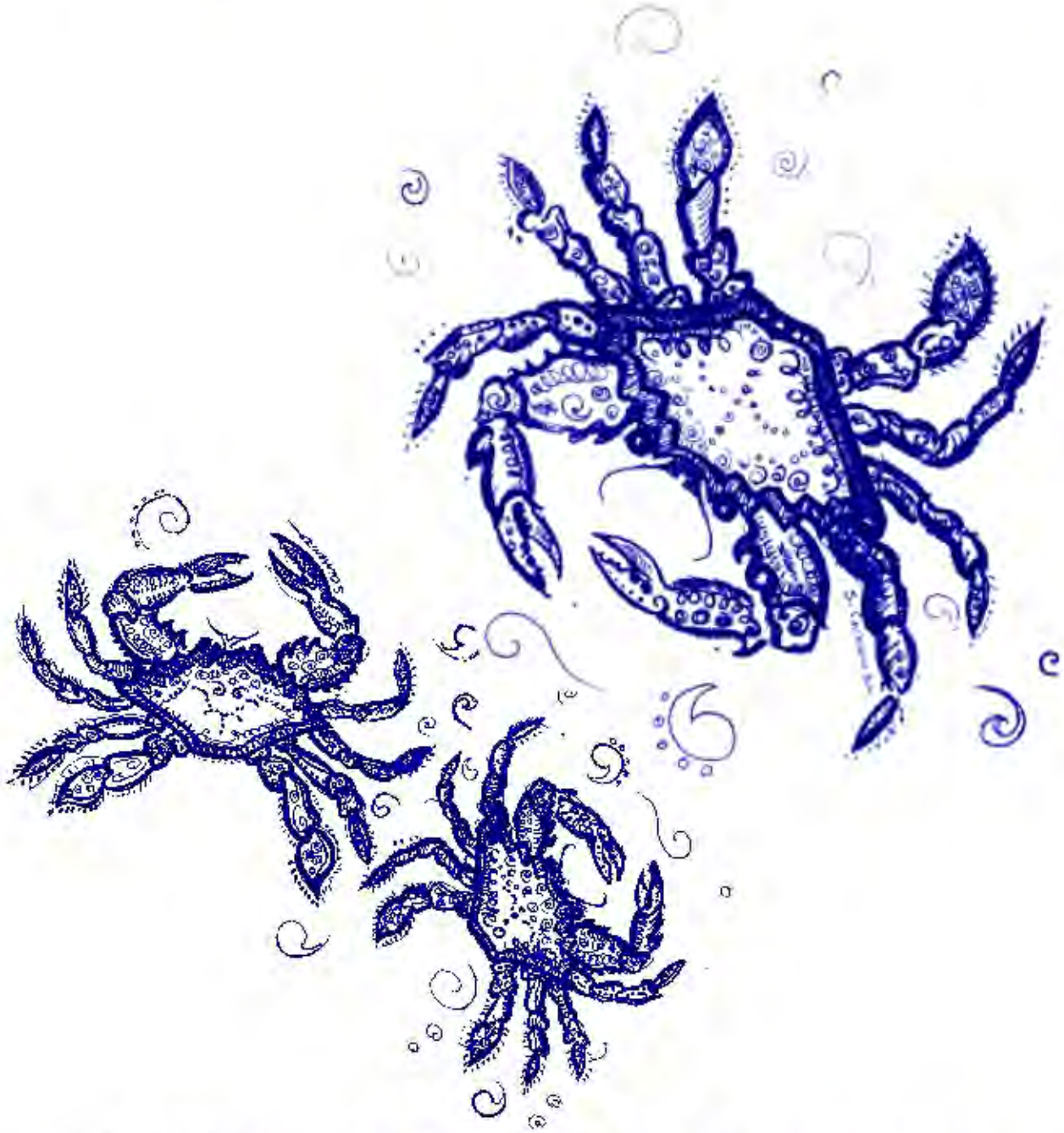
Proceedings:

Blue Crab Mortality Symposium



Gulf States Marine Fisheries Commission

July 2001 **Number 90**

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PROCEEDINGS: BLUE CRAB MORTALITY SYMPOSIUM

held in conjunction with

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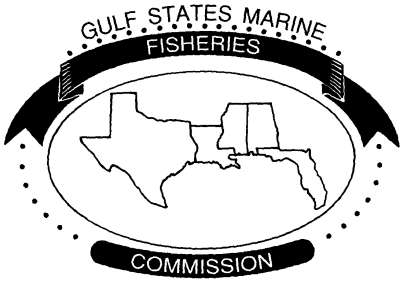

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Preface

A symposium on sources and measurement of blue crab (*Callinectes sapidus* Rathbun) mortality was held in conjunction with the Annual Meeting of the Crustacean Society in Lafayette, Louisiana, on May 28 and 29, 1999. The symposium was sponsored by the Crab Subcommittee of the Gulf States Marine Fisheries Commission (GSMFC). The symposium addressed sources of juvenile and adult blue crab mortality in the form of both review papers and original research findings. The information provided by this Proceedings should stimulate additional questions, investigations, and insights into the sources of mortality on the blue crab population and its implications for the blue crab fishery.

Appreciation is extended to Ms. Cindy Yocom and Ms. Lucia Hourihan for their assistance in the final editing of the proceedings. Thanks also goes to numerous reviewers who provided valuable comment on the papers submitted for this publication.

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Proceedings of the Blue Crab Mortality Symposium 1-17

Effects of Environmental Contaminants on the Blue Crab *Callinectes sapidus*

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Abstract. — A variety of organic and inorganic contaminants, including polycyclic aromatic hydrocarbons (PAHs), organohalogens, pesticides, organometallics and heavy metals, can be present in the blue crab's estuarine environment. Our knowledge of the effects of these contaminants on blue crabs decreases from the molecular, cellular, organismal to the population level. For example, much has been learned about the molecular and cellular mechanisms used by the blue crab to detoxify organic contaminants and heavy metals. In addition, the mechanisms underlying the toxicity and sublethal effects of some classes of contaminants are known. Recent studies have shown that PAHs enhance ecdysone (molt hormone)-dependent gene transcription and cell proliferation. At the organismal level PAHs inhibit growth and molting of juvenile blue crabs, suggesting that PAHs act as endocrine disrupters in the crab. Tributyltin inhibits growth of blue crab oocytes and reduces hatching success of embryos. Heavy metals such as mercury, copper, and cadmium inhibit hatching of blue crab embryos and reduce survival of megalopa and juvenile crabs. Most studies on the effects of contaminants on crabs have been carried out in the laboratory under conditions that may not be environmentally relevant. Little is known about the effects of contaminants on crabs at the population level. A few studies suggest that decreases in populations of blue crabs and grass shrimp have occurred in estuarine creeks impacted by agricultural insecticide runoff.

KEY WORDS: Blue crab, polycyclic aromatic hydrocarbons, pesticides, persistent organochlorines, organometals, heavy metals.

A variety of anthropogenic chemicals, referred to as xenobiotics, can be present in the blue crab's (*Callinectes sapidus*) estuarine environment. Organic xenobiotics include aromatic hydrocarbons, organometallics, organohalogens, and various pesticides, all of which have the potential to affect blue crab growth, reproduction and development. Blue crabs collected from a number of contaminated sites have been found to contain elevated concentrations of each site's contaminants (Marcus and Mathews, 1987; Hale, 1988; Mothershead et al., 1991; Murray et al., 1992). Xenobiotics enter crabs from water, sediment or food via the gill or stomach and accumulate in the lipid-rich hepatopancreas (Figure 1). The crustacean hepatopancreas has many of the functions associated with the vertebrate liver, pancreas and small intestine. These include synthesis and secretion of digestive enzymes, uptake of nutrients and accumulation of nutrient reserves (Wright and Ahearn, 1997). The hemolymph functions as an important avenue for transporting xenobiotics and xenobiotic metabolites. After xenobiotics enter the crab, their fate is determined by the processes of accumulation, biotransformation and elimination. The relative importance of these different processes for a particular xenobiotic depends on a

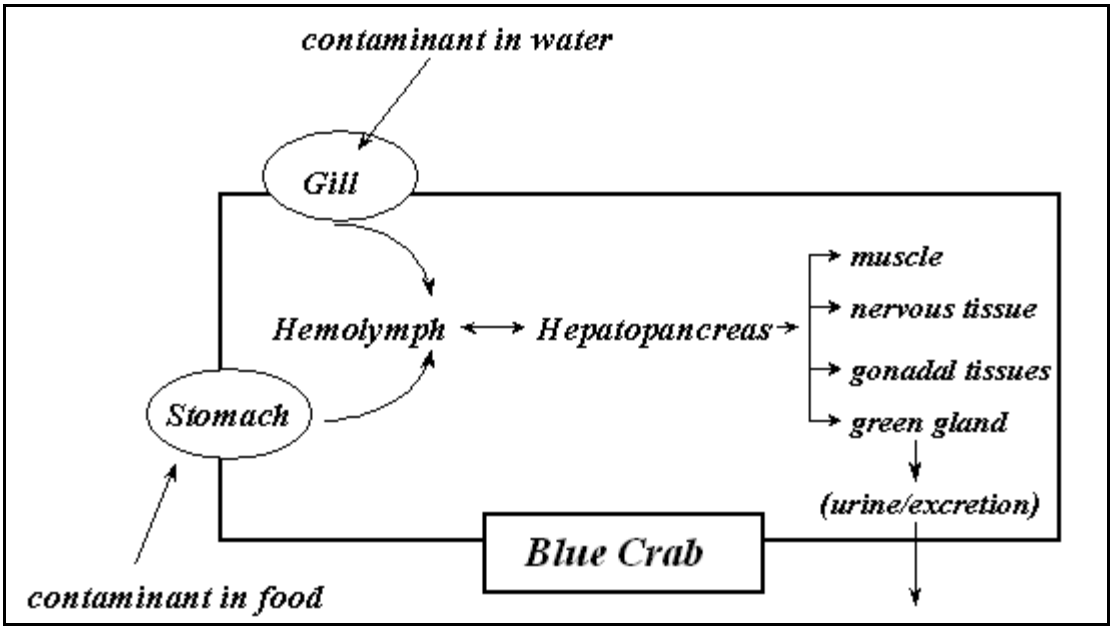

FIGURE 1. — Uptake and bioaccumulation of organic contaminants by blue crabs.

number of factors including the physical-chemical properties of the xenobiotic, the ability of the crab enzyme systems to metabolize the compound and the amount of storage lipid in the crab. Known biotransformation pathways of xenobiotics and their effects in blue crabs are shown schematically in Figure 2.

The first part of our review discusses how blue crabs respond to and are affected by exposure to xenobiotics. While the focus is on the blue crab, there are references to studies done with other crustacean groups, since it is assumed that most crustaceans respond to xenobiotics in a similar manner (James, 1989a; Livingstone, 1991; Kleinow et al., 1992). In the second part of our review we will describe how blue crabs are affected by exposure to toxic metals.

Organic Contaminants

Metabolism of Xenobiotics

Most organic contaminants of concern are hydrophobic. A number of enzyme systems can add polar groups to these compounds which increases their water solubility and thus facilitates their elimination. However, for some compounds the metabolites are more toxic than the parent compound. For example, the binding of certain reactive benzo(a)pyrene metabolites (i.e., arene oxides) to DNA in liver cells of mammals initiates carcinogenesis (Ames et al., 1972). The reactions carried out by biotransformation enzyme systems can be broadly divided into two groups: phase 1 reactions which include oxidation, reduction and hydrolysis; and phase 2 reactions which involve conjugation of sulfate, sugars or peptides to polar groups such as -COOH, -OH, or -NH_2 groups which, in some cases, were added to the xenobiotic during phase 1 reactions. Phase 2 metabolites tend to be highly water soluble and can be more rapidly eliminated from crabs.

One of the most investigated of phase 1 enzyme systems is the cytochrome P-450 dependent monooxygenase (also called mixed function oxidase or MFO) system which oxidizes xenobiotics by hydroxylation, O-dealkylation, N-dealkylation, or epoxidation. Inhibition of cytochrome P-450 by detergents and by treatment with phospholipase C indicate that phospholipids are necessary for MFO activity in blue crabs (Singer and Lee, 1977; Lee and Quattrochi, 1987). Thus, the MFO system in crabs, as in other animals, is a multi-component system composed of phospholipid, cytochrome P-450 and NADPH cytochrome P-450 reductase. Partial purification of cytochrome P-450 from blue

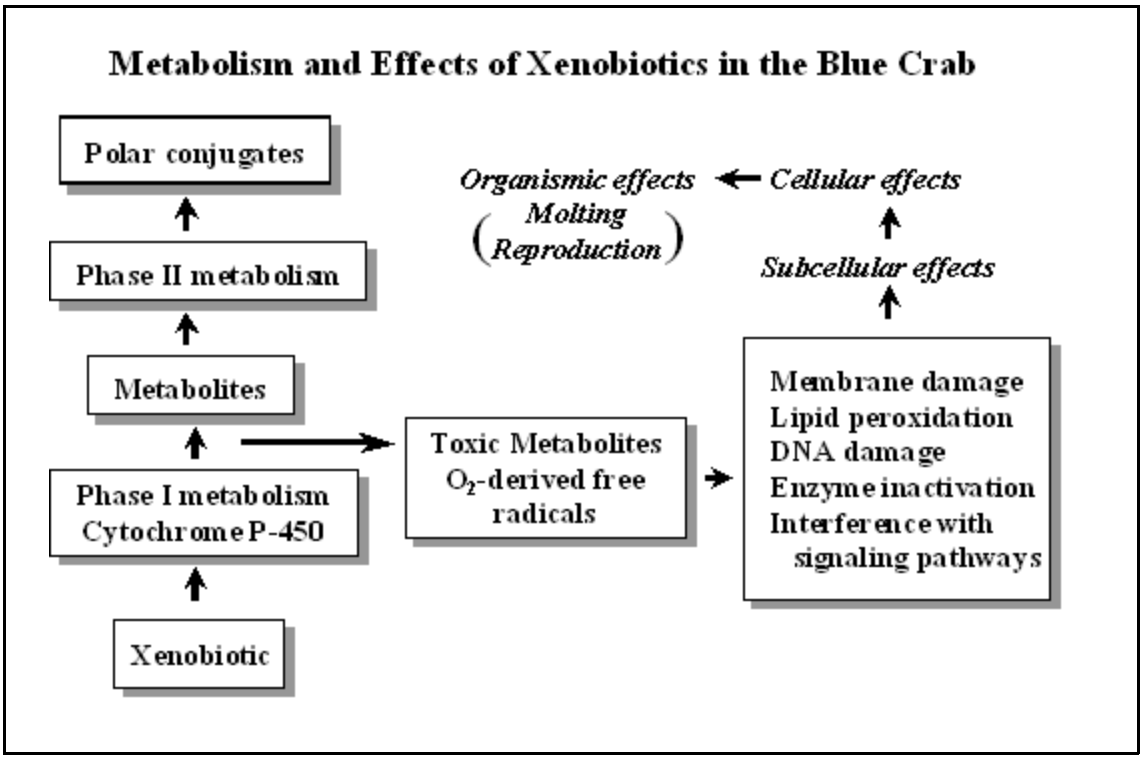

FIGURE 2. — Biotransformation and effects of xenobiotics in blue crabs.

crab hepatopancreas has been achieved by using sodium cholate solubilization of microsomes, affinity chromatography (Octylamine-Sepharose 4B) and hydroxyapatite chromatography (Conner and Singer, 1981).

Phase 2 reactions involve conjugation of phase 1 products with a polar or ionic moiety. The most common moieties involved in these conjugation reactions are glutathione, glucose, and glucuronic acid. In general these conjugation products are water soluble so they are more easily eliminated from the animal than the parent compound. Glutathione-S-transferase catalyzes the conjugation of the nucleophilic tripeptide, glutathione (GSH) to electrophiles which are produced by P-450 systems acting on various xenobiotics. Several electrophilic substrates have been shown to be conjugated to glutathione by blue crab glutathione-S-transferase (Tate and Herf, 1978; Johnston and Corbett, 1986a; Keeran and Lee, 1987).

Phase 1 metabolites containing phenolic or carboxylic acid groups or other nucleophilic centers can undergo glycosylation with uridine diphospho-D-glucuronic acid or uridine diphospho-D-glucose. In crustaceans the sugar moiety is more often glucose than glucuronic acid (Kleinow et al., 1992). In blue crabs an example is the glycoside conjugated to 3-methyl-4-nitrophenol, a metabolite of the organophosphate insecticide fenitrothion (Johnston and Corbett, 1986b). *In vivo* studies have shown that blue crabs form various conjugates of the metabolites of tributyltin oxide, benzo(a)pyrene and chlorobenzoic acid. A significant amount of these metabolites is bound to macromolecules, including GSH-S-transferase (Lee, 1989).

In vivo and *in vitro* studies have shown that blue crab hepatopancreas plays a major role in xenobiotic metabolism (Sheridan, 1975; Lee et al., 1976; Johnston and Corbett, 1986a, 1986b; James, 1989b; Rice et al., 1989; Oberdorster et al., 1998). Cytochrome P-450 and glutathione-S-transferase and other phase 2 enzyme systems have been found in crustacean hepatopancreas (James et al., 1979; James, 1987; James, 1990; Keeran and Lee, 1987; Almar et al., 1988; James and Boyle, 1998). In the blue crab, the cytochrome P-450 dependent MFO

activity of the hepatopancreas is low due to inhibitors released when the tissue is homogenized (James et al., 1979; Lee, 1981, 1986). Activity of MFO is high in the blue crab stomach and green gland (Singer et al., 1980), but low in blood, gill, reproductive tissues, eyestalk, and cardiac muscle (Singer and Lee, 1977). Glutathione S-transferase activity is high in blue crab hepatopancreas and gills (Lee et al., 1988).

Different cells types are found in the crustacean hepatopancreas including E-, F-, R- and B-cells (Al-Mohanna and Nott, 1986; Wright and Ahearn, 1997). The F-, R-, and B-cells are derived from embryonic or E-cells (Biesiot and McDowell, 1995). The R-cells are storage cells with large amounts of lipid, while the F- and B-cells are thought to be important in protein synthesis. (Al-Mohanna et al., 1985; Ahearn, 1988). Lee (1989) introduced a number of ^{14}C- xenobiotics into blue crab food and determined the distribution of the xenobiotics and their metabolites within the hepatopancreatic cells. For compounds not readily metabolized (i.e. hexachlorobiphenyl, Mirex, and DDE) radioactivity is primarily found in the storage lipid in the R-cells. For compounds more extensively metabolized (i.e.. benzo(a)pyrene, tributyltin, pentachlorophenol, 1-chloro-2,4-dinitrobenzene) much of the radioactivity is found in the cytosol of the F-cells (Lee, 1989). It appears that initially these compounds enter R-cell lipids and are then transferred to and metabolized by F-cells, with the principal product being water-soluble conjugates which are eliminated from the crab. The cytochrome P-450 in blue crabs is associated with the endoplasmic reticulum of F-cells (Lee, 1986); whereas, the highest activity of glutathione-S-transferase is found in F-cell cytosol (Keeran and Lee, 1987).

Organismal Responses to Different Classes of Xenobiotics

Blue crabs are exposed in estuaries to various classes of contaminants including polycyclic aromatic hydrocarbons (PAH), organophosphorus pesticides, organochlorine compounds, and organometallics. Each of these classes has very different effects on blue crabs depending on the physical-chemical properties of the compounds as well as the relative importance of the processes of accumulation, biotransformation, and elimination.

Polycyclic Aromatic Hydrocarbons

Polycyclic aromatic hydrocarbons are present in estuaries and nearshore coastal waters as a consequence of crude oil production, shipping and use of petroleum hydrocarbons. They are metabolized by crustacean cytochrome P-450 systems (Lee et al., 1976; Lee, 1981; James, 1989a, 1989b). The polar metabolites produced by the P-450 system can be conjugated to glutathione, glucose, or sulfate (Sanborn and Malins, 1980; Little et al., 1985; Reichert et al., 1985). A variety of PAHs taken up from food and water by blue crabs are oxidized, conjugated and eliminated (Lee et al., 1976; Moese and O'Connor, 1985). Exposure of fish to PAH is correlated with reduced plasma estradiol concentrations, disruption of vitellogenesis, and decreased egg production (Hall and Oris, 1991; Johnson et al., 1993). Exposure of juvenile blue crabs to benzene, dimethylnaphthalene, and the water-soluble fraction of South Louisiana crude oil inhibits growth and molting (Cantelmo et al., 1981, 1982; Wang and Stickle, 1987). Recent studies show that several PAHs enhance ecdysone (molt hormone)-dependent gene transcription and ecdysone-dependent cell proliferation (Oberdorster et al., 1999). Long-term pyrene exposure of grass shrimp, *Palaemonetes pugio*, affects molting and reproduction of exposed males, and offspring of exposed females (Oberdorster et al., 2000). Thus, PAHs can be considered to be endocrine-disrupting chemicals in fish, shrimp and crabs.

Organophosphorus Pesticides

Organophosphate and organochlorine compounds are designed to be arthropod (insect) poisons and, therefore, are inherently toxic to blue crabs and other crustaceans. Organophosphate pesticides impair the nervous system by binding to and inhibiting acetylcholinesterase. Crustaceans are more sensitive to these pesticides than marine fishes by several orders of magnitude (Eisler, 1969; Odenkirchen and Eisler, 1988). Blue crabs are also sensitive to a number of organophosphate insecticides (Schimmel et al., 1983). Johnston and

Corbett (1985, 1986a, 1986b) have reported on the effects and metabolism of the widely used organophosphate insecticide, fenitrothion, by blue crabs. Fenitrothion is oxidized by the crab's MFO system to fenitrooxon, which is a well known cholinesterase inhibitor.

Organochlorine Compounds

Blue crabs can be exposed to a variety of organochlorine compounds in contaminated estuaries, with effects on growth, reproduction, and development (Bookhout et al., 1976, 1980; Koenig et al., 1976; Schimmel et al., 1979). Several organochlorine compounds, including polychlorobiphenyls, tetrachlorophenol and pentachlorophenol inhibit limb regeneration in fiddler crabs, *Uca pugilator*, and grass shrimp, *Palaemonetes pugio*, whereas DDT accelerates regeneration (Weis et al., 1992). Sheridan (1975) showed that DDT was metabolized to DDE and DDD (dechlorination products) when blue crabs were exposed to DDT in the water. Storage and metabolism of DDT takes place in the hepatopancreas. Highly chlorinated compounds such as Mirex and hexachlorinated biphenyls are metabolized at a very slow rate, if at all, and these compounds accumulate in the hepatopancreas of the blue crab (Lee, 1989, 1993). Mirex is toxic to blue crabs at concentrations as low as 0.5 ppb (Tagatz et al., 1975).

Organometallics

The most common organometallic compounds in the blue crab's environment are probably methyl mercury and tributyltin. Marine animals accumulate and only slowly eliminate methyl mercury which is taken up primarily from the food (Riisgard and Famme, 1986; Schultz and Newman, 1997). The high toxicity of methyl mercury may be due to its affinity for sulfhydryl groups which can affect a variety of cellular functions including DNA repair (Massaro, 1992, 1997). The formation of conjugates of methyl mercury with glutathione has been reported in mammals (Urano et al., 1988). Inorganic mercury and methylmercury reduce the rate of limb regeneration in the fiddler crab (Weis et al., 1992). However, the concentrations used in these studies are much higher than exist in even contaminated environments. Other than this data, little information is available on the effects of inorganic and methylmercury on crustaceans.

Tributyltin (TBT), which has been used as an anti-foulant in marine paints, is toxic to most marine invertebrates. TBT enters organisms through the lipid membranes and is metabolized by phase 1 and 2 reactions. Blue crabs exposed to TBT upregulate P-450 isozymes (Oberdorster et al., 1998). The cytochrome P-450 systems in the hepatopancreas oxidize TBT to a series of hydroxylated derivatives followed by conjugation of the hydroxybutyldibutyltin to glucose or sulfate (Rice et al., 1989; Lee, 1991, 1996). TBT inhibits growth, as measured by protein and lipovitellin accumulation, of blue crab oocytes at concentrations of 2 µg TBT/liter, whereas hatching success of embryos is reduced by 50% at 0.047 µg TBT/liter (Lee et al., 1996). Exposure of regenerating fiddler crabs to TBT (0.5 µg/liter) results in retardation of regeneration, delayed ecdysis, and deformities of limbs (Weis et al., 1987, 1992).

Conclusions

There is much information available on the fate and metabolism of xenobiotics in blue crabs. The biochemical mechanisms involved in the toxicity and sublethal effects of some classes of xenobiotics are known, such as the action of organophosphorus pesticides to inhibit acetylcholinesterase and thus interfere with the nervous system (Fukuto, 1990). Little, if anything, is known about the effects of xenobiotics on blue crabs at the population level. The increases in the use of juvenile hormone mimics such as methoprene, designed to disrupt chitin synthesis in insect larvae, mosquitoes and gypsy moths, is a threat to juvenile blue crabs and other crustaceans, which inhabit the same habitat as the target insects. The increased development of regions adjacent to estuaries in the southeastern United States appears to have affected grass shrimp populations in impacted estuarine creeks (Scott et al. 1999). Population decreases are correlated with increases in concentrations of polycyclic aromatic hydrocarbons, and in some areas where farms are adjacent to estuaries, population decreases are correlated with various pesticides (Scott et al.,

1999). It would be predicted that blue crabs, which are important members of the food web in these creeks, would be similarly affected. In view of the complex life cycle of blue crabs, it is important to examine the effects of xenobiotics on growth, development, molting and reproduction as they relate to population effects.

Metals

Trace metals are natural components of seawater and sediments. Some of these metals (cobalt, copper, iron, manganese, molybdenum, nickel, selenium and zinc) are essential for the function of a wide variety of proteins, including enzymes, oxygen-binding proteins, proteins involved in electron transport, and DNA-binding proteins. When present in excess, trace metals can become toxic to the organisms that depend on them. Other metals, such as cadmium, mercury, lead, and silver, do not have any known biological function and are toxic to organisms above certain threshold levels.

Adverse environmental effects associated with redistribution of trace metals, due to mining and fossil fuel combustion, have long been recognized. The fact that metal pollutants are persistent in the environment makes these contaminants especially hazardous. In this section of our review we will first examine the present knowledge about metal (essential and toxic) uptake and inter-organ transport in the blue crab. The emphasis will be on copper and cadmium since these trace metals have been most extensively studied. We will then discuss the molecular defense mechanisms used by the crab for protection against metal toxicity. Next we will consider how metals, when the defense mechanisms are overwhelmed, exert their toxic effects at the cellular/molecular and organismal (growth/molting, development and reproduction) levels. Finally, we will relate the extensive studies carried out under controlled laboratory conditions to the limited number of studies carried out in the field.

Metal Accumulation and Transport

There are two possible routes of exposure to trace metals in the environment: food and water. Blue crabs accumulate cadmium from food in the hepatopancreas and cadmium from water in the gills. Only small amounts of the metal accumulate in muscle tissue (Engel, 1983; Brouwer et al., 1984, 1992). In contrast, copper from food and water appears to primarily accumulate in the hepatopancreas irrespective of the source. Very little, if anything, is known about the processes involved in uptake and export of trace metals from tissues in the blue crab or any other decapod crustacean. However, in view of the very conserved nature of the mechanisms and proteins involved in the uptake, intracellular distribution, and export of copper in the cells of organisms as diverse as yeast and humans (Valentine and Gralla, 1997), it seems likely that similar mechanisms occur in crustacea as well, to help maintain copper homeostasis. There is indeed increasing evidence that decapod crustaceans are capable of regulating copper body burdens within narrow limits. The shore crab *Carcinus maenas* and the shrimp *Palaemon elegans,* for example, maintain constant body copper concentrations under varying external dissolved copper levels, until a threshold of dissolved metal concentration is reached (170 µg Cu/liter and 100 µg Cu/liter, respectively), beyond which net accumulation of copper begins (White and Rainbow, 1982, 1985). The same appears to apply to copper accumulation by the crayfish *Procambarus clarkii* and by larvae of the mud crab *Rhithropanopeus harrisii* (Sanders et al., 1983; Anderson et al., 1997).

The oxygen-binding protein, hemocyanin, of the blue crab has a large number of high-affinity copper-binding sites, in addition to the two coppers that make up the active site (Brouwer et al., 1982, 1983). This *in vitro* observation appears to have biological implications. When *Carcinus maenas* is exposed to elevated levels of water-borne copper, the metal is taken up by the gills. Subsequent binding to circulating hemolymph proteins, mainly hemocyanin, ensures the transport of copper in a less toxic form to the tissues (Rtal et al., 1996; Truchot and Rtal, 1998). In addition to copper, blue crab hemocyanin can bind a large number of cadmium ions (Brouwer et al., 1983). When blue crabs are exposed to water-borne cadmium, the metal rapidly appears in the gill and hemolymph, where it is bound to hemocyanin. During

depuration, cadmium is transferred from the gill, via the hemolymph, to the hepatopancreas (Brouwer et al., 1984). Uptake of cadmium and zinc across the gill epithelia into the hemolymph where it is bound to hemocyanin and passed on to the tissues (hepatopancreas) is a common pathway in decapod crustacea (Wright, 1977b; Bjerregaard, 1990; Martin and Rainbow, 1998). The rate of cadmium uptake by the gills of the blue crab increases with decreasing salinity (Hutcheson, 1974), similar to what is found for cadmium uptake by *C. maenas* and *P. pugio* (Wright, 1977a; Engel and Fowler, 1979). This indicates that cadmium is taken up as Cd^{2+} and not as $CdCl_2$. Indirect evidence suggests that Cd^{2+} is taken up through Ca^{2+} ion channels in the plasma membrane of the gill of the shore crab *C. maenas* (Wright, 1977c; Lucu and Obersnel, 1996). The toxicity of water-borne cadmium may therefore lie mainly in perturbation of calcium metabolism (Hogstrand et al., 1996).

Detoxification Mechanisms. First Line of Defense: Metallothionein and Glutathione

Metal ions are both essential and toxic elements. To cope with potentially hazardous levels of heavy metal ions, organisms have developed an integrated metal-regulatory network to control the concentration and availability of these elements. A major component of this network is a family of low-molecular weight (6500 Da; 57-62 amino acids), cysteine-rich (18-21 cysteines/mole), metal-binding proteins called metallothioneins (Kagi and Kojima, 1987). These proteins are expressed in many different cell lines and tissues following exposure to heavy metals such as cadmium, copper, mercury, silver and zinc; glucocorticoid hormones; interferon; interleukin-I; bacterial endotoxin; UV radiation, and oxidative stress (Hamer, 1986; Cousins, 1985; Engel and Brouwer, 1989; Bauman et al., 1991; Roesijadi, 1992). In mammals there are at least two major MT isoforms, designated as MT-I and MT-II. Nuclear magnetic resonance (NMR) spectroscopy (Otvos and Armitage, 1980) and X-ray diffraction studies (Robbins et al., 1991) have shown that the cadmium/zinc form of mammalian MT is a dumbbell-shaped molecule, composed of a N-terminal, 9-cysteine/3-metal cluster and a C-terminal, 11 cysteine/4-metal cluster.

The presence of MT has been demonstrated in several decapod crustacea, and the proteins have been characterized with different degrees of detail (Engel and Brouwer, 1989; Roesijadi, 1992). The first crustacean MT amino acid sequences published were those of the two MT isoforms of *Scylla serrata* (Lerch et al., 1982). Whereas mammalian MTs have 20 cysteine residues and bind 7 g atoms of Cd/mole of MT, the crab MTs have 18 cysteine residues and bind 6 g atoms Cd/mole of MT. The amino acid sequences of MTs from the American lobster *Homarus americanus* (Brouwer et al., 1989), *Carcinus maenas* (Pedersen et al., 1994), *Callinectes sapidus* (Brouwer et al., 1995) and the freshwater crayfish *Astacus astacus* (Pedersen et al. 1996) show a high degree of structural similarity to the MTs from *S. serrata.*

The structure and function of blue crab MTs have been studied in great detail. Anion-exchange chromatography shows four apparent CdMT isoforms in the hepatopancreas of crabs fed cadmium-enriched diets (CdMT-Ia/Ib and CdMT-IIa/IIb) (Brouwer et al., 1995). CdMT-Ib differs from MT-Ia only in having an extra N-terminal methionine. Similarly, CdMT-IIb is identical with IIa except for an extra Met at its N-terminal position. The same N-terminal heterogeneity has been observed for CdMTs from *C. maenas* and *A. astacus* (Pedersen et al., 1994, 1996). The 3D structure of blue crab Cd_6MT-I has been determined by 2D NMR spectroscopy (Narula et al., 1993, 1995). The protein is folded into two separate domains. Each domain contains a cluster of three metal ions, tetrahedrally coordinated to the sulfur atoms of the nine cysteine residues present in each domain.

When blue crabs are fed copper-enriched diets, two CuMT isoforms are found in the hepatopancreas: CuMT-Ia/Ib and CuMT-II (Schlenk and Brouwer, 1991; Brouwer et al., 1992; Schlenk et al., 1993). The copper-binding properties of the CuMT isoforms are very different (Brouwer and Hoexum-Brouwer, 1998; Brouwer, 1996). CuMT-II is induced to a much greater extent than CuMT-I. CuMT-I and CdMT-I are the same protein, with different metals bound to it. CuMT-II is a unique MT isoform, which can be induced by copper, but

not by cadmium. We have cloned and sequenced the cDNA that encodes CuMT-II. The protein consists of 63 amino acids, 21 of which are cysteines (Syring et al., 2000). The blue crab CuMT-II amino acid sequence is very different from the CdMT-I and CdMT-II sequences. CuMT-II shows greatest homology with a Cu-specific MT from the snail, *Helix pomatia* (Dallinger et al., 1997). The presence of closely-related copper-specific MTs in mollusks and crustaceans, both of which are dependent on hemocyanin for oxygen transport, suggests that CuMT is involved in regulation of copper associated with hemocyanin metabolism.

Short-term copper exposure of hepatopancreas tissue explants shows that Cu taken up by the cells during the first 60 minutes combines with glutathione (GSH). Thereafter, Cu binds to newly-synthesized MT, with concomitant decrease in Cu(I)-GSH (Brouwer and Hoexum-Brouwer, 1998). Copper, when bound to GSH, does not participate in free radical chemistry (Hanna and Mason, 1992), and formation of Cu-GSH complexes in the cell is a common mechanism for rapid detoxification of excess copper (Freedman et al., 1989; Lin et al., 1993). The Cu(I)-GSH complex can transfer its metal to blue crab apoMT (Brouwer and Hoexum-Brouwer, 1998), and GSH-CuMT complexes appear to exist in the hepatopancreas of lobsters and blue crabs (Brouwer and Brouwer-Hoexum, 1991, 1992; Brouwer et al., 1993; Brouwer, 1996). Recent studies indicate that reduced glutathione (GSH) and glutathione disulfide (GSSG) are critical modulators of zinc transfer from ZnMT to zinc-dependent enzymes (Jacob et al., 1998; Jiang et al., 1998). It appears therefore that MT and GSH/GSSG play a critical role in detoxification and intracellular distribution of copper and zinc.

When blue crabs are exposed to cadmium in the water, the metal accumulates in the gill. Most of the cadmium is bound to CdMT-II, while CdMT-I is virtually absent, indicating that the expression of the two cadmium-inducible MT genes is tissue specific (Brouwer et al., 1984, 1995). Only a small fraction of the cadmium is found in the hepatopancreas. Surprisingly, when crabs are exposed to copper in the water, most of the copper accumulates in the hepatopancreas, and only a small portion is found in the gills. It appears that copper is efficiently exported from the gill epithelial cells into the hemolymph with subsequent uptake by the hepatopancreas, a tissue that is heavily dependent on copper for hemocyanin synthesis (Rainer and Brouwer, 1993).

Detoxification Mechanisms. Second Line of Defense: Antioxidant Defense Systems

Copper can catalyze the production of highly toxic hydroxyl free radicals from intracellularly generated hydrogen peroxide (Halliwell and Gutteridge, 1990). It is therefore essential that intracellular levels of free copper be kept at a minimum by sequestering copper in complexes, such as MT and GSH, that render the metal unable to take part in redox reactions with activated oxygen species (superoxide and hydrogen peroxide). In addition to copper chelators, cells contain a variety of antioxidant defenses that limit oxidative damage that may result from metal-catalyzed formation of activated oxygen species. The enzyme superoxide dismutase (MnSOD in mitochondria and CuZnSOD in cytosol) catalyzes the conversion of superoxide into oxygen and hydrogen peroxide (Fridovich, 1997). Catalase and GSH-peroxidase remove hydrogen peroxide and organic peroxides. Glutathione disulfide (GSSG), formed in the reaction catalyzed by GSH-peroxidase, is recycled by the enzyme GSH-reductase. Cells also contain nonenzymic antioxidants such as the lipid soluble α-tocopherol that can limit lipid peroxidation (Buettner, 1993) and the water-soluble vitamin ascorbate and the intracellular tripeptide glutathione that remove free radicals from the cytosol (Reed, 1990).

Long-term exposure of blue crabs to copper in food leads to increased activity of two antioxidant enzymes: GSH-peroxidase and MnSOD. Surprisingly, no CuZnSOD is found. Activities of catalase and GSH-reductase, and the intracellular levels of GSH are unaffected by copper (Brouwer and Hoexum-Brouwer, 1998). In conclusion, blue crabs use the metal-chelators GSH and MT as a first line of defense against excess Cu. The antioxidant enzymes SOD and GSH-peroxidase constitute a second line of defense to help prevent or repair oxidative damage from Cu not sequestered by the

chelators.

SOD is present in the cytosol (CuZnSOD) and mitochondria (MnSOD) of all oxygen-respiring eukaryotes. However, blue crabs and all other crustaceans that use hemocyanin for oxygen transport do not have CuZnSOD. Blue crabs have replaced CuZnSOD with a MnSOD that is retained in the cytosol by virtue of having an abnormal mitochondrial-targeting sequence (Brouwer et al., 1997; Grater and Brouwer, 1998). The paradigm that all aerobic eukaryotes contain intracellular CuZnSOD and that MnSOD occurs exclusively in the mitochondria appears not to apply to a large group of marine arthropods (Brouwer et al., 1997). We hypothesize that the replacement of a copper-dependent SOD by a manganese-dependent SOD may be associated with the high requirement of copper for hemocyanin synthesis. This hypothesis is corroborated by the observation that crustacea that are dependent on hemoglobin for oxygen transport [such as brine shrimp, (cerio)daphnia, barnacles, and copepods] have normal cytosolic CuZnSOD (Brouwer, unpublished data).

Metal-catalyzed Oxidative Damage

To examine if the defense mechanisms against copper toxicity (CuMT-II, GSH, GSH-Px and MnSOD) are sufficient to protect against copper-mediated oxidative tissue damage, hepatopancreas tissues from control and copper-exposed blue crabs were analyzed for lipid peroxidation and protein oxidation. Levels of malondialdehyde, a common product of lipid peroxidation, were significantly greater in the copper-exposed crabs than in control animals, indicating that the defense mechanisms induced by copper exposure were not entirely sufficient to prevent oxidative damage to cellular membranes. However, protein oxidation was kept to a minimum. It seems therefore that copper chelation and increased antioxidant defenses are effective (in view of the large amounts of copper accumulated in the cells) in limiting oxidative tissue damage (Brouwer and Hoexum-Brouwer, 1998). Similar results have been reported for *Scylla serrata* (Reddy, 1997).

Organismal Responses: Embryo/Larval Development, Growth and Molting

Growth of blue crab oocytes and hatching of embryos are inhibited by copper and cadmium (Lee et al., 1996). Under optimum conditions of salinity and temperature, 95% of blue crab megalopa survives to third crab instar in the presence of 50 ppb cadmium. In 150 ppb of cadmium the survival is reduced to 20%. The effects of cadmium and mercury on survival of megalopae and juvenile crabs are much more pronounced at lower salinities (Rosenberg and Costlow, 1976; Frank and Robertson, 1979; McKenney and Costlow, 1981).

Most studies on MTs in aquatic organisms have been directed toward the examination of induced MTs in organisms exposed to elevated concentrations of metals. Few have studied MTs in order to understand their biological function in the absence of such exposure. Investigations on the involvement of MT in copper and zinc partitioning during the molt cycle of the blue crab have shown that three significant changes occur in the metals bound to MT. The first is at the beginning of premolt when the metals bound to MT change from predominantly copper to zinc. These changes are thought to be correlated with reduced hemocyanin biosynthesis and an increased rate of Zn-carbonic anhydrase synthesis in preparation for molting. The second change occurs within 90 min after ecdysis, when there is a transient pulse of CuMT, probably correlated with the catabolism of hemocyanin. The CuMT complex may then be sequestered in lysosomes and eliminated into the gut and out in the feces. The third change occurs during the papershell stages, when MT once again becomes primarily a copper protein, preceding the biosynthesis of hemocyanin. These investigations give further support to the hypothesis that the function of MT in organisms that are not metal-stressed is in the regulation of nutritional metals associated with the degradation and synthesis of metalloproteins (Engel, 1987; Engel and Brouwer, 1987, 1989, 1991, 1993).

The processes of limb regeneration and molting in decapod crustaceans are generally coupled with one another under the control of the neuroendocrine system (Weis et al., 1992). Inorganic mercury, methyl mercury, and cadmium reduce the rate of limb regeneration in the fiddler crab *Uca pugilator*.

Retardation of regeneration is generally

accompanied by a delay in ecdysis, so that limbs are usually fully formed by the time of molting (Weis et al., 1991, 1992). The effects of cadmium are greatly enhanced at reduced salinities (Weis, 1978, 1985). The potential effects of trace metals on reproduction by blue crabs or decapod crustaceans have, to our knowledge, not been studied.

Field Data

Blue crabs are important members of the estuarine food web. Because of their omnivorous feeding characteristics and association with sediments, blue crabs may potentially accumulate significant amounts of metals. Foundry Cove, located on the Hudson River, was heavily contaminated with cadmium by effluent discharged from a Ni-Cd battery plant between 1953 and 1979 (Kneip and Hazen, 1979). The area has now been remediated in an effort to remove the metal-contaminated sediments. High levels of cadmium (7-11 µg/g tissue) are found in the hepatopancreas of blue crabs collected in the cove, and the metal appears to be bound to MT (Wiedow et al., 1982). The hepatopancreas and gills of the field-exposed crabs also have elevated concentrations of copper. The gill has a MT that contains mostly cadmium and no copper; whereas, the MTs in the hepatopancreas contain cadmium, copper, and zinc (Engel and Brouwer, 1984a) identical to what is observed when crabs are exposed to waterborne cadmium and copper under controlled laboratory conditions. Blue crabs collected from Baltimore harbor have high copper concentrations in the digestive gland. Most of the copper is bound to two MT isoforms (Engel and Brouwer, 1984b; Engel et al., 1985) similar to results obtained after dietary copper exposure in the laboratory.

Hepatopancreas, gill, and muscle tissues from blue crabs with shell disease from the Pamlico River, North Carolina, and from non-diseased crabs from the Albemarle-Pamlico estuarine system in North Carolina have been analyzed for 13 different trace metals. Sediments from the Pamlico River show enrichment of arsenic, cadmium, manganese, titanium, and vanadium which is reflected in higher concentrations of these metals in the crabs. However, no trend is evident with regard to diseased versus non-diseased crabs. The higher metal concentrations in the edible portions of the crabs do not pose a significant health risk to humans (Weinstein et al., 1992; Gemperline et al., 1992). Similarly, analysis of metals in tissues from crabs collected from two estuaries in Connnecticut indicated no risk to human health (Jop, 1997). At present there are two fish consumption advisories for mercury in blue crabs: Point Comfort in Lavaca Bay, Texas and Brunswick, Georgia. Both are Superfund sites where the sources of the mercury were chlor-alkali plants. The concern is for human health and not for populations of blue crabs. From the available data, there does not seem to be any measurable effect of mercury on blue crab recruitment, survival, and reproduction within the affected area of Lavaca Bay (Engel and Thayer, 1998).

Conclusions

A variety of organic and inorganic contaminants, including polycyclic aromatic hydrocarbons, organohalogens, pesticides, organometallics, and heavy metals, can be present in the blue crab's estuarine environment. Our knowledge of the effects of these contaminants on blue crabs decreases from the molecular, cellular, organismal to the population level (Figure 3). For example, much has been learned about the molecular and cellular mechanisms used by the blue crab to detoxify organic contaminants and heavy metals. In addition, the mechanisms underlying the toxicity and sublethal effects of some classes of contaminants are known. Recent studies have shown that polycyclic aromatic hydrocarbons (PAHs) enhance ecdysone (molt hormone)-dependent gene transcription and cell proliferation. At the organismal level, PAHs inhibit growth and molting of juvenile blue crabs, suggesting that PAHs act as endocrine disrupters in the crab. Tributyltin inhibits growth of blue crab oocytes and reduces hatching success of embryos. Heavy metals such as mercury, copper and cadmium inhibit hatching of blue crab embryos and reduce survival of megalopae and juvenile crabs. However, most studies on the effects of contaminants on crabs have been carried out in the laboratory under conditions that may not be environmentally relevant. To date there is little compelling evidence that contaminants

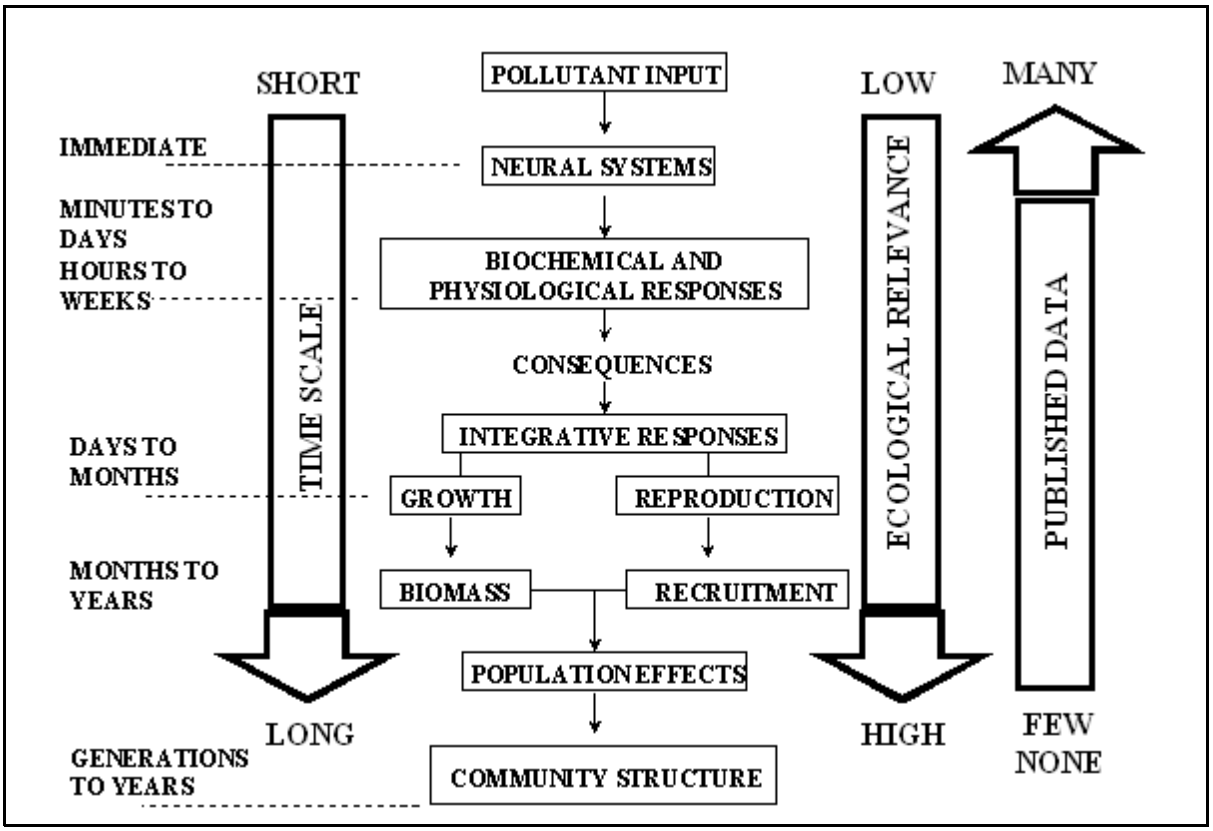

FIGURE 3. — Correlations between time, effects of contaminants, ecological relevance of effects and published data on effects. Adapted from Engel and Vaughan, 1996.

have had direct effects on blue crab populations. A greater threat to blue crab populations may be posed by increased nutrient loading, alterations of freshwater inflow, and physical destruction of estuarine and coastal habitats that accompany increasing human population densities and development near the coast (Engel and Thayer, 1998).

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Post Settlement Mortality of Juvenile Blue Crabs: Patterns and Processes

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Abstract. – Predation-induced mortality can be an important determinant of population size for many benthic invertebrates such as the blue crab. Using information from the 1993 Blue Crab Symposium and more recent studies, we attempt to define the role of predation in determining the abundance of recently settled juvenile blue crabs. We conclude that 1) exceptionally high rates of predation continue to be recorded on juvenile blue crabs, especially in the Gulf of Mexico; 2) overall predation rates are most often lowest in vegetated habitats, although the smallest settlers survive better in low density vegetation, while larger settlers survive better in high density vegetation; and 3) cannibalism on early settlers by larger juveniles may explain this size selective survival.

KEY WORDS: predation-induced mortality, blue crab

For epibenthic organisms with complex cycles, early post-settlement periods are often filled with predation-induced mortality (see reviews by Olafsson et al., 1994 and Hunt and Scheibling, 1997). Consequently, many benthic invertebrates including such well-studied species as the blue crab (*Callinectes sapidus*), preferentially settle in structurally complex "nursery habitats" (e.g., Forward et al., 1996) that afford shelter from predators (Heck and Thoman, 1981; Wilson et al., 1990; Pile et al., 1996). When shelter becomes limiting in "nursery habitats," post-settlement mortality will usually determine juvenile abundance (Wahle and Steneck, 1991; Butler and Hermkind, 1997). When larval supply is insufficient to saturate nursery habitats, juvenile abundance will be determined primarily by larval (or post-larval) abundance.

More complicated scenarios can occur when slightly older juveniles cannibalize the most recent settlers in nursery habitats. This can set up several possibilities for density-dependent population regulation (Moksnes, 1999), and several species of crabs are known to exhibit high levels of cannibalism [Fernandez, 1999 (Dungeness crab *Cancer magister*); Lovrich and Sainte-Marie, 1997 (snow crabs *Chionoecetes opilio*); Schulman, 1996 and Moksnes et al., 1997 (blue crabs *C. sapidus*)]. What is not generally known, however, is whether such intraspecific predation significantly affects population dynamics.

Blue crabs have been the subject of intense study on both the Atlantic and Gulf coasts of the United States, owing to the economic importance of the blue crab fishery. In 1993, blue crab researchers met at the International Estuarine Research Federation meetings to summarize what was known about larval and juvenile blue crab biology (Olmi and Orth, 1995). This symposium resulted in a number of conclusions about the relative roles of post-larval supply and post-settlement mortality along the Atlantic and Gulf Coasts (Rabalais et al., 1995; van Montfrans et al., 1995; Heck and Coen, 1995). Major conclusions were: 1) post-larval

(megalopal) supply appeared to be much greater (one to two orders of magnitude) in Gulf coast than Atlantic coast estuaries; 2) despite the large differences in megalopal abundances, juvenile abundances in nursery habitats were roughly equal in Gulf and Atlantic coast estuaries; and 3) as estimated by tethering studies, losses of juveniles to predators were greater in the Gulf, which explains why, despite large megalopal abundance, juvenile numbers in the Gulf were similar to those along the Atlantic coast. Therefore, larval supply appeared to be more important in determining population size in Atlantic estuaries, while post-settlement mortality appeared to be most important in Gulf estuaries.

A number of studies have been carried out since the results of the 1993 symposium were published, and the results of another symposium on blue crab biology in 1999 are currently in press (Eggleston, in press). Our intention is to focus on what has been learned since the publication of the proceedings on the symposium in 1993 (Olmi and Orth, 1995) regarding the role of predation in determining the abundance of recently settled blue crabs. We emphasize our work in the northern Gulf of Mexico but also discuss other data from the Gulf of Mexico and the Chesapeake Bay. We ask whether the previous generalizations are supported by recent data. We then incorporate recent information on cannibalism to elucidate how intraspecific predation may help explain puzzling mortality patterns of early settlers in nursery habitats.

Post-Larval Supply

By the early 1990s researchers concluded that post-larval supply along the northern Gulf of Mexico appeared to be much greater than that on the Atlantic coast. This conclusion was based on comparing the results of similar megalopal sampling efforts in Texas, Louisiana, Mississippi and Alabama with those in Atlantic coast states from Delaware to South Carolina (Rabalais et al., 1995; van Montfrans et al., 1995). On average, collections in the Gulf were between 10 and 100 times greater than those in the Atlantic states (Rabalais et al., 1995), although it should be noted that the database on megalopal supply in the Gulf was not as extensive as that in other places such as the Chesapeake Bay.

Post larval supply sampling efforts were repeated in 1997 and 1998 along the Alabama coast, and it was again found that megalopal supply was about an order of magnitude greater than that reported from the Atlantic coast (Spitzer et al., in press). However, mean megalopal supply had decreased when compared to data from the early 1990s (Figures 1a &1b). This decrease may have been partially caused by hurricanes that interrupted sampling efforts during the peak recruitment period in 1998. Such disturbances could easily alter mean recruitment rates because post larval settlement typically occurs in small numbers interspersed with large, episodic settlement events that can contribute up to 50% of the total annual settlement of blue crabs (Perry et al., 1995; van Montfrans et al., 1995). If 1998 sampling efforts missed these large peaks, recruitment estimates could be severely underestimated. Perry et al. (in press) found similar patterns in Mississippi waters, although the smaller collections in the late 1990s were still at least an order of magnitude higher than mean Atlantic coast numbers. Therefore, based on data from Mississippi and Alabama in the latter part of the 1990s, megalopal numbers in the Gulf were still much greater than those along the Atlantic coast, although the difference was not as large as originally reported (Rabalais et al., 1995) but more on the order of ten times greater.

Juvenile Abundance

Despite differences in megalopal supply, juvenile abundance in submerged aquatic vegetation (SAV) and fringing marsh along the northern Gulf of Mexico in the early 1990s (36-92/m^2: Williams et al., 1990; Heck and Coen, 1995) was the same order of magnitude as that reported from Chesapeake Bay (45-90/m^2: Orth and van Montfrans, 1987; 10-27/m^2: Pile et al., 1996; Figure 2). When studies on juvenile abundance were conducted in Alabama during 1997-1998, results were qualitatively similar to those found previously. However, in 1998 there were elevated numbers of juvenile blue crabs present in the fringing marsh (Figure 2), which we attributed to the large amount of SAV detritus that was found in the marsh during the sampling period (Spitzer et al., in press). This complex habitat, not normally present, may have

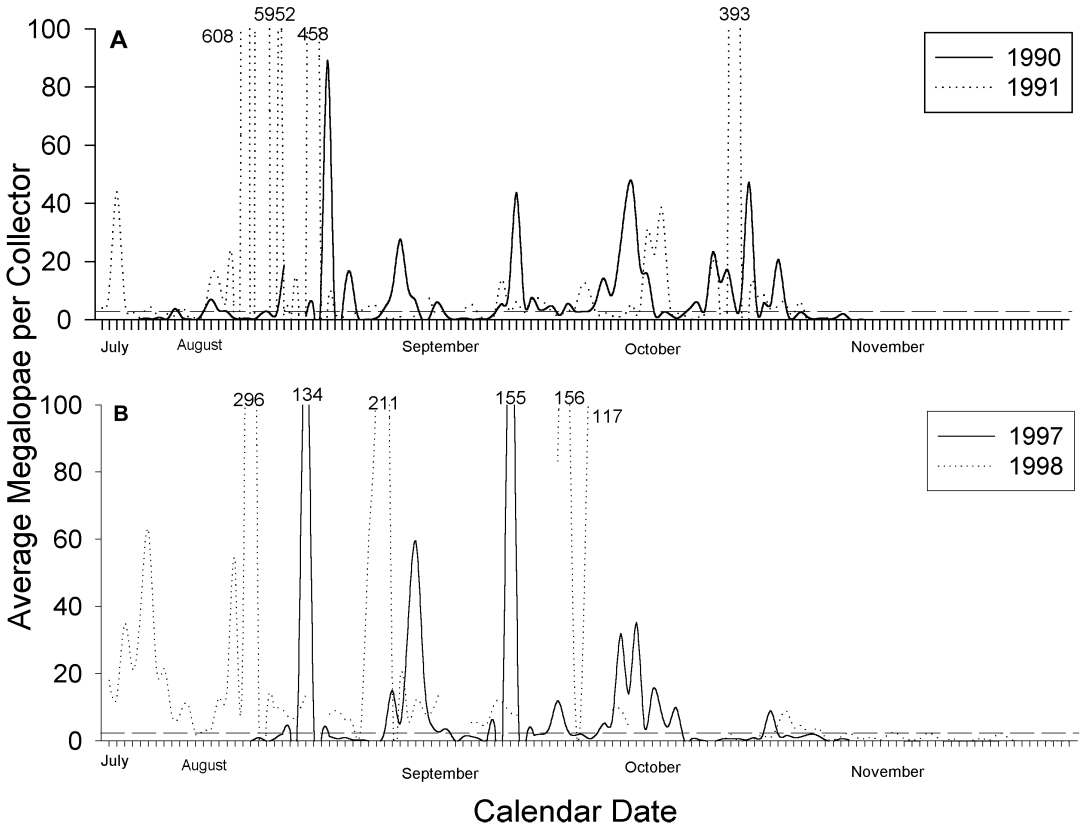

FIGURE 1. — Average number of megalopal recruits at Point aux Pins (PAP) Alabama (Lat: 30° 23'; Lon: 88° 15') during a) 1990 and 1991 and b) 1997 and 1998. Dashed line indicates the average megalopal recruitment in the Chesapeake Bay.

provided juvenile blue crabs additional refuge from potential predators.

Densities of macroinvertebrates and fishes are often positively correlated with seagrass biomass (see Orth et al., 1984 and Heck and Crowder, 1991 for reviews), which is usually explained as a result of the increased food and refuge thought to be provided by dense vegetation (Heck et al., 1997). Surprisingly, we did not consistently find significant positive correlations between SAV biomass and the abundance of blue crabs at our study sites in either the early or late 1990s (Heck et al., in press; Spitzer et al., in press; Table 1). We now believe that the non-significant correlations between SAV biomass and juvenile crab abundance may be due to interactions between size dependent cannibalism and size dependent protection provided by different amounts of vegetation (see Cannibalism below).

Predation Rates

Juvenile blue crab (5-20 mm CW) mortality, as estimated by tethering studies, was greater in the northern Gulf of Mexico during the early 1990s (85% consumed/day: Heck and Coen, 1995; Heck et al., in press) than estimates obtained on the Atlantic coast [New Jersey, 25% (Wilson et al., 1990) and Virginia, 68% (Pile et al., 1996)] using identical methods. Similar results were found in 1997-1998 when the studies were repeated in Alabama waters. Mortality estimates varied from year to year and from site to site (Figure 3), but there was no consistent relationship between vegetation biomass and juvenile blue crab survival. We hypothesize that the lack of a positive relationship between vegetation biomass and tethering losses resulted from density-dependent cannibalism nullifying the effects of SAV refuge and minimizing differences in predation potential among habitats (see Cannibalism below).

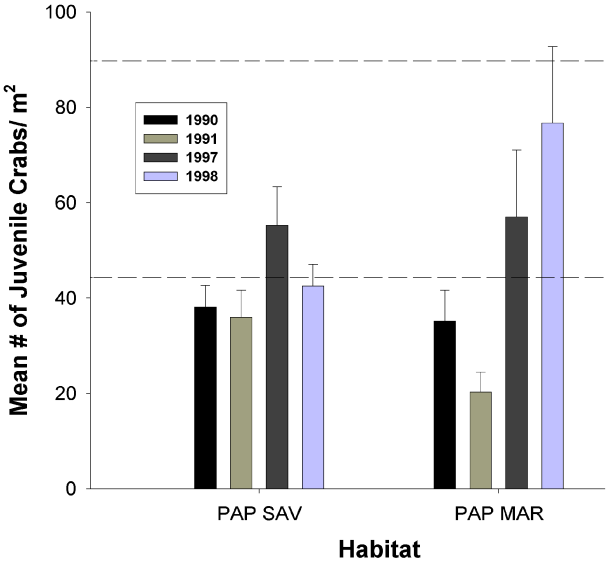

FIGURE 2. — Mean abundance of juvenile blue crabs per m^2 in both submerged aquatic vegetation (SAV) and fringing marsh (MAR) at Point aux Pins (PAP) during 1990, 1991, 1997 and 1998. Dashed lines indicate the reported average range of juvenile blue crab densities in the Chesapeake Bay.

Mortality estimates also varied seasonally within sites. In 1998, early in the recruitment season (July), juvenile blue crab mortality was extremely high (approximately 94%) regardless of the habitat occupied (Figure 4). In September, mortality estimates were lower (approximately 58%) than those in July and did not seem to be related to differences in the amount of vegetation between months. One possibility for the lowered predation losses in September could be predator swamping during that month's extraordinarily large settlement events. Predator swamping has been proposed by van Montfrans et al. (1995), along with concomitantly reduced cannibalism by larger blue crabs, as processes that could favor a life history containing large, episodic recruitment events. Subsequently (in October), mortality estimates increased to approximately 82%, with a significant refuge value provided by vegetated habitats.

Megalopae-Juvenile Correlations

Strong correlations between larval supply and juvenile abundance have been observed for both the American lobster (Incze et al., 1997; Wahle and Incze, 1997) and the rock lobster (Pearse and Phillips, 1994), and one might expect the same to be true for other decapod species such as the blue crab. However, this was not the case at our study sites in Alabama. Significant correlations between megalopal supply and juvenile abundance were infrequent, usually associated with episodic large recruitment events, and short-lived (Figure 5 & 6). Within one to two weeks, juvenile abundance always returned to background levels, leaving no indication of the large recruitment events.

TABLE 1. — Summary of correlations (Pearson and Spearman) between juvenile blue crab abundance and vegetation biomass at Point aux Pins during 1990, 1991, 1997 and 1998 (* = $p<0.05$; ** = $p<0.01$).

Study Year	Pearson			Spearman		
	r	p	n	r	p	n
1990	-0.16	0.45	24	-0.23	0.28	24
1991	0.40	*0.04	27	0.37	0.06	27
1997	0.62	**.008	17	0.47	0.055	17
1998	0.12	0.62	20	0.23	0.32	20

The decoupling of larval supply and juvenile abundance may be a result of emigration from vegetated habitats or mortality within SAV habitats. In Chesapeake Bay, where Pile et al. (1996) found few significant relationships between small and large instars, juveniles were inferred to begin moving out of SAV after the fifth instar (7.5-9.1 mm CW: Pile et al., 1996). However, densities of juvenile crabs on unvegetated substrate were always quite low compared to densities in SAV (Orth and van Montfrans, 1987; Pile et al., 1996). Alternatively, density dependent mortality from predation and/or disease might account for the decoupling of megalopal and juvenile abundances. Our data and those of others show strong evidence for very high levels of predator-induced mortality in early juveniles, with the magnitude of predation losses increasing with decreasing latitude (see Heck and Coen, 1995 for a summary). Recently, Etherington and Eggleston (2000) found conflicting evidence for density-dependence between early and late instars in North Carolina, depending on whether sites with high post-settlement movement of juveniles were included or not. Despite differences among these studies, each shows evidence for

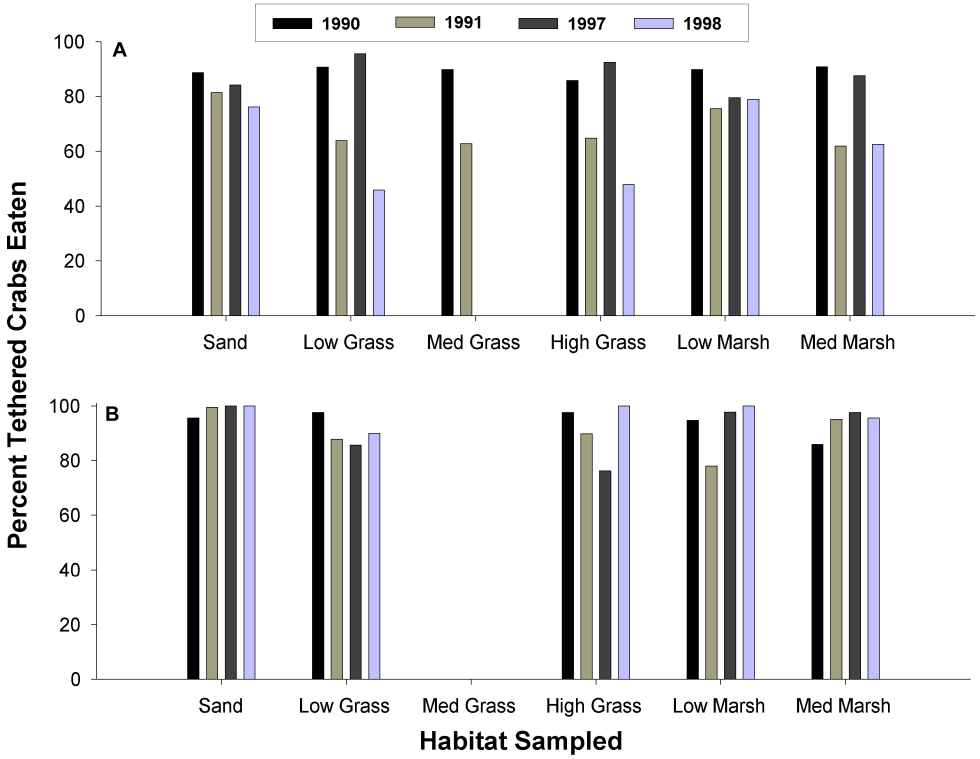

FIGURE 3. — Percentage of juvenile blue crabs eaten during tethering studies conducted during September of 1990, 1991, 1997 and 1998 at a) Point aux Pins and b) Mobile Delta, Alabama (Lat: 30° 40'; Long: 87° 58').

density-dependent mortality at high settler densities, with the implication that locations with high densities of settlers will often experience high rates of post settlement losses.

Cannibalism

We have learned from several studies that cannibalism can have important effects on brachyuran population dynamics. For example, Fernandez et al. (1993) and Fernandez (1999) found that cannibalism of megalopae by young-of–the-year Dungeness crabs could decimate cohorts of settlers, and Lovrich and Sainte-Marie (1997) concluded that cannibalism reduced cohort strength of snow crabs (*Chionoecetes opilio*) during the first four years after settlement. In another example, Moksnes et al. (1998) suggested that shore crabs (*Carcinus maenas*) were the dominant predators on settling post-larvae and early juveniles of their own species.

More to the point, it has become clear that cannibalism by early juvenile instars can cause substantial mortality among the most recent blue crab settlers, and that intra-year class cannibalism can be a major factor influencing megalopae

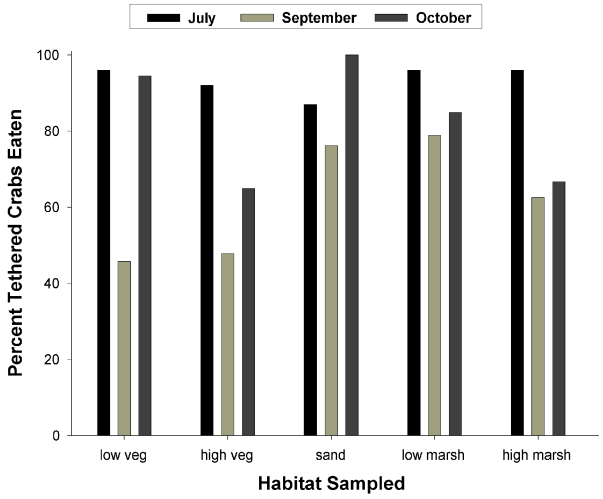

FIGURE 4. — Percentage of juvenile blue crabs eaten during seasonal (July, September and October) tethering studies conducted in 1998 at Point aux Pins.

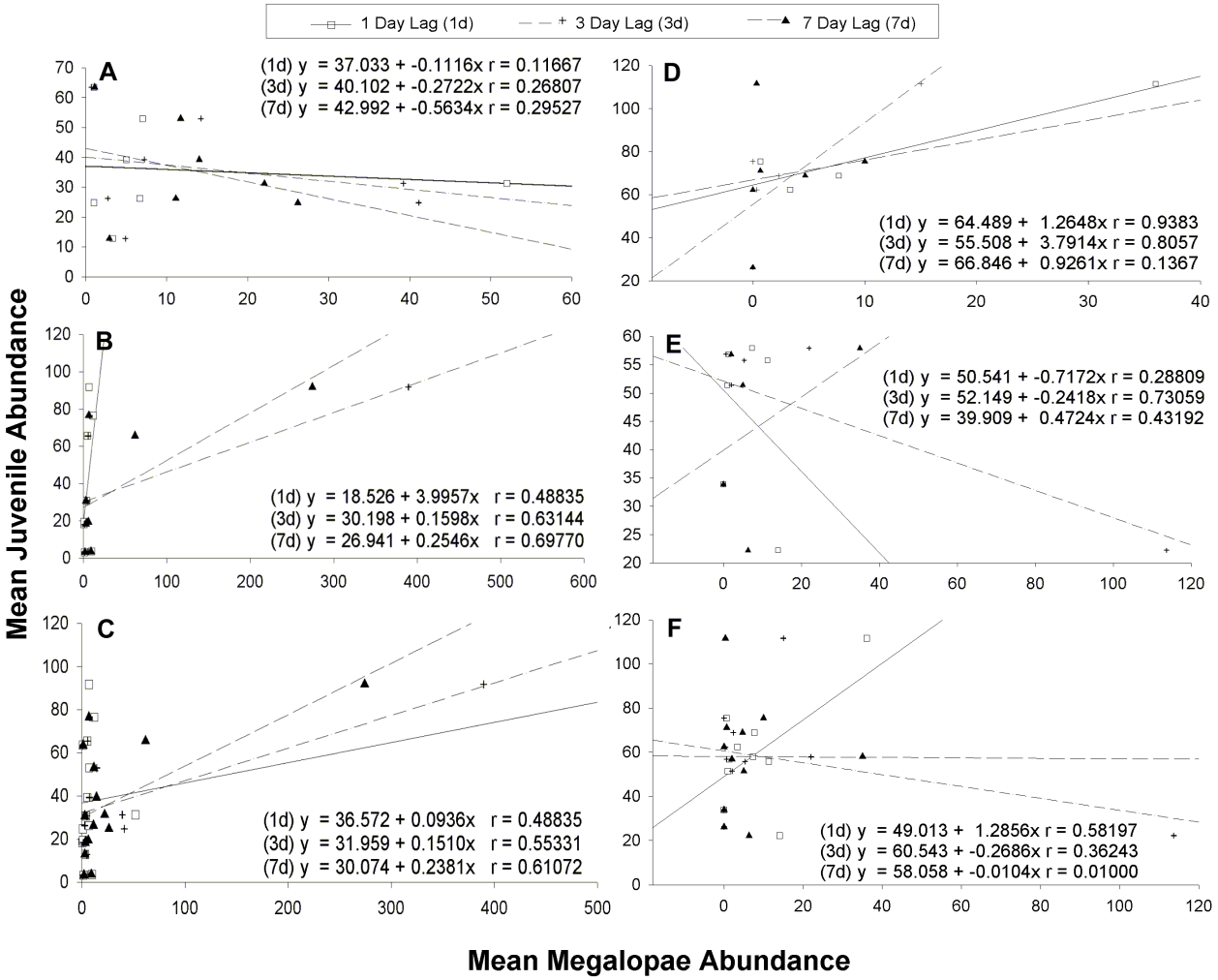

FIGURE 5. — Relationship between megalopal abundance and juvenile abundance with 1- 3- and 7-day lags in submerged aquatic vegetation at Point aux Pins during a) 1990, b) 1991, c) 1990-91 combined, d) 1997, e) 1998 and f) 1997-98 combined. Significant correlations (when present) indicated by * ($p<0.05$).

and early juvenile blue crab numbers (Moksnes et al., 1997). In an unpublished master's thesis, Schulman (1996) provided an assessment of the interaction between the survival of juvenile blue crabs and shoot density of artificial eel grass (*Zostera marina*). In this field tethering study, separate evaluations of the effect of increasing shoot density for instars 2-3, (CW 3.1-5.9 mm) 7-9 (CW 10.7-16.1 mm), and larger juveniles (CW 11.7- 34.8 mm) showed quite different results. For example, instars 2-3 showed greatest survival at low shoot densities, while instars 7-9 and larger juveniles showed the expected pattern of increasing survival with increasing shoot density (although the curves describing this relationship were shaped quite differently) (Figure 7). These survival data corresponded with density patterns that showed greater numbers of instars 2-3 in low-density eelgrass (Figure 8) and greater numbers of the two larger size classes in higher density eelgrass. Schulman's (1996) explanation for these patterns was that cannibalism by larger juveniles prevented instars 2-3 from surviving well in high-density vegetation, which was where the survival of larger juveniles was best. In sparse vegetation, the earliest instars were not preyed upon in great numbers, probably because they were so small that they were an unprofitable prey item for many non-crab predators. However, larger juveniles would be easily preyed upon in sparse vegetation, and this

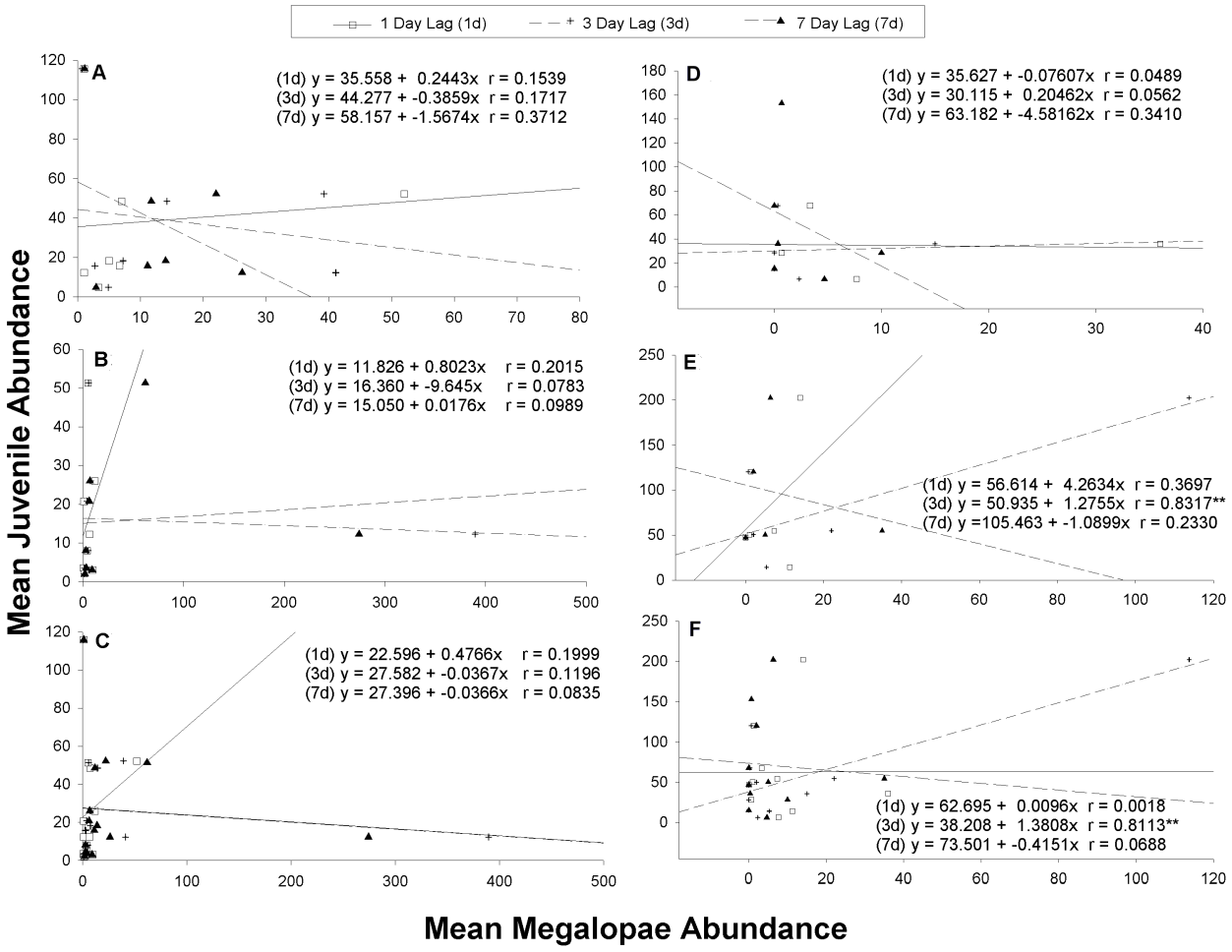

FIGURE 6. — Relationship between megalopal abundance and juvenile abundance with 1- 3- and 7-day lags in fringing marsh at Point aux Pins during a) 1990, b) 1991, c) 1990-91 combined, d) 1997, e) 1998 and f) 1997-98 combined. Significant correlations (when present) indicated by * ($p<0.05$).

explains why they were found primarily in denser seagrass.

Consistent with Schulman's (1996) expectations, data from Moksnes et al. (1997) showed that ninth instar blue crabs (CW 14.2-16.1 mm) consumed high numbers of megalopae and third instar (CW 4.3-5.9 mm) crabs, but many fewer of the larger fifth instar (CW 7.5-9.1 mm) crabs at eel grass densities of 400 shoots m^2. Subsequent to the fifth instar, intraspecific aggression was hypothesized to result in juvenile crabs leaving vegetated habitats (Moksnes et al., 1997).

Clearly, these experiments need to be repeated in the same and other locations, but if true, they explain what has been a puzzling aspect of our own work on blue crab survival in vegetated habitats. As reported by Heck and Coen (1995) and shown in subsequent data (see Figure 4), we have found little relationship between the survival of 5-20 mm CW blue crabs and the biomass of vegetation in Alabama seagrass habitats. We propose that this is a result of high survival of the smallest crabs in sparse vegetation and low survival in dense vegetation, and just the opposite patterns of survival for larger crabs. In this way, any significant relationship between vegetation density and survival is effectively cancelled out by opposite results for the survival of early and late juveniles in different vegetation densities. Therefore, there is no significant relationship between vegetation biomass and the survival of the entire 2-16 mm CW size class of juvenile crabs.

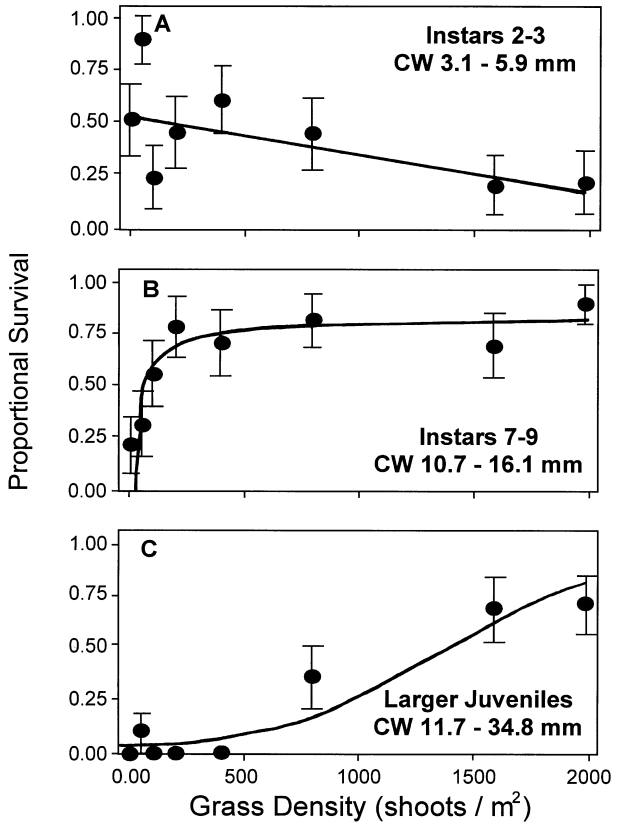

FIGURE 7. — Survival defined as the proportion of total number of individuals tethered that survived (excluding molted and dead-on-tether), and best fit survival response function for a) small crabs, b) medium juveniles and c) large juvenile crabs from Schulman's (1996) experiment.

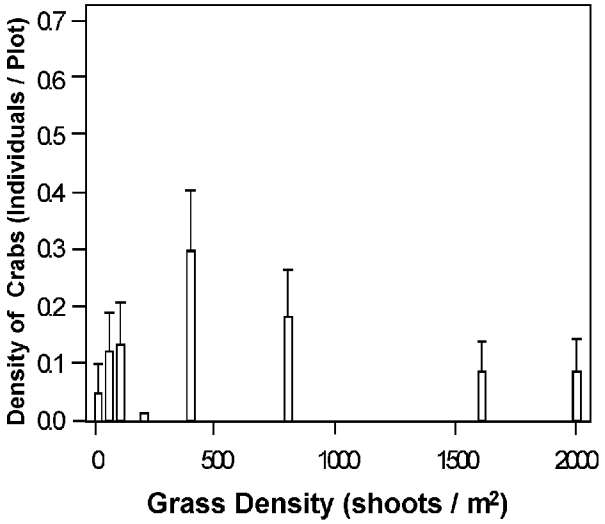

FIGURE 8. — Abundance distributions of small crabs (CW 3.1-5.9 mm) sampled throughout the late summer portion of Schulman's (1996) experiment.

Conclusions

Based on our review of previously summarized and recently published evidence on post-larval and early juvenile blue crabs we conclude that: 1) densities of megalopae reaching nursery habitats continue to be higher on the Gulf coast than those along the Atlantic coast, although less so than in the early 1990s; 2) there are few significant correlations between megalopal supply and juvenile abundance in the northern Gulf of Mexico, but when they do occur it is shortly after a large, episodic recruitment event, and usually within two weeks the correlation is no longer significant; 3) exceptionally high rates of predation continue to be recorded, indicating that most early juvenile blue crab mortality must be due to predation; 4) predation rates are most often (but not always) lower in vegetated habitats than on unvegetated substrates, but there is a size-specific effect of vegetation on survival, such that the smallest crabs survive best in low density vegetation while larger juveniles survive best in high density vegetation; 5) cannibalism by larger juveniles on the earliest settlers may drive this size selective pattern of survival.

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Proceedings of the Blue Crab Mortality Symposium 28-41

A Review of Incidental Fishing Mortalities of Blue Crabs

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Abstract. — The literature on the effects of capture and handling in actively fished blue crab (*Callinectes sapidus*) traps and penaeid shrimp gear and of confinement in ghost traps is reviewed. Blue crab traps are very inefficient with respect to size selectivity, and high numbers of sublegal individuals are captured that must be culled and released. Blue crab bycatch is very high in the large penaeid shrimp fishery. Blue crabs captured in traps and shrimp gear are subjected to physiological stress and injuries while in the gear and during culling. Immediate and delayed mortalities and reduced future growth rates may occur. Estimates of mortality ranged from 6-8% for trap-caught blue crabs and 6-36% for trawl- and skimmer net-captured blue crabs. There are many abandoned or lost traps that continue to ghost fish for extended periods. Estimates of annual blue crab mortality in ghost traps ranged from 25 to 40-60 per trap.

KEY WORDS: Blue crab, mortalities, ghost fishing, bycatch

Determination of both natural and fishing mortality rates is a critical step in a stock assessment of blue crabs (*Callinectes sapidus* Rathbun). The fishing mortality component can be divided into 'accounted mortality' (reported harvest) and 'unaccounted mortality' consisting of bycatch discards, ghost fishing, and juveniles released from actively fished traps (Chopin et al., 1996). Calculations of blue crab mortality typically do not include unaccounted mortality because this component is largely directed toward juveniles.

Incidental fishing mortalities of blue crabs in the Gulf of Mexico may be a significant component of overall mortality. Saila (1983) concluded that the effects of fishing on discarded nontarget organisms, including conspecifics which are outside size and sex restrictions imposed by fishery managers, are especially evident in fisheries which target decapods. Traps are inefficient with respect to size selection and may retain excessive numbers of sublegal (<127 mm CW) blue crabs (Guillory and Prejean, 1997; Guillory and Hein, 1998a, 1998b; Guillory, 1998a). Additionally, crab traps are often congregated in areas with a relatively high probability of contact with other user groups and of becoming ghost traps. Because blue crab traps do not deteriorate quickly, they may ghost fish for extended periods. Finally, high numbers of blue crabs are caught in the penaeid shrimp fishery. Effort in the shrimp fishery is especially high in Louisiana and Texas, and their adjacent offshore waters and large numbers of juvenile blue crabs are captured in shrimp trawls.

The objective of this report is to review literature on blue crab mortality resulting from capture and handling in actively fished crab traps and penaeid shrimp gear and from confinement in ghost traps. Although emphasis is placed on literature from the northern Gulf of Mexico, pertinent blue crab research from the Atlantic Coast and supplemental literature on other decapod species are also referenced.

Trap Capture and Handling

Cronin (1949) recognized the potential deleterious effects of trap capture and handling on blue crabs and recommended that, to minimize mortality, animals to be used for tagging projects should be collected with a trotline and stored in baskets with wet seaweed or grass. Although the popular perception is that culled sublegal blue crabs caught in traps and released are unharmed, recent scientific literature suggests that capture and handling adversely affects many decapods (see comprehensive bibliography of Murphy and Kruse, 1995).

INCIDENTAL FISHING MORTALITIES

The effects of trap capture and handling are most pronounced on blue crabs from 100-126 mm CW because blue crabs of that size are commonly caught in traps but must be released to comply with minimum size regulations. Excessive retention of sublegal blue crabs in traps has been recognized since the introduction of the gear (Green, 1952). The percentage of undersized crabs in traps exceeds 50% in some areas of Louisiana where there are high densities of sublegal crabs (Guillory and Merrell, 1993). The increased use of one-half inch square mesh traps in Louisiana has exacerbated the problem of sublegal catch because square mesh traps catch significantly higher numbers of undersize crabs than do hexagonal mesh traps (Guillory, 1998a; Guillory and Hein, 1998b; Guillory and Prejean, 1997). A significant reduction in catch of sublegal crabs has been achieved by use of escape rings (Guillory, 1989; Guillory and Merrell, 1993; Guillory and Hein, 1998a, 1998b) and escape rings are now required in three of five Gulf states (Guillory et al., 1998).

Fishing practices of most commercial blue crab trap fishermen are not conducive to high survival rates of culled sublegal blue crabs. Many fishermen empty their catch directly into boxes for later culling or use table graders that separate the catch and allow the sublegals to fall into a box for discard. Regardless of the technique used, sublegal blue crabs are usually held for extended periods before being released into the water. These practices not only prolong exposure to air but also increase the probability of injuries.

Physical injuries and physiological stresses from trap capture and handling may result in immediate or delayed effects to blue crabs. Immediate mortalities occur in the trap or during culling. Delayed effects on released blue crabs include mortality, reduced growth, and behavioral modifications.

Immediate Effects

Immediate mortalities of blue crabs may result from: 1) excessive injuries and predation from conspecifics and other bycatch, 2) stress associated with hypoxic conditions while captive in the trap, and 3) exposure to air and sunlight during holding and culling.

Blue crabs are notoriously aggressive even under optimal conditions and are probably more aggressive in crowded baited traps. Small blue crabs (Spier et al., 1996) and soft-shelled crabs that undergo ecdysis in the trap (V. Guillory, personal observation) may suffer high mortalities in traps due to conspecific predation by larger individuals. Damage to the carapace or appendages of blue crabs that are captured in traps is common. Eldridge et al. (1979) noted that over one-half (56.7%) of blue crabs in their study appeared to sustain damage associated either with trap capture or transit to the laboratory and damaged appendages were documented in 25% of trap-caught blue crabs in South Carolina (McKenna and Camp, 1992). Smith and Hines (1991) found that 18-25% of blue crabs in the Rhodes River in Chesapeake Bay and 19-35% of blue crabs at six other sites along the Atlantic and Gulf coasts had missing or regenerating limbs. Smith and Hines (1991) suggested that unsuccessful predation encounters by conspecifics may have been the principal source of nonlethal injuries but recognized that sublegal blue crabs captured in traps and subsequently released were also subject to limb loss.

High trap mortalities of blue crabs due to hypoxic water conditions have been reported in Alabama (Tatum, 1982), Chesapeake Bay (Van Engel, 1982), Texas (More, 1969), and Louisiana (V. Guillory, personal observation). Blue crabs are oxygen conformers (Batterton and Cameron, 1978) and have a high rate of oxygen consumption (Ayers, 1983) that is temperature sensitive (Laird and Haefner, 1976). Environmental hypoxia severely stresses blue crabs whose rate of oxygen consumption is further elevated by high temperatures (Lowery and Tate, 1986).

Physiological stress from confinement and crowding of blue crabs in traps and culling boxes and from exposure to air, sunlight, and elevated temperatures may be substantial. Lynch and Webb (1973) found that blue crabs caught by commercial trap fishermen had increased levels of serum glucose, and developed hyperglycemia when held out of water. Research on other decapods suggests that additional physiological stresses may result from exposure to air and sunlight. The inability to ventilate gills may lead to anaerobic metabolism and accumulation of toxic metabolites and exposure to air and sunlight results in gill dehydration, eye

damage, and physiological changes (increased pumping rates, decreased oxygen uptake, and increased hemolymph lactic acid and ammonia levels) (Dufur and McMahon, 1978; McMahon et al., 1978; Vermeer, 1987; Winkler, 1987). Exposure to air for relatively short time periods resulted in physiological stress and mortalities in Caribbean spiny lobster, *Panulirus argus* (Lyons and Kennedy, 1981). Myer-Rochrow and Tiang (1981) concluded that rock lobsters exposed to bright sunlight were affected in several ways, including impaired vision, inability to adjust to differing ambient light intensities, and alteration of normal diurnal activity rhythms.

Delayed Effects

Physical injuries and physiological stresses that occur during trap capture and handling contributes to delayed effects, including mortality, reduced growth, and possible behavioral modifications. Several publications have provided data on delayed mortality of trap-caught blue crabs held in transport containers or aquaria/tanks. Springborn (1984) and McKenna and Camp (1992) found mortalities of less than 6% after two hours and 7% after 14 days, respectively. A mortality of 43% after 56-hours was observed by Souza et al. (1980); however, they attributed the high death rate to frequent handling and crowded conditions. Method of capture influenced survival of peeler crabs in Haefner (1971); mortality after five days in shedding tanks was 80% and 48% for blue crabs caught in traps and dip nets, respectively. Delayed mortalities of other trap-caught decapods generally ranged from 3-15% (Table 1).

Blue crabs may be more susceptible to bacterial infections because of injuries and stress from trap capture and handling. Potentially pathogenic bacteria present on external surfaces may enter through wounds or other routes not ordinarily breached in nonstressed animals. Johnson (1976) found that 86% of trapped and 15% of trawled blue crabs in her study had bacterial infections. She observed an 80% mortality within 12 days and noted that paramoebiasis contributed to the high mortality. Sindermann (1971) reviewed work showing that bacteraemias in American lobster (*Homarus americanus*) and other invertebrates often occur in animals immediately after capture.

TABLE 1. — Delayed mortality of trap-caught decapods.

Species Name	Mortality (%)	Author(s)
Paralithodes camtschaticus red king crab	3 5.2 7.2-14.8	Byersdorfer and Watson, 1992 Stevens and MacIntosh, 1993 Zhou and Shirley, 1995
Neophrys norvegicus Norway lobster	3	Chapman, 1981
Chionoecetes bairdi tanner crab	11	Stevens and MacIntosh, 1993
Panulirus cygnus rock lobster	14.6	Brown and Caputi, 1986
Panulirus argus Caribbean spiny lobster	13.1	Hunt et al., 1986

The effects of trap capture and handling on blue crab mortalities may be influenced by several factors such as culling time, length of exposure to air, care in handling, and degree of injury. Inferences drawn from research conducted on other decapods (Onizuka, 1972; Edwards and Bennet, 1980; Schlieder, 1980; Lyons and Kennedy, 1981; Brown and Caputi, 1983; Simonson and Hochberg, 1986; Kennelley et al., 1990; Kaiser and Spencer, 1995; Zhou and Shirley, 1995) showed that mortality increased with exposure time, temperature, number of times caught and handled, and degree of injury and was greater on warm, windy, dry days than cool, calm, and damp days.

Injuries or stresses that occur in the trap or during handling may reduce growth rates of released blue crabs and delay recruitment into the fishery. Larger sublegal crabs that would normally enter the fishery after one additional molt [assuming a 30% increase in carapace width per molt (Gray and Newcombe, 1938)] may require additional molts before reaching harvestable size. Van Engel (1958) suggested that injuries may reduce the growth increment at molting from 25-33% to less than 10%. Ary et al. (1987) found that chelotomized blue crabs had growth increments of 2.5-4.7% less than did controls. Multiple limb loss was found to significantly reduce the molt increment and percent weight gain in the first post-autotomy molt (Smith 1990a). Reduced growth rates following limb loss/injury or handling stress have also been reported for other decapods (Table 2).

INCIDENTAL FISHING MORTALITIES

Behavior of released sublegal blue crabs may be altered by injuries or stresses that occur during capture and handling. Smith (1992) demonstrated experimentally that autotomy had a negative impact on mate competition in male blue crabs. Male blue crabs with limb loss were at a significant disadvantage when guarding sexually receptive females against other size-matched blue crab males. Limb loss and other injuries or physiological stress may reduce the ability of blue crabs to evade predators. Limb loss slowed escape behavior, altered random directional movement in small- and medium-sized blue crabs, and significantly increased predation of tethered blue crabs (Smith, 1990b). Aberrant defensive and escape behavior was observed in Caribbean spiny lobster after exposure-induced stress (Vermeer, 1987). Increased predation of released sublegal Hawaiian spiny lobster (*Panulirus marginatus*), rock lobster (*Panulirus cygnus*), and spanner crab (*Ranina ranina*) has been observed or postulated because of increased vulnerability while falling through the water column and disorientation upon landing on the bottom (Brown and Caputi, 1983; Gooding, 1985; Kennelly et al., 1990) or from impaired vision related to exposure to bright light (Myer-Rochrow and Tiang, 1981).

The repeated capture and release of sublegal blue crabs may compound the delayed effects of trap capture. Mortality was 100% for Dungeness crabs (*Cancer magister*) handled four times per month for two consecutive months, 10% for unhandled controls, and intermediate for Dungeness crabs handled 1-3 times (T. Shirley, personal communication; cited in Kruse, 1993). Guillory (1993) found that approximately half of the blue crabs escaped from ghost traps and noted that many later entered other ghost traps or were captured by commercial fishermen. Sublegal blue crabs may become conditioned to using traps as a feeding station and may repeatedly reenter traps after being released, as suggested for small American lobsters (Smolowitz, 1978a). With multiple recaptures, dessication may become a major stress factor. Smaller blue crabs dehydrate at a faster rate than larger individuals because water loss in decapods is directly proportional to surface area (Herreid, 1969; Vermeer, 1987).

TABLE 2. — Studies investigating reduced growth in decapod species due to [1]limb loss or injury, and [2]handling stress.

Species Name	Author(s)
Cancer pagurus edible crab	[1] Bennett, 1973
Panulirus argus Caribbean spiny lobster	[1] Davis and Dodrill, 1980 [1,2] Davis, 1981 [1] Hunt and Lyons, 1986
Panulirus sygnus rock lobster	[2] Brown and Caputi, 1985
Menippe mercenaria stone crab	[1] Savage and Sullivan, 1978
Homarus americanus American lobster	[2] Aiken and Waddy, 1986

Blue Crab Bycatch in Shrimp Gear

The penaeid shrimp fishery may contribute significantly to juvenile blue crab mortality. Fishing effort is high, and a variety of gears (several types of trawls, skimmer nets, and stationary and boat-based wing nets) are used that capture high numbers of blue crabs. More than 25,000 commercial shrimp licenses were issued in Louisiana and Texas in 1995 (Gulf States Marine Fisheries Commission, 1996). In recent years bycatch has captured the attention and scrutiny of interest groups and the public. According to Crowder and Murawski (1998), the term bycatch has been variously used to define catches or mortalities due to interactions with fishing gear. As used here, bycatch is defined as blue crabs captured in the shrimp fishery and discarded.

Comprehensive statewide bycatch surveys of the inshore penaeid shrimp fisheries have been conducted in Texas (Lamkin, 1984; Bessette, 1985; Fuls, 1996) and Louisiana (Adkins, 1993; Rogers et al., 1993). In addition, Watts and Pellegrin (1982) surveyed bycatch in the east Texas and central and west Louisiana inshore and offshore shrimp fisheries for the 1973-78 period. In Texas, blue crab bycatch averaged approximately 2.6% by number and 5.4% by weight in survey trawls and 3.9% by number in commercial bycatch samples (Fuls, 1996). In the Galveston Bay, Texas bait shrimp fishery, blue crab bycatch weight averaged 4% from May-November, 1984 (Bessette, 1985) and >15% in five of eight months sampled in 1982

(Lamkin, 1984). In Louisiana, biomass of blue crabs comprised 9.0% of surveyed 1989 shrimp fishery bycatch (Adkins, 1993) and 15.3% of inshore commercial trawl samples (Rogers et al., 1993). Watts and Pellegrin (1982) found that the percent composition by weight of blue crab bycatch was as follows: 2.5-5.1% from 0-10 fathoms in Louisiana; 0.3-2.2% from >10 fathoms in Louisiana; 0.5-3.2% from 0-10 fathoms in Texas; and, 1.8-18.1% from >10 fathoms in Texas. In North Carolina, blue crabs comprised 16.6% and 12.5% of the total catch biomass in otter trawls and skimmer nets, respectively (Coale et al., 1994).

The total number of blue crabs captured in the Gulf of Mexico penaeid shrimp fishery is high, and greatly exceeds the number harvested by crab fishermen. Based upon an estimated 1989 trawl bycatch of 227.8 million pounds in the Louisiana shrimp fishery and the percent of blue crabs in the catch by weight (Adkins, 1993), the 1989 Louisiana blue crab bycatch would have been approximately 20.5 million pounds or 380 million blue crabs. This assumes an average blue crab size of 68 mm CW (Rogers et al. 1993; Fuls, 1996), which corresponds to an average weight of 25 g (Guillory and Hein, 1997). This figure is probably an overestimate because bycatch samples were taken from estuarine or nearshore Gulf habitats, with none from further offshore where fewer blue crabs occur. Using bycatch data and estimated shrimp fishing effort, Hammerschmidt et al. (1998) calculated that more than 100 million blue crabs were caught as bycatch in the Texas inshore shrimp fishery in 1994. These estimates of blue crab bycatch compare to estimates of 130.3 million and 17.2 million blue crabs in the trap fisheries of Louisiana and Texas, respectively. The numbers of blue crabs harvested in the 1997 Louisiana and Texas blue crab fisheries were calculated by dividing the total landings by the generally acknowledged average weight of a commercially harvested blue crab (1/3 pound, or 151 g).

Blue crabs caught in shrimp gear, as in traps, are subject to stress and injuries. McKenna and Camp (1992) found that 36% of trawl-caught hard blue crabs had injuries with appendages being most frequently damaged. Injuries associated with capture in shrimp gear and handling ranged from 5-75% in other decapods (Scarratt, 1973; Spurr, 1978; Ganz, 1980; Wassenberg and Hill, 1989, 1993; Kaiser and Spencer, 1995). Blue crabs caught in shrimp gear are generally subjected to shorter capture and handling times than are sublegals caught in traps; however, the greater biomass of catch in trawls and skimmer nets may result in more injuries, greater physiological stress, and higher mortality. For example, the recapture rate of sand crabs taken in trawls was only one-third that of sand crabs captured in traps (Potter et al., 1991), suggesting that mortality of sand crabs (*Portunus pelagicus*) is higher after trawl capture than after trap capture.

Delayed mortality estimates for blue crabs captured in trawls ranged from 5.7% after two hours (Hines et al., 1993) to 36% after two weeks (McKenna and Camp, 1992). Mortality after capture in skimmer nets averaged 7.7% after two hours (Hines et al., 1993). These mortalities are significant when the estimated total number of blue crabs captured in shrimp gear is considered. Mortalities of other decapods caught in shrimp gear ranged from 2-57%, depending on species, depth of capture, time, environmental conditions, and other factors (Edwards and Bennett, 1980; Chapman, 1981; Reilly, 1983; Blackburn and Schmidt, 1988; Wassenberg and Hill, 1989, 1993; Hill and Wassenberg, 1990; Stevens, 1990; Kaiser and Spencer, 1995).

Gear type, tow and culling time, catch sorting conditions, amount and level of physical injury, molt stage, and total catch biomass affect bycatch mortality in shrimp gear (Smith and Howell, 1987; Wassenberg and Hill, 1989). Blue crab mortality was slightly higher after capture in skimmer nets than in trawls (Hines et al., 1993). Other authors (Coale et al., 1994; Adkins, 1993; Hein and Meier, 1995), however, suggested that overall bycatch mortalities were lower in butterfly or skimmer nets than in trawls. Skimmer or wing nets catch less mud and debris and are emptied more frequently than trawls and are often fished at night when temperatures are cooler and humidity higher.

Stress and incidence of injuries and damage, and subsequent mortalities are directly proportional to tow and culling time. Survival of blue crab bycatch varies with exposure time and averaged 9.6 days for early-culled blue crabs and 6.7 days for late-culled blue crabs (McKenna and Camp, 1992).

Mortality rates of sand crabs exposed for 10, 20, and 30 minutes were <5%, 5%, and 14%, respectively (Wassenberg and Hill, 1989). Environmental conditions such as temperature may be directly related to degree of stress on bycatch. Mortality of blue crab bycatch varied with season (26% in winter and 80% in summer), and warmer temperatures during the summer may have been a contributing factor (McKenna and Camp, 1992). McKenna and Camp (1992) found no significant difference in delayed mortality rates between damaged and undamaged blue crabs; however, mortalities of other decapods have been shown to increase with injury level (Onizuka, 1972; Edwards and Bennett, 1980; Kennelly et al., 1990; Kaiser and Spencer, 1995).

Soft or papershell stage blue crabs have high mortality rates when captured in shrimp gear. Highest mortalities of trawl-caught blue crabs coincided with the presence of many papershell and soft crabs (McKenna and Camp, 1992). Immediate mortalities of trawl-caught Dungeness crabs were 0.9% for hard, 1.8% for recently molted, and 20.4% for softshell crabs (Reilly, 1983). Smith and Howell (1987) and Wassenberg and Hill (1989) also found high immediate mortalities of trawl-caught soft or peeler stage individuals of other decapods. Damage and physiological stress associated with trawl capture may be reduced by mandated trawl modifications that decrease retention of bycatch. Turtle-excluder devices (TEDs) or bycatch-reduction devices (BRDs) have been demonstrated to reduce both fish (Branstetter, 1997; Watson et al., 1997) and blue crab bycatch (Rogers et al., 1993).

The effect of salt-boxes on bycatch survival is a controversial issue in the northern Gulf of Mexico (Adkins, 1993). Salt boxes are onboard containers with a hypersaline solution of seawater and NaCl used by shrimp fishermen to separate bycatch from shrimp. Catch is placed in the salt box; the fish float and are discarded while invertebrates such as penaeid shrimp and blue crabs sink. Thirty-seven percent of Texas inshore shrimpers have salt boxes and use them 55% of the time (Bumguardner and Colura, 1997). Colura and Bumguardner (1996) concluded that tow time and culling time were more important than salt-box use for bycatch survival. Of the species tested, blue crabs were least affected by salt-box exposure, with an LE_{50} of 67 minutes. This experiment, however, was conducted under optimum, controlled conditions. Mortalities may increase under typical conditions associated with commercial fishing. Additionally, Adkins (1993) suggested that shrimp fishermen add other chemicals to their salt boxes to increase the specific gravity of the solution, and that the mixture kills all bycatch.

Discards that survive trawling and sorting activities and escape initial predation from birds, aquatic mammals, and fishes which often prey upon bycatch discards (Hill and Wassenberg, 1990; Kennelly et al., 1993; Wassenberg and Hill, 1993) may be subjected to future increased predation rates because of altered behavior (Crowder and Murawski, 1998) or succumb to bacterial and viral infections (Kennelly et al., 1993).

Ghost Fishing

Several terms have been used loosely and interchangeably in the literature to discuss ghost fishing. Breen (1990) suggested that standard 'ghost fishing' terminology be used: 'lost traps' are lost or discarded fishing gear, which may or may not be capable of ghost fishing; 'derelict traps' are lost or abandoned traps that are no longer capable of ghost fishing; 'ghost traps' are lost or abandoned traps that continue to fish.

There are several ways in which an actively fished trap can become a ghost trap. Traps may be simply abandoned by fishermen or lost due to uncontrollable factors (i.e., tides, currents, storm surges). Negligence by the fishermen in properly assembling and maintaining buoys and attachment lines, inadvertent clipping of float lines by vessel propellers, intentional cutting of buoy lines, and the use of plastic containers as floats which may deteriorate also contribute to the proliferation of ghost traps (Guillory, 1996). Regardless of the mechanism, the number of lost or abandoned traps is substantial.

Blue crabs enter ghost or derelict traps for several reasons (Guillory, 1993): autobaiting by fishes (Davis, 1942; Whitaker, 1979; Guillory, 1993) or blue crabs that die in the trap; prior conditioning of previously caught sublegal blue crabs to enter traps; attraction to captured males by premolt females (Bishop et al., 1983, 1984; Christian et al., 1987); and shelter for premolt crabs

of both sexes. Although dead individuals in traps have been shown to repel conspecifics of several species (Hancock, 1974; Miller, 1977; High and Worlund, 1979), blue crabs are cannibalistic and are attracted to crushed blue crabs in traps (Savoie and Casanova, 1982; Guillory, 1993).

Overall ghost fishing mortality is dependent upon the rate of trap deterioration, the length of time the trap fishes, the number of ghost traps and the mortality rate per trap. Mortalities will continue until the trap deteriorates sufficiently for holes to develop in the wire mesh and captured individuals are able to escape. The life expectancy of various mesh type crab traps has been estimated several times. Galvanized blue crab traps with anti-corrosive zinc anodes began to deteriorate after about 250 days (Whitaker, 1979) or one year (Southern Fisherman, 1956). Deterioration of galvanized trap wire is rapid once the underlying iron wire core is exposed (Van Engel, 1962). Vinyl-coated hexagonal trap wire was introduced during the 1970s to retard corrosion and was widely accepted by the late 1970s in the Gulf of Mexico (Steele and Perry, 1990). Depending on salinity, the life expectancy of a vinyl-coated trap will average two years or more (Shively, 1997). In recent years, vinyl-coated square mesh traps, which are constructed of a heavier gauge wire than the traditional hexagonal mesh traps, have become increasingly common in Louisiana (Guillory, 1996). Square mesh traps probably have a longer life expectancy than hexagonal mesh traps, although no data are available.

Estimates of trap loss are high. Casey (1990) speculated that annual trap loss in the Chesapeake Bay blue crab fishery was generally in the 10-30% range. According to surveyed commercial blue crab fishermen in Louisiana and Texas, an average of 257 (Guillory, 1998b) and 103 (Shively, 1997) traps per fisherman were either lost or stolen each year. Assuming a conservative annual trap loss of 10% and approximately 500,000 commercial crab traps and up to 33,000 recreational traps in use (Guillory, 1997), approximately 50,000 ghost traps may be added each year in Louisiana. The total number of ghost traps in Louisiana coastal waters has probably increased over time. Stevens (1996) concluded that the number of ghost traps would eventually peak due to the arithmetic increase in lost traps and the exponential decay process. Stevens (1996) showed that trap decay can be modeled as an exponential process and described with a half-life. For instance, if 7,000 traps were lost each year with a half-life of one year, then the number of ghost traps would eventually reach a maximum of 14,000 after 10 years and achieve a steady state. Annual trap loss in other decapod fisheries is given in Table 3.

Ghost fishing and mortality of captured animals is a serious problem in many other decapod trap fisheries. Ghost trap mortalities result from adverse environmental conditions in the traps, cannibalism, predation by fish bycatch, injuries from fish and other crabs, starvation, or disease (Breen, 1990; Guillory, 1993). Mortality of blue crabs in ghost traps has been quantified in Louisiana (Arcement and Guillory, 1993; Guillory, 1993), South Carolina (Whitaker, 1979), and Chesapeake Bay (Casey and Daugherty, 1989; Casey and Wesche, 1977 and 1980). In general, catch rates for blue crabs (Whitaker, 1979; Arcement and Guillory, 1993; Guillory, 1993) and other decapods (Pecci et al., 1978; Breen, 1987) in ghost traps are lower than rates of actively fished traps, although the cumulative catch over time may be substantial. Blue crab mortalities in Louisiana averaged 25.8/trap for one year (Guillory, 1993) and 17.3/trap

TABLE 3. — Estimates of annual trap loss in commercial decapod trap fisheries.

Species Name	Loss (%)	Author(s)
Chionecetes opilio snow crab	8	Miller, 1977
Homarus americanus American lobster	20-25	Sheldon and Dow, 1975
Cancer magister Dungeness crab	11	Breen, 1987
	23	Tegelberg, 1974
	18	Northup, 1978
		Muir et al., 1984
	10	Pacific States Marine Fisheries Commission, 1978
Paralithodes camtschaticus red king crab	10	High and Worlund, 1979
	20	Kruse and Kimker, 1993
all trap fisheries	20	Kruse and Kimker, 1993
	10-20	Breen, 1990
	10-30	Laist, 1986

in traps without escape rings and 5.3/trap in traps with escape rings over a three-month period (Arcement and Guillory, 1993). Whitaker (1979) concluded that total annual mortality in South Carolina ghost traps averaged approximately 40 blue crabs per trap and generally ranged from 20-60 blue crabs. Table 4 lists other fisheries in which ghost fishing mortalities have been estimated.

Mortalities in ghost trap studies in Chesapeake Bay varied seasonally. High mortalities occurred in ghost traps from January to March (7.7 crabs/trap and 100% mortality; Casey and Wesche, 1977) and lower mortalities in August and September (7.5 crabs/trap and 33% mortality; Casey and Wesche, 1980). Arcement and Guillory (1993) and Guillory (1993) reported that 38-60% of blue crabs entering ghost traps died in Louisiana.

The lower mortality estimates obtained in Chesapeake Bay compared to Louisiana and South Carolina may be partly related to study design; Casey and Wesche (1977, 1980) monitored ghost traps that were not initially baited as were traps used by Whitaker (1979), Arcement and Guillory (1993), and Guillory (1993). Baiting ghost traps for monitoring is recommended because most traps that are lost are probably baited and being actively fished. In addition, unless blue crabs are identified with durable tags and small mesh bottom screens are used to collect loose tags, many blue crabs that die between trap checks will be missed because they are crushed into small fragments by other blue crabs. Guillory (1993) recovered 42 loose tags in monitored ghost traps, and in most cases intact carcasses were not present in the trap.

Highest mortalities in ghost traps occur immediately after a trap converts from an actively fishing to a ghost fishing mode (Whitaker, 1979; Arcement and Guillory, 1993; Guillory, 1993) and blue crabs that were attracted to the original bait in the trap are still present. Mortality in a ghost trap is directly related to the number of blue crabs that are present in the trap (Arcement and Guillory, 1993; Guillory, 1993). Entry of blue crabs declines as traps deteriorate. Casey and Wesche (1977) calculated the average number of blue crabs in traps at different stages of deterioration: good traps -- 11.2; fair traps -- 5.3; and, poor traps -- 2.3. Approximately half of the crabs in a three-month study (Arcement and Guillory, 1993) and two-thirds of the crabs in a 12-month study (Guillory, 1993) died within the first two weeks. Blue crabs attracted to the original bait had an overall mortality of 71% while crabs entering the traps later had an overall mortality of 51% (Guillory, 1993). From 25-50% of blue crab mortality in South Carolina ghost traps took place immediately (Whitaker, 1979). Breen (1990) cautioned that some ghost traps periodically empty but may later attract decapods due to seasonal effects or to autobaiting. Sampling programs that rely on infrequent counts of crabs in ghost traps can be misleading (Guillory, 1993).

Any measure that reduces sublegal catch in actively fished traps will likewise reduce capture and handling effects (Brown and Caputi, 1986; Brown and Dibden, 1987). Arcement and Guillory (1993) showed that escape rings will reduce ghost fishing mortality. Ghost fishing mortality was also reduced in vented Dungeness crab (High, 1976), American lobster (Pecci et al., 1978; Smolowitz, 1978b), and Hawaiian spiny lobster (Paul, 1984) traps. Traps with escape rings have a shorter confinement time for escaping blue crabs than traps without escape rings (Arcement and Guillory, 1993), which may have important implications for delayed post-escape mortality. The presence of stone crabs (*Menippe mercenaria*) and heavy fouling decreases entry of blue crabs in ghost traps, leading to decreased mortalities per trap (Whitaker, 1979). Recovery rates and probably mortality rates for tagged red king crabs (*Paralithodes*

TABLE 4. — Ghost fishing mortalities in decapod trap fisheries.

Species Name	Mortality (%)	Author(s)
Cancer magister	23	High, 1985
Dungeness crab	19	Muir et al., 1984
	50	Breen, 1987
Scyllarides squammosus	<4	Parish and Kazman, 1992
slipper lobster		
Homarus americanus	12-18	Sheldon and Dow, 1975
American lobster	25	Pecci et al., 1978
Paralithodes camtschaticus	4-12	High and Worlund, 1979
red king crab		
Chionoecetes bairdi	39	Kimker, 1992
tanner crab		

camtschaticus) were inversely related to length of residence in traps (High and Worlund, 1979). Finally, ghost fishing mortality varies with blue crab abundance and location (Casey and Daugherty, 1989).

Ghost trap data underestimate total mortality because many blue crabs escape and are subjected to delayed mortalities as a result of injuries, physiological stress, and lack of food while in the trap. Arcement and Guillory (1993) and Guillory (1993) found that 34-56% of blue crabs escaped from ghost traps. Starved tanner crabs exhibited delayed mortalities (Paul et al., 1994); 40-100% of the crabs died during a 230-day, food rich observation period following various starvation regimes. Delayed mortalities of decapods escaping from ghost traps may be directly related to length of residence in the trap. The tag recovery rate of red king crabs confined for 10-16 days in simulated lost traps was significantly lower than those confined in traps for only 1-4 days before release (High and Worlund, 1979).

The Louisiana blue crab fishery will be used to illustrate the potential impact of ghost fishing. Annual trap loss was estimated at approximately 50,000 traps (Guillory, 1997). This, coupled with a mortality of 25 blue crabs per trap (Guillory, 1993), would yield a potential mortality of 1,250,000 blue crabs per year. This very conservative estimate assumes that each lost trap will ghost fish for one year and does not include older ghost traps. The effects of ghost traps on other decapod fisheries have been estimated at 7% of annual Dungeness crab landings in British Columbia (Breen, 1987) and 3-6% of annual American lobster landings of the East Coast of the United States (Smolowitz, 1978a).

Conclusions

Although incidental, or unaccounted, fishing mortalities of juvenile blue crabs are substantial in the northern Gulf of Mexico, the magnitude of their effects on blue crab populations is unknown. Perry et al. (1998) found large annual variation in recruitment of small crabs in Mississippi Sound and noted that exceptionally high numbers of early crabs did not provide for greatly elevated numbers of later stage juveniles. Fishery-independent data from this study and others suggest that estuarine carrying capacity sets population limits and production in excess of carrying capacity is lost. The lack of quantitative knowledge of carrying capacity prohibits evaluation of the importance of incidental fishing mortalities relative to numbers available for recruitment to the fishery. Additionally, other factors may partially ameliorate the potential effects of incidental fishing mortalities on blue crab populations; predation, parasites and diseases, and environmental parameters may be reduced with high incidental fishing mortalities. Although the impact of increased survivorship of early juvenile crabs to the commercial fishery is not clear, an increased survival of sublegal crabs through the use of escape vents, optimum mesh size, degradable panels, and reduced culling will result in more animals available to the fishery.

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Length-based Estimates of Total Mortality For Gulf of Mexico Blue Crab

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Abstract. – Hoenig's (1987) length-based method was used to estimate total instantaneous mortality rates for Gulf of Mexico blue crab (*Callinectes sapidus*, Rathbun). Carapace width data from Gulf states' monitoring and assessment programs, and von Bertalanffy (1938) growth parameters K and CW_∞, were used as input parameters for Hoenig's formula. K and CW_∞ were estimated to be 0.663 and 276 mm, respectively, based on a maximum age of six years. Total mortality estimates were derived for each Gulf state for which carapace width data were available. Estimates ranged from 0.572 for Louisiana in 1967 to 1.279 for Mississippi in 1975. The grand mean across states and years was 0.971. Trend analysis indicated all states except Louisiana showed similar inter annual trends.

Key words: blue crab, *Callinectes sapidus*, total mortality, stock assessment

Mortality estimates are one of the most important parameters required when conducting stock assessments. Mortality rates are critical for determining the abundance of populations since one of the objectives of stock assessment is to estimate stock responses to various levels of fishing mortality (F). Fishing mortality is usually estimated by subtracting an estimate of natural mortality (M) from an estimate of total mortality (Z). Therefore, estimating Z is an essential first step in the assessment procedure.

For several reasons, there are currently no

estimates of total mortality rates for the blue crab (*Callinectes sapidus*, Rathbun) in the Gulf of Mexico. First, the blue crab is a lower priority species than other Gulf commercial species such as brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*), Gulf menhaden (*Brevoortia patronus*) and red snapper (*Lutjanus campechanus*). Second, because of this relative unimportance there has been inadequate research funding to estimate stock assessment parameters. Third, there are considerable problems associated with ageing blue crabs. It is usually necessary to age organisms prior to estimating mortality rates.

None of the methods used to age fish are suitable for blue crabs. Fish are usually aged by four methods: direct observation in a captive environment; mark and recapture experiments; analysis of size frequency histograms; and anatomical inspection of somatic features such as scales, otoliths or bones, and spines or fin rays. Direct observation in a captive environment may include bias since captive organisms may experience dissimilar growth rates in comparison to organisms in the natural environment. Mark and recapture methods are difficult for crabs since they undergo ecdysis, and tags may be shed while molting. Assigning ages to modal groups in size frequency histograms is difficult because the spawning period for blue crabs in the Gulf is protracted. Finally, blue crabs, like all invertebrate species, lack somatic features used in ageing vertebrate species. Since ageing blue crabs is particularly challenging, length-based methods are a significant contribution toward estimating mortality rates. Hoenig's method is an extension of Beverton and Holt's (1957) technique and corrects for bias created when the average carapace width of crabs wider than the width at full recruitment to the sampling gear, approaches the carapace width at full recruitment (Hoenig, 1987).

This report is the result of a request by the Blue Crab Technical Task Force of the Gulf States Marine Fisheries Commission. The Task Force is currently in the process of revising their Blue Crab Fishery Management Plan (Steele and Perry, 1990). The total mortality estimates contained in this report were incorporated in the revision as part of the stock assessment section. Objectives of this paper are to: (1) derive estimates of instantaneous total mortality for each Gulf coast state for years in which carapace width data are available from state fisheries agencies; (2) investigate inter annual trends within states; and (3) compare inter annual trends among states.

Materials and Methods

Carapace width data were obtained from assessment and monitoring programs in each Gulf state. Data collected by trawls were used in order to improve comparability of results across states. Mississippi, Alabama and Louisiana used 4.9 m otter trawls while Florida and Texas used 6.1 m otter trawls. Differing trawl sizes as measured by headrope lengths were not considered to be a substantial problem since Hoenig's formula accounts for such differences in computing sizes at full recruitment to the sampling gear.

The first step in developing length-based estimates of total mortality was to derive estimates of Gulf blue crab carapace widths-at-ages to be used in the von Bertalanffy growth equation. Carapace widths-at-ages for post-larval to one-year-old crabs were based on St. John's River, Florida data from Tagatz (1968). Tagatz estimated growth by month for reared blue crabs hatched in April, July and October (Table 1). Although reared blue crabs may not accurately represent growth rates in their natural habitat, these data were the best available estimates for carapace widths-at-ages in the Gulf of Mexico.

Maximum age of Gulf blue crabs was estimated to be six years. This estimate was based on the following: Fischler (1965) who found crabs attaining an age of at least five years in a tagging study conducted in North Carolina, Rothschild and Ault (1992) who assumed a maximum age of six years in their assessment of Chesapeake Bay blue crabs, and Smith (1997) who inferred a maximum age of five and a half years based on a molt-process model.

A first estimate of maximum carapace width, obtained by the modified Wetherall et al. (1987) technique, was compared to an estimate obtained from the approach of Beverton (1963). The modified Wetherall technique is described by,

$$(\overline{CW} - CW') = \beta_0 + \beta_1(CW') \quad (1)$$

where $\overline{CW}$ is the mean carapace width of crabs CW' in width and larger, CW' is the lower bound of a size interval in a size frequency distribution, and β_0 and β_1 are the respective estimated y-intercept and slope of the fitted line. Calculating $\overline{CW}$ by starting with the largest size class and fitting a straight line to the resultant data pairs provides an estimate of maximum carapace width, CW_∞, as the point where the fitted line intercepts the x-axis or,

$$CW_\infty = -\frac{\beta_0}{\beta_1} \quad (2)$$

Beverton's approach divides the maximum size occurring in a well sampled stock, CW_{max}, by the constant 0.95,

$$CW_\infty = \frac{CW_{max}}{0.95} \quad (3)$$

and is based on the observation that, in general, the oldest individuals of a stock grow to reach about 95 percent of their asymptotic size. Upon estimating CW_∞ this value was coupled with the estimated maximum age of blue crabs to provide an additional width-at-age data pair for the von Bertalanffy analysis.

TABLE 1. — Carapace widths (mm) by month of St. Johns River, Florida blue crabs hatched in April, July and October (Tagatz, 1968).

Month	Month Hatched			Mean Carapace Width
	April	July	October	
1	1[1]	1[1]	1[1]	1.0
2	5	5	5	5.0
3	12	12	8	10.7
4	23	23	10	18.7
5	46	46	12	34.7
6	58	46	15	39.7
7	90	58	29	59.0
8	113	58	46	72.3
9	113	72	72	85.7
10	113	90	90	97.7
11	113	113	113	113.0
12	142	142	142	142.0

[1] Larvae

von Bertalanffy growth is described as,

$$CW_t = CW_\infty(1 - e^{-K(t - t_0)}) \quad (4)$$

where CW_t is the estimated carapace width at time, t; e is Euler's number (~2.7183); K is the von Bertalanffy growth coefficient; and t_0 is the time at which carapace width is theoretically zero. This continuous growth function doesn't literally describe the incremental growth of blue crabs, but since model fitting is essentially a data smoothing technique and members of a cohort molt at different times, the average growth of a cohort becomes a smooth curve (Sparre et al., 1989). Rothschild et al. (1992) and Smith (1997) considered incremental growth functions but Rugolo et al. (1997) concluded that the von Bertalanffy model adequately described blue crab widths-at-ages.

Once the von Bertalanffy growth model was developed, CW_∞ and K were used in Hoenig's formula to compute annual estimates of instantaneous total mortality rates,

$$Z = \log_e\left[\frac{(e^{-K}(\overline{CW} - CW_\infty)) + CW_\infty - CW_r}{(\overline{CW} - CW_r)}\right] \quad (5)$$

where CW_r is the carapace width at full recruitment to the sampling gear and $\overline{CW}$ is the mean carapace width of crabs measuring CW_r and greater.

Multiple regression with dummy variables was used to compare interannual trends of estimated mortality rates among states,

$$\hat{Z} = \hat{\beta}_0 + \hat{\beta}_1(Year) + \hat{\beta}_2(Fla) + \hat{\beta}_3(Ala) + \hat{\beta}_4(Miss) + \hat{\beta}_5(La) + \hat{\beta}_6(Year \times Fla) + \hat{\beta}_7(Year \times Ala) + \hat{\beta}_8(Year \times Miss) + \hat{\beta}_9(Year \times La) \quad (6)$$

with each state coded with dummy variables (Table 2). Statistical tests of significance were performed at the α=0.05 level of significance.

Results

Maximum carapace width was estimated to be 268 mm (Figure 1) by the Wetherall et al. (1987) approach and 274 mm by the Beverton (1963) technique. Sparre et al. (1989) considered the Wetherall approach to be the better of the two therefore 268 mm was used as an estimate of CW_∞.

Carapace widths-at-ages derived from Tagatz (1968) were averaged across hatching months to obtain general growth rates (Table 1). Two additional data pairs were used to estimate von Bertalanffy growth, 179 mm at age two (based on the expected number of molts between age one and age two crabs, and the expected growth-per-molt) and 268 mm at six years. These 14 data pairs were then used to fit the von Bertalanffy growth equation,

$$CW_t = 276(1 - e^{-0.663(t-0.169)})$$

The estimate of K=0.663 was similar to those reported by Rothschild et al. (1991) and Rugolo et al. (1997) who estimated growth coefficients f 0.506 and 0.587, respectively, for Chesapeake Bay crabs.

The estimated total mortality averaged across states and years was 0.971 (Table 3). Considering spatial (states) and temporal effects (years), the lowest estimate was observed for Louisiana in 1967 (0.572) and the highest for Mississippi in 1976 (1.279). Disregarding temporal effects, the mean

TABLE 2. — Variables used to code the states for multiple regression analysis.

State	Dummy Variable			
	FL	AL	MS	LA
Florida	1	0	0	0
Alabama	0	1	0	0
Mississippi	0	0	1	0
Louisiana	0	0	0	1
Texas	0	0	0	0

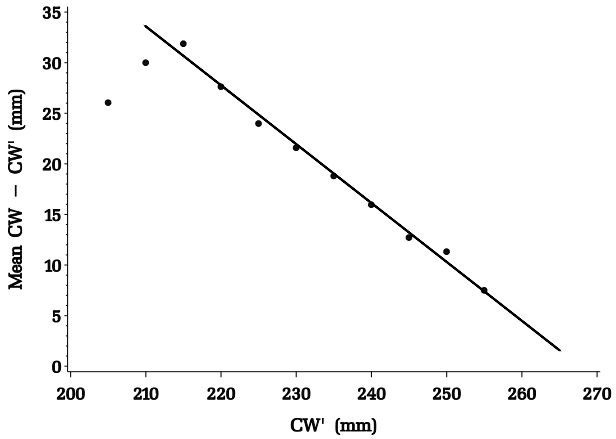

FIGURE 1. — Wetherall et al. (1987) plot used to estimate CW_∞, the average carapace width of very old Gulf of Mexico blue crabs.

estimate for Louisiana was lowest for all states (0.748) followed by Mississippi (1.020), Florida (1.072), Texas (1.103) and Alabama (1.145).

Results of multiple regression analysis yielded a significantly fitting full model (R^2=0.746, p=0.0001) with no significant state×year interaction (p=0.9684). The full model was decomposed into five simple linear models representing each state,

$$\begin{aligned}
\textit{Florida}: \quad \hat{Z} &= 0.854200 + 0.007909(\textit{Year}) \\
\textit{Alabama}: \quad \hat{Z} &= 1.018952 + 0.005271(\textit{Year}) \\
\textit{Mississippi}: \quad \hat{Z} &= 1.077785 - 0.002869(\textit{Year}) \\
\textit{Louisiana}: \quad \hat{Z} &= 0.653224 + 0.005731(\textit{Year}) \\
\textit{Texas}: \quad \hat{Z} &= 0.969529 + 0.005581(\textit{Year})
\end{aligned}$$

Statistical analysis indicated that interannual trends for all states were similar except for Louisiana which resulted in a common slope but a significantly different y-intercept (Figure 2).

Discussion

An important component of Hoenig's length-based formula is von Bertalanffy's growth coefficient, K. Assuming a maximum age of six years, maximum carapace width of 268 mm and widths-at-ages of Tagatz (1968), the von Bertalanffy growth function estimated K at 0.663

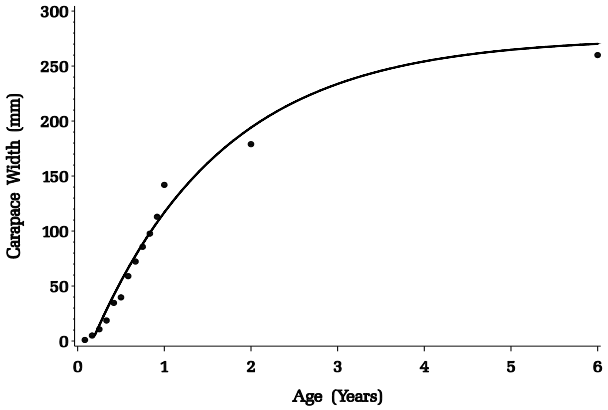

FIGURE 2. — von Bertalanffy growth curve for Gulf of Mexico blue crabs.

(Figure 2). Rothschild et al. (1991) and Rugolo et al. (1997) also modeled growth using the von Bertalanffy model for Cheasapeake Bay blue crabs. Rothschild et al. (1991) estimated K=0.506 by modifying the continuous function to account for molting, and assumed a maximum carapace width of 178 mm and maximum age=6 years. Rugolo et al. (1997) estimated K=0.587 using the standard approach and assumed a maximum carapace width of 260 mm and maximum age=8 years. The higher growth coefficient for Gulf crabs is due to temperature dependent growth behavior. Blue crabs stop growing in water temperatures below 9°C therefore Chesapeake Bay crab growth ceases in November and begins again the following April (Miller and Houde 1998). The temperature of Gulf waters seldom drops below 9°C therefore growth continues throughout most years. It is not uncommon for Gulf crabs to reach maximum size within their first year whereas Chesapeake Bay crabs may not reach maximum size until their second summer (Smith 1997).

Although the von Bertalanffy growth function was used to model growth rate, caution should be exercised when applying this technique to blue crabs because of sex specific growth characteristics. Although males grow throughout their lifetimes, females undergo a terminal anecdysis at which time growth stops. This occurs at sexual maturity which occurs at about age one in the Gulf. Therefore, the von Bertalanffy growth function performs well for describing growth rates for both sexes less than a year old, but may be biased for older crabs. Beyond one year of age, carapace widths of females are overestimated while males are underestimated. The amount of bias introduced into estimates of K because of this phenomenon is unknown, but it is important to note that most of blue crab growth occurs prior to one year of age.

TABLE 3. — Estimated annual total mortality rates for blue crabs by state for the U.S. Gulf of Mexico. The grand mean for years and states combined was 0.971.

Year	State				
	FL	AL	MS	LA	TX
1967				0.572	
1968				0.715	
1969				0.797	
1970				0.694	
1971				0.782	
1972				0.694	
1973				0.649	
1974			1.163	0.610	
1975			1.168	0.701	
1976			1.279	0.675	
1977			1.060	0.781	
1978			0.954	0.805	
1979			1.112	0.713	
1980			1.078	0.739	
1981			0.733	0.679	
1982			0.921	0.789	0.886
1983		1.158	0.904	0.804	1.040
1984		1.042	0.772	0.702	1.123
1985		1.065	1.004	0.679	1.159
1986		1.116	1.155	0.682	1.063
1987		1.206	1.168	0.789	0.970
1988		1.259	1.083	0.704	1.163
1989	1.050	1.176	0.888	0.698	1.186
1990	1.013	1.126	1.059	0.634	1.169
1991	1.024	1.106	0.893	0.654	1.201
1992	1.109	1.003	1.025	0.915	1.164
1993	1.123	1.092	0.842	0.807	1.039
1994	1.143	1.207	1.029	0.859	1.166
1995	0.935	1.253	0.889	0.940	1.178
1996	1.039	1.157	0.928	0.913	1.114
1997	1.128	1.216	1.195	0.869	1.136
1998	1.153		1.208	0.885	1.002
Mean	1.072	1.145	1.020	0.748	1.103
SE	0.022	0.020	0.029	0.017	0.022

Annual total mortality was estimated using estimates of K, maximum carapace width, and state specific estimates of: 1) size at full recruitment to the sampling gear and 2) mean carapace width of crabs larger than the size at full recruitment. Considering temporal (years) and spatial (states) effects, the lowest estimate occurred in 1967 for Louisiana (0.572) while the greatest occurred in

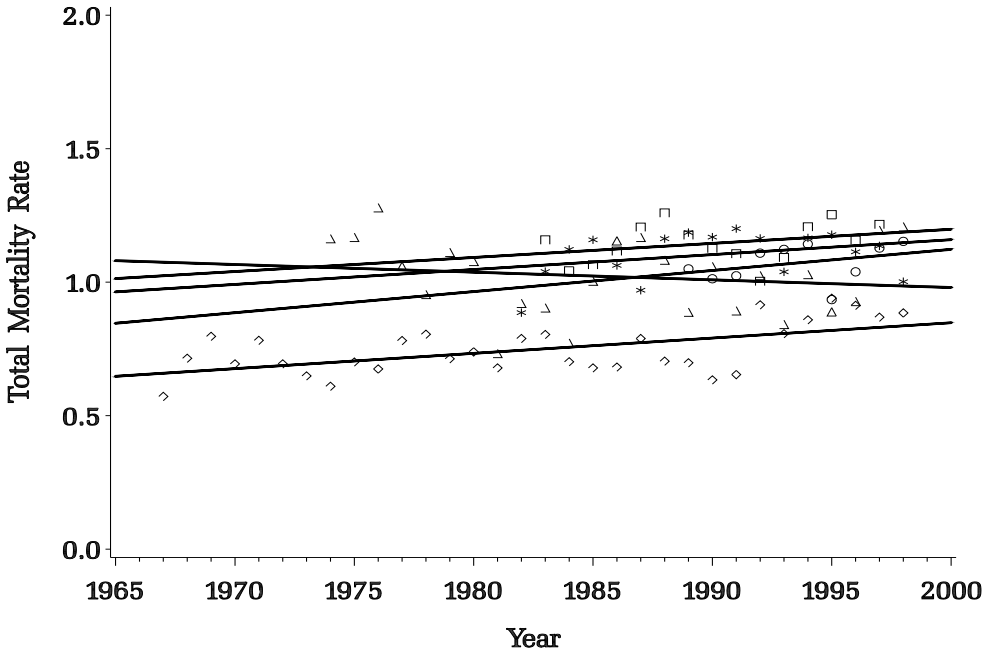

FIGURE 3. — Overlay plots of blue crab total mortality estimates by years for Gulf coast states. Symbols represent individual states; circles, Florida; squares, Alabama; triangles, Mississippi; diamonds, Louisiana; stars, Texas. Fitted lines represent from top to bottom, adjacent to the y-axis; Mississippi, Alabama, Texas, Florida and Louisiana.

1976 for Mississippi (1.279, Table 3). The low estimate for Louisiana occurred early in the fishery's history when fishing mortality was relatively low. The remaining states did not have comparable carapace width data as early in their respective fisheries; however, it is assumed that fishing mortalities were similarly low. Explaining the high Mississippi estimate is difficult since it occurred during a year in which landings were not particularly high. Apparently natural mortality played a larger role than fishing mortality in influencing the high estimate of total mortality.

Regression analysis resulted in a significantly fitting model describing annual trends in total mortality estimates for each Gulf coast state ($p=0.0001$, $R^2=0.746$). Results showed no significant temporal trend for any state; however, the y-intercept for Louisiana was significantly different from at least one of the other states. Inspection of Figure 3 reveals that the trend lines for Florida, Alabama, Mississippi and Texas are grouped together while that of Louisiana is separate. Estimates of $\overline{CW}$ and CW_r were computed for each state with years combined to gain insight into the variation of mortality estimates among states (Table 4). $\overline{CW}$ For Louisiana was greater (101 mm) than all other states except Florida (127 mm); however, the Florida estimate was influenced by a relatively large size at full recruitment (90 mm) in comparison to Louisiana (25 mm). Thus a relatively large number of crabs in Louisiana waters survive to reach a larger size than in other Gulf states which results in lower mortality estimates. It is interesting to note that even though mortality estimates were significantly lower for Louisiana, the temporal pattern was similar for all states indicating that factors affecting mortality rates appear to be similar throughout the Gulf.

Another interesting result was the apparent compensatory nature of the estimates. Although landings have increased substantially during the period of these analyses, total mortality has remained relatively constant. This suggests that natural mortality was high during years of low fishing mortality and natural mortality was low during years of high fishing mortality. Such a result complicates the use of modeling surplus production

TABLE 4. — Blue crab size at full recruitment to sampling gears and mean size of crabs greater than the size at full recruitment for each Gulf coast state (disregarding temporal effect).

	Florida (n=12,425)	Alabama (n=11,785)	Mississippi (n=644)	Louisiana (n=24,003)	Texas (n=48,392)
$\overline{CW}$	127	77	79	101	93
CW_r	90	30	25	25	50

which regresses landings on estimates of total mortality (Csirke and Caddy, 1983).

Since the trend lines for four states were statistically coincident, mortality estimates for these states were combined across years to arrive at general Gulf-wide estimates of total mortality (along with the composite estimate for Louisiana since it was significantly different from the other states). Although estimates of total mortality for Louisiana crabs were less than other states, the magnitude of difference did not appear to be great when expressed as percent annual mortality (Figure 4). Estimated percent annual mortality for Louisiana was 52.7% while the estimate for the remaining states was 65.9%. Mortality estimates for blue crabs were similar to other warm water species. Most individuals in a cohort die within the first year and very few survive beyond the third year. These are characteristics of an "r-selected strategist" which is characterized by the production of a large number of young, interannual fluctuations in production, rapid growth, early attainment of maturity and a short life span (Van Engel, 1987).

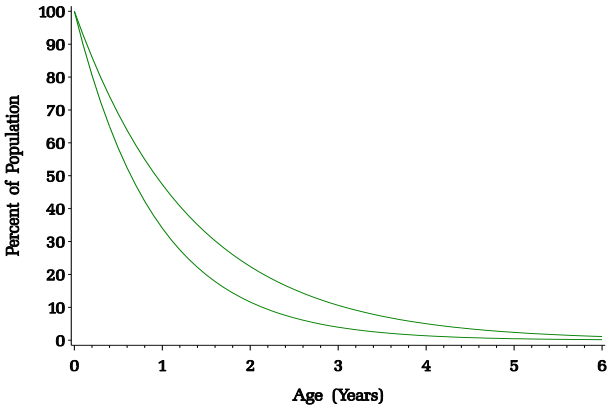

FIGURE 4. — Cohort decline as estimated by length-based method of estimating total instantaneous mortality rates for northern Gulf of Mexico blue crabs.

In summary, northern Gulf of Mexico blue crab growth was modeled using the von Bertalanffy growth equation. The growth coefficient, K, and asymptotic carapace width, CW_∞, were estimated to be 0.663 and 276 mm, respectively. These were similar to estimates derived by Rothschild and Ault (1992) and Rugolo et al. (1997) who studied Chesapeake Bay blue crabs. K and CW_∞ were then used in Hoenig's (1987) method of estimating total mortality for each Gulf state for years in which carapace width data were available. Estimates ranged from 0.572 for Louisiana in 1967 to 1.279 for Mississippi in 1976, with a Gulf-wide grand mean of 0.971.

Regression analysis with dummy variables indicated no significant linear trend among years for any state but the y-intercept for Louisiana was significantly less than at least one of the remaining states. Since trend lines for Florida, Alabama, Mississippi and Texas appeared similar, and since no annual linear trend was detected for any state, yearly mortality estimates were collapsed into a composite estimate for the four grouped states (1.076) and Louisiana (0.748). Although the estimate of total mortality for Louisiana crabs was less than the other states, the magnitude of difference did not appear to be great when expressed as percent annual mortality. Estimated percent annual mortality for Louisiana was 52.7% while the estimate for the remaining states was 65.9%.

In general, blue crabs of the northern Gulf experience total mortality rates similar to other warm water species. Mortality rates are high with 95% of a cohort dying within the first three years of life. This is characteristic of an r-selected strategist which produce a large number of young, exhibit interannual fluctuations in production, rapid growth, early attainment of maturity and a short life span.

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Infection and Mortality Studies with *Hematodinium perezi* in Blue Crabs

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Abstract. — Blue crabs, *Callinectes sapidus*, from the Delmarva Peninsula experience recurring epizootics of a pathogenic dinoflagellate. The parasite, *Hematodinium perezi*, fulminates in late summer and autumn causing significant mortalities in high salinity embayments and estuaries. Mortality rates during epizootics are difficult to estimate because dead crabs quickly deteriorate. Host mortality was investigated in naturally- and experimentally-infected crabs. Detection of the parasite, its proliferation in the hemolymph, and distribution in lower Chesapeake Bay were also examined. The dinoflagellate was highly pathogenic, killing 100% of naturally infected crabs, and 86% of inoculated crabs over 35 and 40 days, respectively. Inoculated hosts began dying 14 days after infection, with a median time to death of 30.3 $\pm$ 1.5 d (se). Proliferation of the parasite was rapid at 20°C, with infections progressing to high levels over one to two weeks. Detection of the parasite was, however, variable. In infection experiments some hosts presented infections after two weeks while others were not detected until four weeks post inoculation. The dinoflagellate was prevalent in the seaside bays of the Delmarva Peninsula. In fall 1996, the prevalence of the disease along the Virginia portion of the Delmarva Peninsula varied from 20-50% in legal crabs. Prevalences of 1-30% were noted for crabs caught between Cape Henry and Cape Charles, i.e., the mouth of the bay. The mortality studies indicate that *H. perezi* represents a significant threat to the blue crab fisheries in high salinity estuaries and may preferentially infect mature females that move to higher salinities to breed.

KEYWORDS: *Callinectes sapidus, Hematodinium perezi*, epizootics, crab fisheries, parasitic dinoflagellate

Hematodinium perezi is a parasitic dinoflagellate found in the hemolymph of blue crabs, *Callinectes sapidus,* and other decapods. The disease occurs in high salinity waters (>11‰) from Delaware to Florida, and into the Gulf of Mexico (Newman and Johnson, 1975; Messick and Sinderman, 1992; Messick and Shields, in press). In Virginia and Maryland, *H. perezi* has caused serious losses to the crab fishery of the Delmarva Peninsula (Messick, 1994; S. Rux and M. Oesterling, VIMS, personal communication). In 1991 and 1992, an epizootic of the parasite affected the blue crab fishery in seaside bays of the Delmarva Peninsula. Watermen reported reduced catches and lethargic, moribund and dead crabs in pots and shedding facilities. The Delmarva Peninsula has several characters that may facilitate epizootics of *H. perezi*, including relatively closed crab populations (i.e., those with little immigration and emigration of juveniles and adults), relatively little water exchange between the open ocean and backwaters, and stressful conditions such as heat stress, seasonal hypoxia, seasonal fishing and predation pressure (Shields, 1994). Similar conditions exist in many small estuaries along the mid-Atlantic and southeastern USA.

In 1997, blue crabs supported the largest commercial fishery within Chesapeake Bay and the second largest fishery in Virginia (Kirkeley, 1997). The crab industry harvests from 80-120 million

pounds from Chesapeake Bay annually; of that, approximately 10-14 million pounds are soft-shell crabs (Kirkeley, 1997; Rugolo et al., 1998a). Declines in crab catches in 1998 and projected declines in 1999 indicate that mortality processes in blue crabs are not well understood. Current models project estimates of natural mortalities, but they do not account for the potential epizootics and mortalities caused by *Hematodinium perezi.* While fishing pressure may be high (Rugolo et al., 1998b), disease and environmental processes have not been well examined; yet, both processes contribute to declines and population cycles in other crustacean fisheries (e.g., Hobbs et al., 1992; Kuris and Lafferty, 1992). Given the importance of the fishery to the region's economy, and the relative effect of the disease in blue crabs, it is imperative that we clarify the epizootiology and pathology of the disease.

Hematodinium spp. threaten other important crustacean fisheries. Recent outbreaks of *Hematodinium*-like parasites have been reported from Alaskan stocks of Tanner crab, *Chionoecetes bairdi* (Meyers et al., 1987, 1990, 1996); Eastern Canadian stocks of snow crab, *C. opilio* (Taylor and Khan, 1995); the Scottish fishery for Norway lobster, *Nephrops norvegicus* (Field et al., 1992; Field and Appleton, 1995); and the French fisheries for the velvet crab, *Necora puber* (Wilhelm and Miahle, 1996) and rock crab, *Cancer pagurus* (Latrouite et al., 1988). In Australia, *H. australis* occurs at low levels in stocks of sand crabs, *Portunus pelagicus,* and mangrove crabs, *Scylla serrata* (Shields, 1992; Hudson and Shields, 1994). An unusual dinoflagellate has also been reported from spot and pink shrimp, *Pandalus borealis* and *P. platyceros* (Bower et al., 1993; Meyers et al., 1994).

Unfortunately, background mortalities due to *Hematodinium* are often difficult to assess because dead crabs quickly become undiagnosable. The timing of host mortalities was investigated in natural and experimental infections as well as the detection and proliferation of the parasite in infected crabs. In addition, the prevalence of the parasite was reported for Chesapeake Bay.

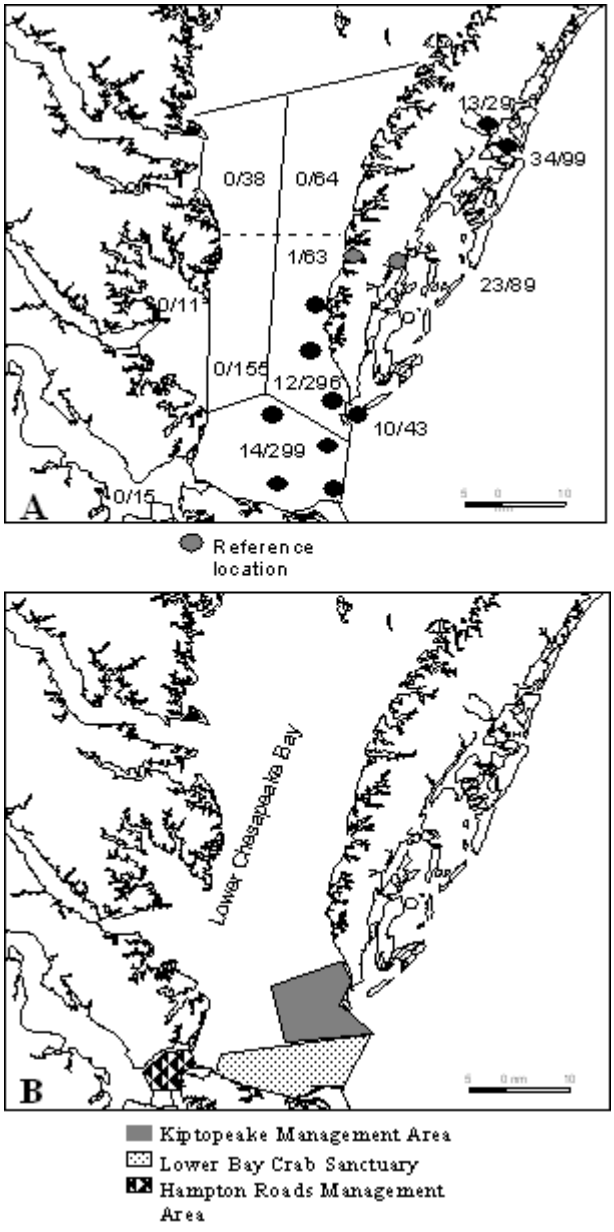

FIGURE 1. — (A) Distribution and prevalence of *H. perezi* in blue crabs from Chesapeake Bay, fall, 1996. Black circles represent locations where the disease was found. Gray dots represent reference locations (Hungars and Red Bank creeks). Numbers indicate infected crabs versus total number sampled. Schematic of aggregate locations used in the analysis (cf. strata used by VIMS Trawl Survey). (B) Crab management areas designated by the Virginia Marine Resources Commission. The Kiptopeake and Hampton Roads areas are closed to dredging in winter. The Lower Bay is closed to pot fishing but open to dredging.

Methods

Crab Collections

Blue crabs were collected from the coastal bays and creeks on the "seaside" (e.g., Red Bank Creek, Wachapreague) and "bayside" (e.g., Nassawadox Creek, Hungars Creek, Cape Charles) of the Delmarva Peninsula and from many locations within the mainstem of the lower Chesapeake Bay (Figure 1). Additional collections were made in the York, James, and Rappahannock rivers. Regular monthly sampling was done via pot and trap fishing at two reference locations: bayside at Hungars Creek and seaside at Red Bank Creek. The broad-scale sampling was done in conjunction with the Virginia Institute of Marine Sciences (VIMS) trawl (April through December, December through March, respectively) and dredge surveys. Additional samples were collected via trawls and crab pots. In most cases, crabs were chilled on ice for transportation to the laboratory. Up to 60 crabs from each trawl or dredge were examined for *Hematodinium perezi*. Low salinity locations (<11‰) were not sampled for the disease, but subsamples (n=60-75) of several hundred crabs were sampled from the York River as a baseline.

Laboratory Analyses

Crab sex; carapace width (with and without spines); condition (maturity, natural vs. trawl damage); molt stage; and collection location were recorded. Crab hemolymph was taken from the axillae of the 5th walking leg with a 27 ga. needle and tuberculin syringe. Hemolymph was examined as a wet smear, with an additional smear being processed and stained as described in Messick (1994). Briefly, acid-cleaned, poly-l-lysine-coated microslides were smeared with 2-3 drops of fresh blood, allowed to sit for 2-3 min, then fixed in Bouin's fixative. The smears were then processed through a routine hematoxylin and eosin procedure. Wet smears were read at 400x using phase contrast; matching prepared smears were read with oil immersion at 1000x. The density of infection was estimated via direct cell counts using a hemocytometer (Neubauer, Bright-line). Intensity was the proportion of parasites (trophonts and plasmodia; Figure 2) to the total number of host cells multiplied by 100, giving parasites per 100 host cells.

For infection studies, *Hematodinium perezi* was maintained in the laboratory by serial passage of infected hemolymph. Raw hemolymph or buffer-washed (see below) parasites from naturally infected crabs was injected directly into naive crabs. Naive crabs were obtained from areas outside the enzootic region, and their hemolymph was examined prior to challenge. Uninfected crabs were acclimated for 3-7days prior to treatment to ensure absence of overt bacterial or protozoal diseases. During experiments, crabs were fed fish and squid semiweekly and held individually in 5gal. (19 l) aquaria (static, box filters with activated charcoal) at 20°±2°C and 24‰ salinity.

Proliferation and Mortality Studies

Observations on the proliferation of the disease were undertaken in two Proliferation Studies. In Proliferation I, naturally infected crabs were held individually for observation and hemolymph sampled regularly as described above. In Proliferation II, unexposed, naive crabs were inoculated with infected hemolymph containing plasmodia of *H. perezi*. Hemolymph was taken from an infected crab, the density of the parasites was counted with a hemocytometer (10^3 plasmodia ml^{-1}), and 100 µl of hemolymph was injected directly into the axillae of the fifth walking leg of uninfected, naive crabs. Both male and female crabs were inoculated (n = 12 and 3, respectively). The onset and course of the infections were monitored via weekly hemolymph smears.

Two mortality experiments were undertaken and are briefly described here (for details, see Shields and Squyars, 2000). In Mortality I, raw, infected hemolymph was the inoculant. In Mortality II, buffer-washed parasites were adjusted to the density of the inoculant used in Mortality I. Mortality II was a close replicate of Mortality I except for the use of centrifugation with buffer washes and the use of mostly plasmodial versus uninucleate stages of the parasite (see below). Controls consisted of injecting uninfected hemolymph (or buffer in Mortality II) into uninfected crabs and handling uninfected crabs similarly. The controls served as comparisons for the onset and severity of the infection in the

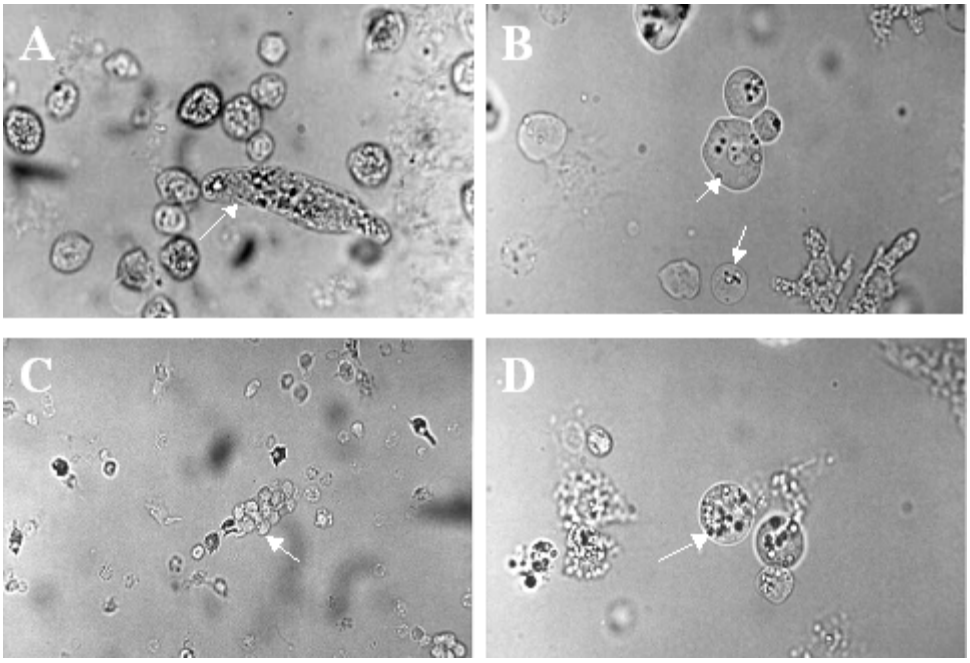

FIGURE 2. — (A) Small plasmodium in the hemolymph (approx. 20 um long) (arrow). (B) Amoeboid trophont (12-14 um) in the hemolymph (arrow). (C) Schizogony of a plasmodial stage (approx. 80 um) (arrow). (D) Rounded trophont (12-14 um, arrow) in the hemolymph.

inoculated crabs, as well as for monitoring survivorship. Crabs were monitored daily for mortalities and bled weekly to assess infection status.

Mortality I consisted of an experimental group (n = 20 crabs) inoculated individually with 100 µl of infected hemolymph containing 1.3 x 10^5 parasites (100% trophonts). Controls (n = 22 crabs) were inoculated with 100 µl of uninfected hemolymph. Mortality II consisted of two experimental groups (n = 10, 10 crabs respectively) inoculated with 100 µl of buffer containing either 1.0 x 10^5 parasites per crab (high dose; 97% plasmodia, 3% trophonts) or 1.0 x 10^3 parasites per crab (low dose, same ratio). Controls (*n* = 8 crabs) were inoculated with 100 µl physiological buffer. In Mortality II, infected hemolymph was diluted 1:1 with filter-sterilized buffer (modified from Appleton and Vickerman, 1998; NaCl 19.31 g/l, KCl 0.65 g/l, $CaCl_2 \bullet 2H_2O$ 1.38 g/l, $MgSO_4 \bullet 7H_2O$ 1.73 g/l, Na_2SO_4 0.38 g/l, HEPES 0.82 g/l, adjusted to pH 7.8, with added glucose 1.0 mg/ml), centrifuged at 4000 rpm for ten minutes, washed twice more as above, and the parasites resuspended in buffer to obtain 1.0 x 10^6 parasites ml^{-1} and 1.0 x 10^4 parasites ml^{-1}.

The proportional hazards model was used to analyze survival data (Cox and Oakes, 1984). The Tarone-Ware log-rank test was used to examine differences between survivorship curves (Wilkinson, 1997). SYSTAT (Wilkinson, 1997) and SAS were used to perform the statistics. A significance level of $p < 0.05$ was accepted as significant.

Results

Proliferation Studies

In aquaria, naturally infected crabs with light infections (0.33 to 3.00 plasmodia/100 host cells) developed heavy infections (>100 trophonts/100 host cells) over two to three weeks (Figure 3). Proliferation of the parasite was faster in moderate

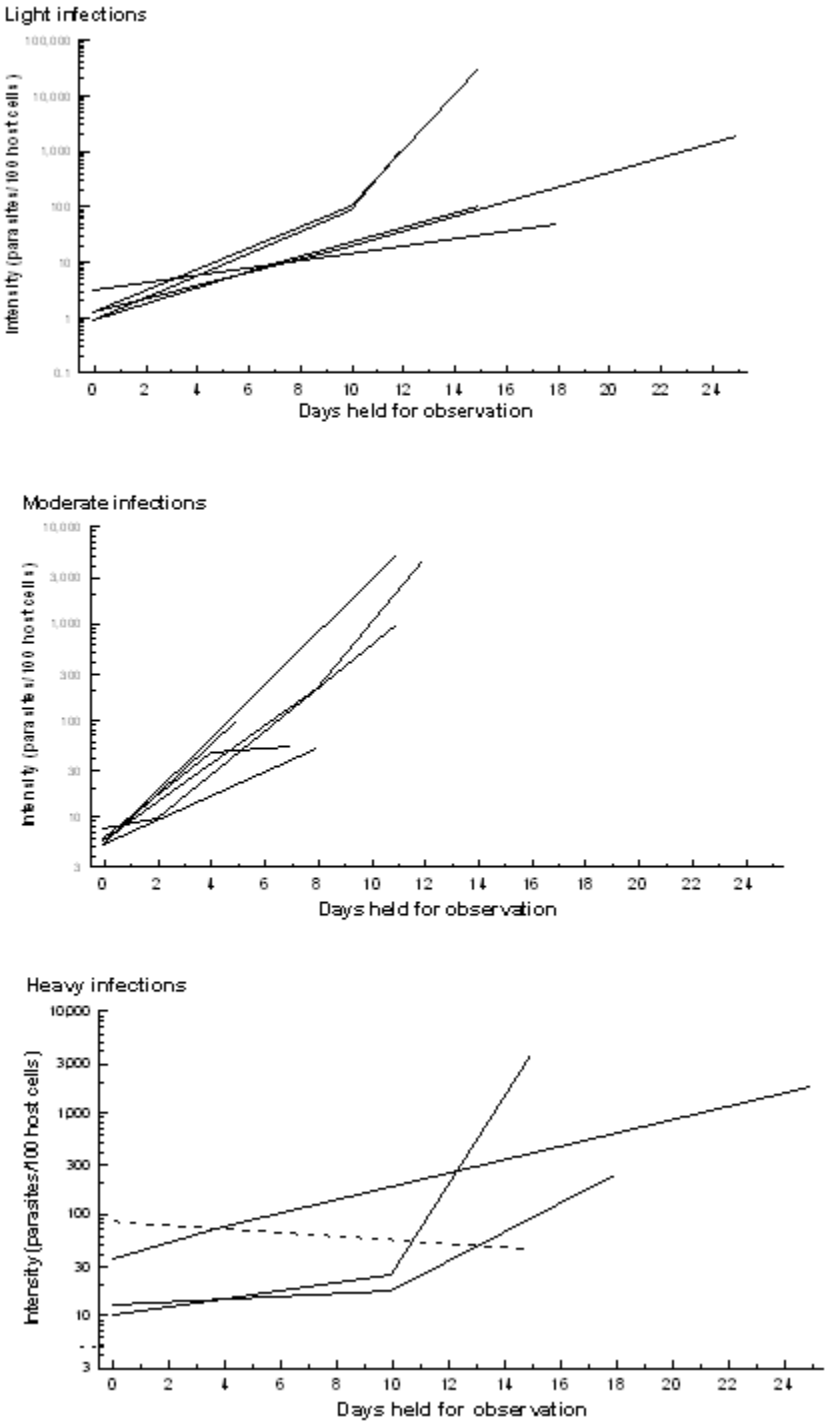

FIGURE 3. — Proliferation of *H. perezi* in naturally infected blue crabs with light infections (0.33-3 parasites/100 host cells), moderate infections (3.1-10 parasites/100 host cells), heavy infections (>10 parasites/100 host cells). Females (dashed lines) and males (solid lines). Endpoints represent crab death.

infections with log growth rapidly pushing intensities to enormous levels (>3000 parasites/100 host cells). Proliferation in heavy infections was not as rapid as the moderate infections, but log growth was apparent in two crabs after ten days in the laboratory.

Survival of the host was not consistent between light, moderate and heavily infected crabs. (Figure 3). Crabs with moderate infections appeared to die more quickly than those with light and moderate infections, and mortalities may have been associated with high parasite intensities. In some cases, heavily infected crabs survived as long as lightly infected crabs (Figure 3). A few crabs survived for up to 35 days before dying from the infection (Figure 4), with one female showing a decline in the intensity of the infection (Figure 3).

Inoculation of 10^2 plasmodia (Proliferation II) successfully transmitted the parasite to naive hosts. In general, no infections were observed before six days post inoculation. Light infections, characterized by plasmodia (1-3 plasmodia/100 host cells), were observed after approximately 13 days in 14 of 15 hosts (Table 1). Moderate infections (3–10 parasites/100 host cells) with plasmodia and trophonts occurred after 16 days, and heavy infections (>10 parasites/100 host cells) occurred after 30 days. Host mortalities to the infection occurred after 17 days, peaked between 45 to 52 days, with the last infected crab dying 55 days after the injection (Figure 4).

An important aspect regarding occult infections was revealed. Densities of less than 0.33 parasites/100 host cells (approximately 1.0 x 10^4 parasites/ml) cannot be effectively diagnosed using hemolymph smears. This was confirmed by reexamining crabs from Hungars and Red Bank Creek (reference locations) after they had been held separately for five to ten days. Several crabs that had been diagnosed as uninfected from field collections had converted to light infections. Hence, there was a minimum prepatent period of at least eight to ten days before infections could be observed.

Mortality Studies

Hematodinium perezi was highly pathogenic (Figures 4 and 5). Inoculated crabs that became infected began dying two weeks after inoculation. The mortality rate of the infected crabs was 86%, while only 20% of the controls died. Uninfected crabs (controls) experienced significantly fewer

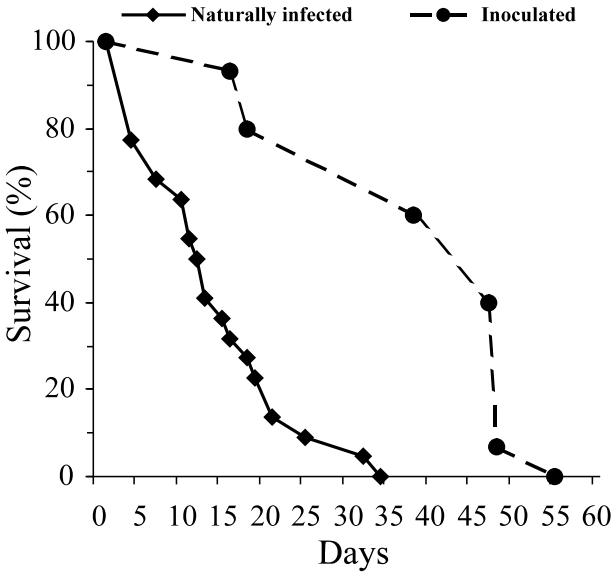

FIGURE 4. — Survival of of naturally infected crabs (Proliferation I; solid line, diamonds) and experimentally inoculated crabs (Proliferation II, dashed line, circles, 10^2 plasmodia per crab) held in the laboratory.

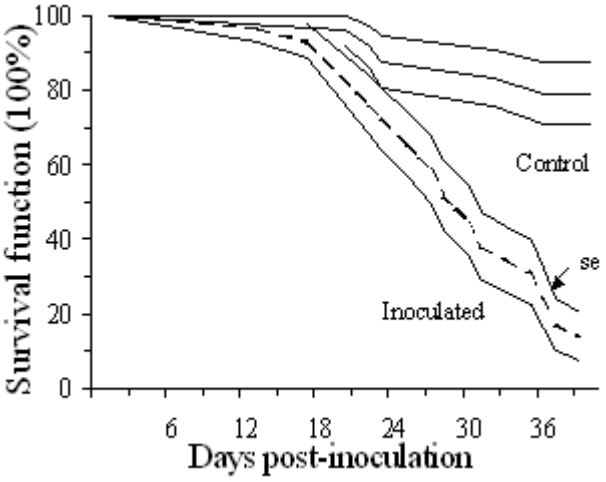

FIGURE 5. — Survival analysis (Kaplan-Meier, Weibull distribution) of experimentally inoculated crabs (Mortality I and II, 10^3 and 10^5 parasites per crab) held at 20° C, 24 ‰. N = 20 uninfected controls, 30 inoculated crabs. The proportional hazards model indicated a significant difference between uninfected and infected crabs (with a 14 day lag) at $P<0.001$.

TABLE 1. — Detection of *H. perezi* in hemolymph of experimentally inoculated blue crabs over the course of infection. Crabs in Proliferation I were given 10^2 plasmodia (n = 15 crabs). Crabs in Mortality experiments (combined results) were given 10^3 or 10^5 plasmodia or trophonts. Mean intensity is given for the Mortality experiments only. Numbers in parenthesis are sample sizes. Only those crabs that developed infections are included.

Days post inoculation	Proliferation II Prevalence (%)	Mortality I and II Prevalence (%)	Mean Intensity (parasites/100 host cells) (± se)
0	0.0	0.0 (21)	0.0 ± 0.0
7	0.0	8.7 (21)	0.037 ± 0.04
14	93.3	36.3 (11)	2.876 ± 1.66
18	100	30.0 (10)	0.256 ± 0.14
21		60.0 (10)	202.27 ± 197.55
26		87.5 (16)	48.27 ± 23.82
32		75.0 (4)	46.6 ± 24.28
35		100.0 (4)	46.74 ± 4.49

mortalities than infected hosts (Chi-square = 19.267, df = 1, $P<0.001$). There were no differences in mortalities between infected crabs in Mortality I and II (Chi-square = 1.212, df = 1, $P= 0.271$). There were also no differences in mortalities between uninfected crabs in the two experiments (Chi-square = 0.652, df = 1, $P = 0.419$); hence the data were grouped for further analysis. The median time to death (MTTD) for infected crabs was 30.3 ± 1.5 (se) days. The MTTD could not be calculated for the controls since they exhibited too few mortalities. Infected crabs had a significantly higher mortality rate that was 7 to 8 times greater than that of the uninfected controls (proportional hazards, Chi-square = 13.503, $P < 0.001$, relative risk = $e^{1.055/0.5174}$).

From Proliferation II and the mortality studies, parasites were detected in the hemolymph approximately two weeks after injection (Table 1). In Proliferation II, 93% of the inoculated crabs had detectable infections after two weeks, but in the mortality experiments, detection was low (30-35%) after 14 to 18 days, reaching 80 to 85% after 26 to 32 days and 100% after 35 days. (Detection was based solely on crabs that developed infections. Four crabs from Mortality II did not become infected and were excluded from the analysis of detection.) Proliferation of the parasite and related hematology of infected crabs in the mortality studies are reported elsewhere (Shields and Squyars, 2000).

Additional Observations

During the course of routine maintenance of the parasite, four crabs presented long-term chronic infections. One crab (#3977) was monitored weekly over the time course of infection (Figure 6). Observations on the other crabs were intermittent. Synchronous sporulation of the parasite occurred at least twice in Crab #3977, with each event lasting less than four days. Parasite density was extraordinarily high (1.6×10^8 dinospores ml^{-1}) during sporulation and dropped to moderate levels (3.3×10^6 trophonts ml^{-1}) thereafter. Dinospores were observed five times over the course of 26 days, beginning 43 days after injection. [Dinospores were only enumerated twice.] Surprisingly, the crab did not die during the mass sporulation events.

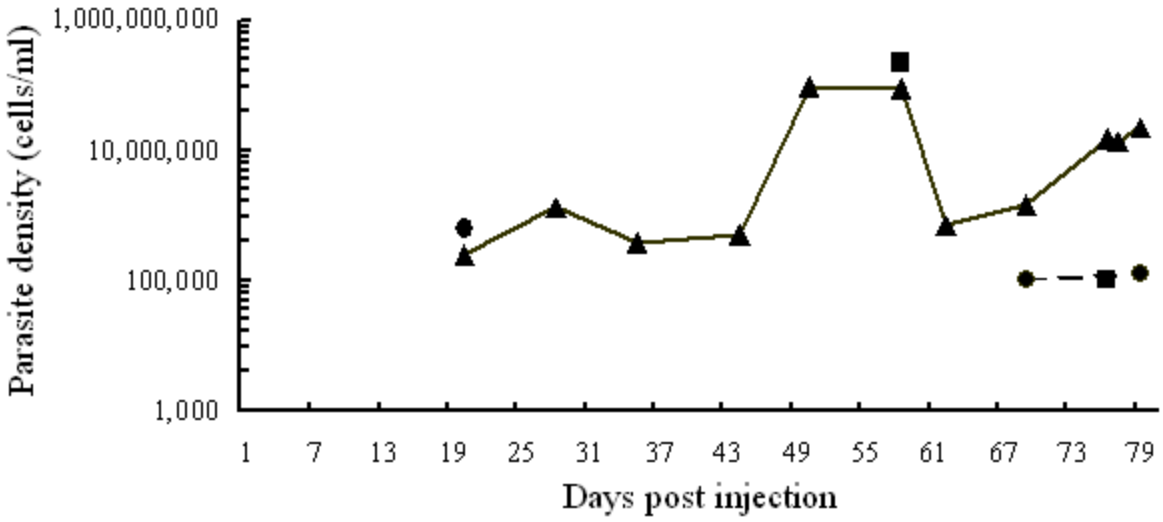

FIGURE 6. — Crab #3977 presenting a chronic, experimental infection of *H. perezi* (plasmodia, circles; trophonts, triangles; dinospores, boxes). The crab died after 80 days.

Prevalence in Lower Chesapeake Bay

In 1996, a total of 3259 crabs were sampled. Of these, 733 were sampled in the winter, 446 in the spring, 871 in the summer, and 1209 in the fall. The collection gear was biased toward mature crabs. Since most of the sampling was done in the mainstem of the bay, more female crabs were collected than males (1940 versus 1239, respectively). A total of 111 crabs were infected, with virtually all of the infections occurring in the fall (Figure 1).

In the fall 1996, a limited outbreak was documented along the Eastern Shore, at the mouth of Chesapeake Bay, and at several stations along the southeastern portion of the bay (Figure 1). The prevalence of the disease along the Virginia portion of the Delmarva Peninsula varied from 20-50% in legal size crabs. Lower prevalences (1-10%) were noted for crabs caught between Cape Henry and Cape Charles, i.e., at the mouth of the bay. In November, the prevalence of the disease was notably higher in crabs caught between Cape Henry and Cape Charles (10-30%).

In 1997, a total of 870 crabs were sampled. Of these, six were sampled in the winter, 148 in the spring, 358 in the summer, and 358 in the fall. At least 47 crabs were infected, with the infected crabs evenly spread through the three seasons. In 1997, *H. perezi* festered at moderate prevalences (1-10%) at both the seaside and bayside reference stations. In the summer and fall 1997, the prevalence and distribution of the disease were higher than that observed in 1996. The disease was present at both reference locations during spring and summer 1997. Hungars Creek had a surprisingly high prevalence of 20% during September 1997. This creek is located over 30 miles from the bay mouth on the bayside of Delmarva Peninsula.

Discussion

Experimental infections of *Hematodinium perezi* were highly pathogenic and proliferated rapidly in the hemolymph. The mortality rate of 86% at 20°C over 40 days is equivalent to that reported for bubonic plague in human populations. Lower mortality rates with longer survival duration have been observed at lower temperatures (12° and 16°C) in naturally infected crabs (Messick et al., 1999). Parasites are lost or become dormant below 10°C. High mortality rates have been noted in *Hematodinium*-like infections in Tanner crab, *Chionoecetes bairdi*, and Norway lobster, *Nephrops norvegicus*. Naturally-infected Tanner crabs experienced 67% mortality (n=11) over 158 days (Meyers et al., 1987). Mortalities occurred in assocation with secondary bacterial infections.

Uninfected controls exhibited no mortalities during the time course (Meyers et al., 1987). Naturally-infected Norway lobsters suffered mortality rates of 86% to 100% over 27 days and 75 days, respectively (Field et al., 1992). Mortality rates were two to four times higher than uninfected lobsters (Field et al., 1992). Infections in blue crabs kill the host very quickly; hence, infected crabs do not acquire the bitter flavor found in Tanner crabs with their lengthy *Hematodinium* infections (Meyers et al., 1987).

Hematodinium infections in blue crabs have four apparent stages: (1) the occult stage occurs when parasites are not detectable in the hemolymph (but detectable in the heart, Shields and Squyars, 2000); (2) the acute stage is when parasites are rarely observed in the hemolymph, and mortalities occur quickly (14 to 40 days); (3) the chronic stage occurs over lengthy periods (up to 90 days) with one to several mass sporulation events (10^8 dinospores ml^{-1} – a density far higher than most algal blooms) or sequelae; and (4) the refractory or immune state, where exposed crabs survive and do not develop infections.

Estimates of host mortality to disease are often difficult to obtain. They are important in predicting the scale or impact of parasites and diseases on a fishery. Blue crab catches fluctuate yearly in Chesapeake Bay but causes for these fluctuations are not well understood. Current models for blue crab populations in Chesapeake Bay are based on population assessments from various surveys (Lipcius and Van Engel, 1990; Abbe and Stagg, 1996; Rugolo et al., 1998a, 1998b). These models project crab abundance for the fishery as a whole but do not separate the larger, low salinity "bayside" fishery from the smaller, high salinity "seaside" fishery in the region. Natural mortality is often assigned a constant term in models, it does not vary with potential epizootics and resulting mortalities caused by *H. perezi.* Differential models of exploitation by region may be warranted

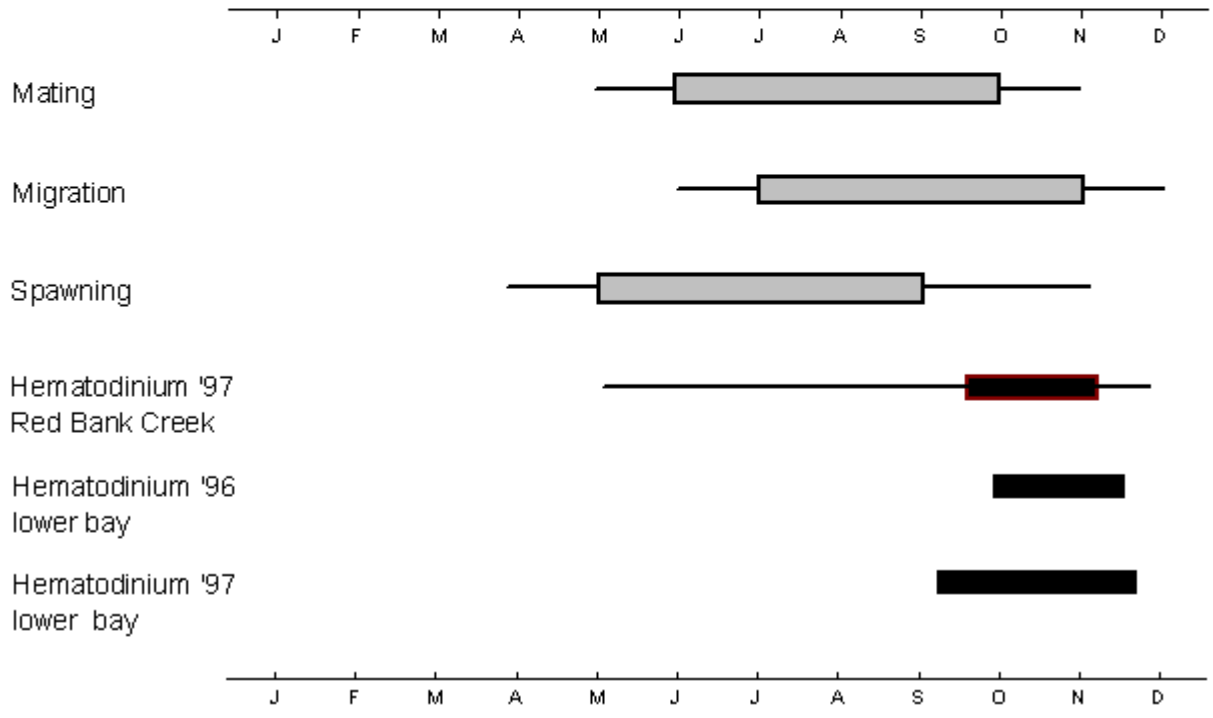

FIGURE 7. — Temporal patterns in reproductive patterns of female blue crabs shown with underlying prevalences of *H. perezi*. Bars represent peak periods of activity; lines, ranges of activity. Red Bank Creek is the "seaside" reference site; lower bay is the mouth, and adjacent strata.

especially during or immediately following epizootics.

Hematodinium perezi was present at low to moderate prevalences in the main spawning grounds of the blue crab near the mouth of Chesapeake Bay. Most of the crabs collected from the lower bay were in or adjacent to the Crab Management Areas/Sanctuaries designated by the Virginia Marine Resources Commission (Figure 1b). These sanctuaries are designed to protect preovigerous and spawning crabs during sensitive portions of their life cycles. The parasite occurred in the spawning grounds during the fall. The peak season for crab reproduction is late spring and summer (Van Engel 1958, 1987; Hill et al., 1989). In 1996, the prevalence of the parasite was low during the prebreeding and ovigerous season (Figure 7), but moderate to high later in the ovigerous season. The moderate prevalence and heavy infections in adult female crabs, coupled with the predilection of the disease for juvenile crabs (Messick, 1994), indicates that during epizootics the disease may threaten reproduction in the sanctuaries and may impact survivorship of the next season's harvest.

Hematodinium perezi occurs in high salinity waters (Newman and Jonson, 1975). However, the occurrence of the disease on both sides of the Delmarva Peninsula indicates that the problem is not strictly a "seaside" phenomenon. Apparently, the parasite fulminates in small foci along the Eastern Shore throughout much of the year with small to moderate outbreaks occurring in the mouth and southeastern portions of the mainstem of Chesapeake Bay during the fall (Messick and Shields, in press). The risk of infection to larval and migrating juvenile crabs has not been well assessed. Larval crabs must pass through high salinity waters, hence, they may risk exposure to infectious stages (dinospores?) of *H. perezi*. The possible impact of the disease on juvenile recruitment to the stock should be incorporated into further analyses of blue crabs in Chesapeake Bay.

Acknowledgments

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Proceedings of the Blue Crab Mortality Symposium 61-68

Infestation Rates of the Ectocommensal Gill Barnacle, *Octolasmis mülleri*, on Blue Crabs, Effects of Salinity and the Impact of the Barnacle on Crab Mortality

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Abstract. — The gooseneck barnacle, *Octolasmis mülleri*, is found only in the gill chamber of crabs. This ectocommensal does not take any nutrition from the host, but could harm the host by obstructing the ventilatory stream. The potential of *O. mülleri* to cause mortality in blue crab, *Callinectes sapidus,* populations was investigated by surveying infestation rates in blue crab populations and assessing the physiological impact of the barnacle on blue crab hosts. In a 2 year survey of 1,406 blue crabs from the Gulf coast of Florida, we found a 39% infestation rate. The number of barnacles per infested crab averaged 26.0 and ranged as high as 610. Smaller samples of blue crabs from low salinity (< 22 ppt) waters in Coastal Louisiana and the Chesapeake Bay yielded infestation rates of 1-2%. Male crabs from Florida suffered a higher (42%) infestation rate than females (19%), the reverse of trends previously reported from other sites. The bias in sex ratios of infested crabs, coupled with the known migrations of the crabs, suggests that the barnacle is not likely to be found on crabs in low salinity waters. *In vitro* studies confirmed that adult barnacles do not survive in low salinity waters, with 100% mortality occurring in 5 ppt water. The physiological effects of the gill barnacle on its crab hosts are minimal in most infestations, with significantly elevated heart rates (1.4X) and significantly increased ventilation rates (1.8X), which probably compensated for the presence of the barnacles in the crabs' ventilatory stream. When the crabs exercised moderately for short periods, there was no measurable effect of the barnacle, presumably due to the crab's well developed aerobic exercise capacity. However, crabs that died during the stress of emersion and high temperature exposure were more likely to be infested by the barnacle. In summary, blue crabs in higher salinity waters are more likely to be infested by *Octolasmis mülleri*, and heavily infested individuals may suffer mortality due to this ectocommensal during periods of environmental stress.

KEY WORDS: blue crab mortality, gill barnacles, *Octolasmis mülleri*

Because blue crabs (*Callinectes sapidus,* Rathbun, 1896) are relatively long-lived and serve as hard substrates in soft bottom estuaries, they are hosts to numerous obligate and accidental

commensals, such as soft coral (Pearse, 1947); bryozoans (Maturo, 1957); hydroids (Overstreet, 1982); gooseneck and sessile barnacles (Van Engel, 1958); tunicates (Pearse, 1947); oysters (Overstreet, 1982); and slipper shells (Gannon, personal observation). *Octolasmis mülleri* (Coker, 1902), an ectocommensal, stalked barnacle, is found in the gill chamber of numerous estuarine and near-shore crab species (Humes, 1941; Walker, 1974). However, blue crabs are the favored host (Humes, 1941). Blue crab populations on the Gulf Coast of Louisiana (Humes, 1941), in the Chesapeake Bay (Van Engel, 1958), and on the West Coast of Florida (Gannon, 1990) have been reported to be commonly infested by *Octolasmis mülleri.*

After undergoing six naupliar stages as a free living planktivore (Lang, 1976), *O. mülleri* enters the crab gill chamber as a cyprid larva and cements itself to the edges of several adjacent gill lamellae (Walker, 1974). It is occasionally found on the gill rakers or on the walls of the gill chamber (Jeffries and Voris, 1983). The adult barnacle filter feeds on particulate matter in the host ventilatory stream. It derives no nutrients directly from the host crab and is thought to harm the host only indirectly by occluding the ventilatory current when infestation levels are great (Walker, 1974). The distribution of *O. mülleri* within the gill chamber of blue crabs has been found to be biased towards the area where the inhalant current first enters the gill chamber (Walker, 1974; Jeffries and Voris, 1983; Gannon, 1990). This area, the hypobranchial (underside) surface of the basal end of the middle gills would be considered the optimal site for filter feeding (Gannon, 1990).

Research on mortality and population levels of the commercially harvested blue crab has traditionally centered on recruitment, over-harvesting, and physical environmental factors (Lipcius and Van Engel, 1990; Jones et al., 1990). There has been little research at the organismal level on the physiological effects of parasites and commensals on their crustacean hosts. A few studies have shown minimal effects of parasites on crustacean hosts; parasitic isopods stimulate decreased metabolic rates in caridean shrimp (Anderson, 1975); and a symbiotic nemertean egg predator has little impact on host fecundity (Shields and Wood, 1993). However, rhizocephalan barnacles and nicothoid copepods do have measurable effects on the fecundity of the blue sand crab, *Portunus pelagius* (Shields and Wood, 1993). Previous research has shown that *O. mülleri* infestation results in elevated heart and ventilation rates (Gannon and Wheatly, 1992) and minor changes in hemolymph chemistry (Gannon and Wheatly, 1995) in exercising blue crab hosts. This study addresses the potential effect of *O. mülleri* on mortality in blue crab populations.

Methods

Infestation Rates

Adult blue crabs were collected at Seahorse Key on the Gulf coast of Florida from May 1987 to March 1989 using plastic-coated wire mesh commercial crab traps. Although sampling was done on a monthly basis, trapping effort was not equal for each month. The crabs were transported to Gainesville, Florida where their gill chambers were inspected for the presence of the gooseneck barnacle, *O. mülleri.* Blue crabs were also collected from the Chesapeake Bay and its tributaries in October and November of 1993 as bycatch from a Virginia Institute of Marine Science (VIMS) trawling program and from commercial trappers. These crabs were frozen, and after thawing their gill chambers were inspected for the presence of *O. mülleri.* Blue crabs were also collected from Louisiana in Lake Barre by a commercial trapper in May 1999 and transported to Birmingham, Alabama where their gill chambers were inspected for the presence of *O. mülleri.*

The salinity of the water from which the Chesapeake Bay trawl samples were taken was measured by the VIMS collectors with a refractometer. The salinities for the commercially collected Chesapeake crabs were estimated using month and location of capture and long term means compiled by Pritchard (1952). The salinity for the Louisiana sample was provided by the Louisiana Department of Wildlife and Fisheries (V. Guillory, unpublished data). The range of salinity for the samples from the Gulf coast of Florida was estimated using refractometer salinity measurements from nearby Waccasassa Bay (B. Lindberg, Univ. of Florida, unpublished data).

Salinity Tolerance of Adult Barnacles

Salinity tolerance of adult barnacles (*O. mülleri*) was determined using barnacles on the gills of crabs obtained from the Gulf Specimen Company, Panacea, Florida. The barnacles were removed from the crab gills and placed in a finger bowl with 500 ml of aerated 35 ppt artificial seawater (Instant Ocean Aquarium Systems, Mentor, Ohio). They were fed freshly hatched brine shrimp every 48 hours prior to experimentation. The barnacles were transferred through a series of decreasing salinities (25 ppt, 15 ppt, and 5 ppt) also created with Instant Ocean. The salinity of each sample was determined with a Wescor Vapor Pressure Osmometer. The barnacles were exposed to each salinity for 24 hours before being transferred to the next lowest salinity level. Their survival was determined by the presence of a visible heartbeat and the ability to retract the cirri when gently probed.

Effects of Barnacle Infestation on Crab Hosts During Exercise

A subset of the adult (150-250 g) male blue crabs collected at the University of Florida Marine Lab in the sampling described above were maintained in filtered, recirculating, aerated seawater (33-36 ppt) at 23-26°C on a 12:12 light:dark cycle. They were fed chopped fish one or two times weekly, but food was withheld 48 hours prior to experimentation. Lacquered copper wire (32 ga.) was inserted on either side of the heart and into the gill chamber to measure heart rate and ventilation rate using an impedance conversion technique previously described (Gannon and Wheatly, 1992; Ansell, 1973). The crabs were placed in a harness made out of baling wire that could be used to hold them in the water column so that their legs did not touch the bottom. This stimulated the crabs to perform continuous motions with their swimming legs, although some crabs required occasional gentle prodding to continue for the entire 15 minute exercise period. After 24 hours of recovery from the implantation of leads and acclimation to the harness and experimental chamber, heart rate (f_h) and ventilation rate (f_{SC}) were recorded while the crabs were at rest, during 15 minutes of swimming, and during one hour of recovery.

Crabs were divided into three classes based on intensity of barnacle infestation. Uninfested crabs had 0.00-0.02g of *O. mülleri* in their gill chambers. Moderately infested crabs had 0.02-0.10 g of barnacles in their gills and heavily infested crabs had 0.10- 1.22 g of barnacles on their gills. These classes were based on a study of the distribution of the barnacle on 512 blue crabs (Gannon, 1990). Because the infestation level could not be determined until the crab was sacrificed, this was a blind experiment. Resting, exercise and recovery f_h and f_{SC} were compared for crabs at the three infestation levels with a factorial ANOVA.

Mortality of Blue Crabs

The blue crabs that were collected at the University of Florida Marine Lab at Seahorse Key were transported by boat to Cedar Key and then by car (with no air-conditioning) to Gainesville, Florida. This exposed the crabs to elevated temperatures and crowded conditions which forced them to ventilate with air. In most monthly samples there was some mortality of crabs during this exposure. The barnacle infestation rates of the crabs that died during transport were compared to infestation rates of the crabs that survived this exposure. In each monthly sample with mortality during transport greater than 10% (n = 10), the infestation rate of dead crabs was compared with the infestation rate of the surviving crabs from that monthly sample using a Wilcoxon Signed-Rank Test (Snedecor and Cochran, 1980).

Results

Infestation Rates

Infestation rates of Seahorse Key, Florida crabs were high (Table 1) with a sharp difference between males and females. The trapping was heavily biased towards males (80% of total catch) unlike the Chesapeake Bay sample (75% female) and the Lake Barre, Louisiana sample (94% female). The Seahorse Key sample was made up of 19 monthly samples over two years (Table 2) from one location. The Chesapeake Bay sample covered a large area within the bay and its tributaries, but only two months (October-November 1993) of sampling effort. The Lake Barre, Louisiana sample was

TABLE 1. — Infestation rates of blue crabs by *Octolasmis mülleri* and estimated salinity ([1]B. Lindberg, Univ. of Florida, unpublished data; [2]V. Guillory, LDWF, unpublished data).

Area	n	Infestation rate	Infestation rate - males	Infestation rate - females	Salinity range
[1]Seahorse Key, FL	1406	39%	41.9%	18.8%	>22 ppt
Chesapeake Bay	405	2%	1.0%	2.3%	8-22 ppt for 86% of crabs
[2]Lake Barre, LA	174	1.2%	0%	1.2%	12.5 ppt

taken in one day at one site. In the sample of crabs from Seahorse Key, Florida the mean number of barnacles found on each infested crab was 26.0 and ranged as high as 610. The median infestation level was four barnacles/crab. Salinity for the Seahorse Key sample was not available from the nearby Cedar Key NOAA station because it was destroyed by a hurricane. However, salinity samples from seven stations in nearby Waccasassa Bay ranged up to 33 ppt and rarely dropped below 22 ppt.

Salinity Tolerance of Adult Barnacles

All barnacles (n = 23) survived 24 h in 35 ppt water (Figure 1), but mortality began to occur after 24 h in 25 ppt water. Mortality of the barnacles increased as salinity decreased to 15 ppt, and at 5 ppt, all barnacles died.

Effects of Barnacle Infestation on Crab Hosts During Exercise

At rest, f_{SC} for heavily infested crabs (Figure 2) was significantly greater than that of uninfested and moderately infested crabs (factorial ANOVA, $P<0.05$). During exercise and recovery, ventilation rates and their variance increased for all classes of crabs, and differences between infestation levels were no longer significant.

A similar pattern was found for heart rate (Figure 3). At rest, f_h was significantly elevated in heavily infested crabs (factorial ANOVA, $P<0.05$). At the end of the recovery period f_h for uninfested crabs was higher than that of infested crabs, but comparison of rates throughout the recovery period (repeat measures ANOVA) indicated no significant difference.

Mortality of Blue Crabs

The barnacle infestation rates in the blue crabs from the Gulf coast of Florida were consistent between the 1987-88 sampling (39% infestation rate) and the 1988-89 sampling (37% infestation rate) although there were great fluctuations (range = 8-82%) between monthly samples (Table 2).

The infestation rate in the monthly samples (n=10 samples with significant mortality) of crabs that died during transport ranged from 17% to 100%. It was greater than that of crabs that survived transport in every monthly sample but one.

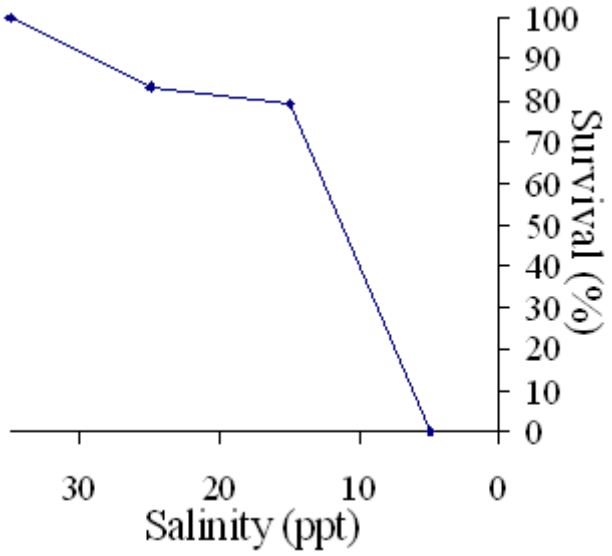

Figure 1. — Survival of adult barnacles after 24 h exposure to different salinity water (n = 23 barnacles).

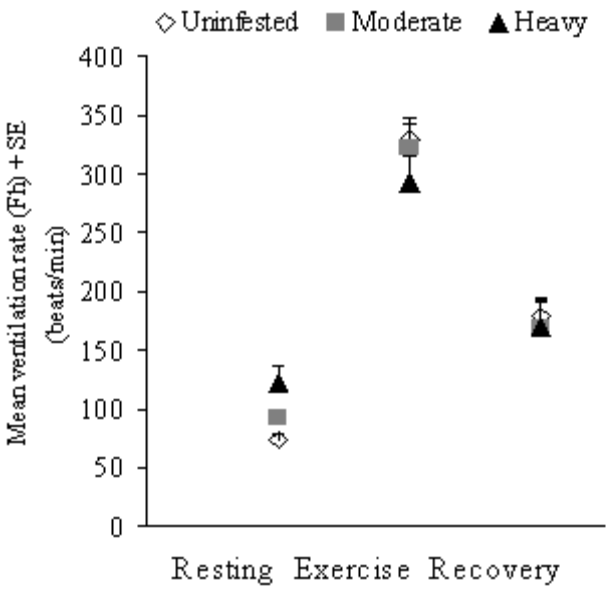

FIGURE 2.— Mean ventilation rate (f_{SC}) during rest, exercise and recovery for blue crabs at three levels of infestation by the barnacle *Octolasmis mülleri*; uninfested (n=9-12), moderately infested (n=7-8) and heavily infested (n=6-10). Error bars indicate +1 standard error.

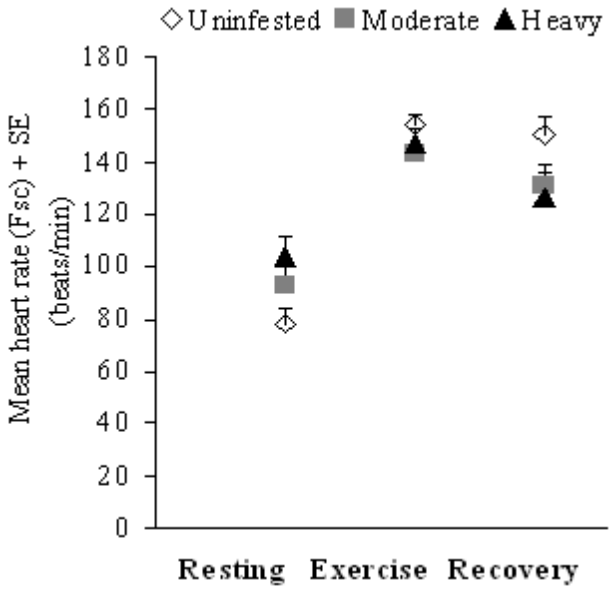

FIGURE 3. — Mean heart rate (f_H) during rest, exercise and recovery for blue crabs at three levels of infestation by the barnacle *Octolasmis mülleri*; uninfested (n=11-13), moderately infested (n=8-11) and heavily infested (n=7-10). Error bars indicate +1 standard error.

Over the two years of sampling, the infestation rate of crabs that died during transport was 51% (n=191 crabs), and the infestation rate of crabs that survived transport was 37% (n=1199 crabs). Differences in the monthly infestation rates were compared with the Wilcoxon Signed-Rank Test (Snedecor and Cochran, 1980). Infestation rates were significantly higher ($p = 0.01$) in the samples of crabs that died during the stress of transport.

Discussion

The blue crab population at Seahorse Key, Florida is commonly infested with *O. mülleri*. The overall infestation rates are similar to those found in crab populations taken from high salinity waters including Grand Isle, Louisiana (37%) by Humes (1941), Beaufort Inlet, North Carolina (49%) by Jeffries and Voris (1983) and around the mouth of the Chesapeake Bay (W. Van Engel, VIMS, personal communication). The infestation rate from Beaufort Inlet may be inflated because of selection for crabs with external balanoid barnacles (Jeffries and Voris, 1983). The presence of external barnacles is correlated with the presence of *O. mülleri* in blue crabs (Gannon, 1990). The low infestation rates found in the Chesapeake Bay in this study are not directly comparable since crabs were sampled only in the winter. The salinity of the water from which these samples were taken ranged from 8-32 ppt, but infested crabs were found only in water >20 ppt. Infestation rates in the Chesapeake crabs were close to 10% in the small subsample that came from water >23 ppt. The crabs taken from coastal Louisiana for the present study also came from low salinity waters (12.5 ppt) and had an extremely low infestation rate (Table 1). This salinity value was unseasonably low due to heavy rains, and typical salinity in Lake Barre is typically slightly above 15 ppt (V. Guillory, LDWF, personal communication). Based on a paucity of barnacle-infested crabs in trawls from low salinity waters around Beaufort Inlet, North Carolina and an unpublished student research project, Walker (1974) suggested that the distribution of *O. mülleri* was limited to higher salinity waters. That contention is supported by the larger samples obtained in this study (Table 1).

In this study a difference between male (41.9%)and female (18.8%) infestation rates was

TABLE 2. — Monthly infestation rates of blue crabs collected at Seahorse Key, FL.

Sample	Rate in Crabs that Survived Transport	n	Rate in Crabs that Died During Transport	n
5/87	29 %	52		
6/87	59 %	41		
7/87	8%	63	54 %	13
9/87	29 %	35		
10/87	66 %	96	100 %	4
11/87	45 %	58		
12/87	45 %	42		
3/88	36 %	14		
4/88	18 %	51	46 %	13
5/88	34 %	100	47 %	30
6/88	53%	64		
7/88	45 %	169	58 %	33
8/88	42 %	55	50 %	26
9/88	14 %	142	25 %	20
10/88	12 %	65		
11/88	82 %	61	84 %	25
1/89	48 %	44	17 %	6
3/89	24 %	68	43 %	14
Total	37 %	1220	52 %	184
	Infestation Rate			
Grand Total	39 %	1406		

noted (Table 1). Chesapeake watermen have long noted a gender bias in infestation rates showing the reverse trend (male infestation rates relatively low and female rates relatively high) (W. Van Engel, personal communication). Humes (1941) also reported a higher infestation rate in females (43%) than males (19%). There are also gender differences in migratory patterns of crabs in Louisiana and the Chesapeake. In both areas adult females migrate to higher salinity waters to spawn, but adult males remain in the brackish waters of the Chesapeake Bay's tributaries and upper reaches (Van Engel, 1958) or the less saline waters of Lake Pontchartrain and the bayous of Louisiana (Darnell, 1959). On the Gulf coast of Florida the migratory patterns are different. Males do not migrate, but females migrate northward to the lower salinity Apalachicola Bay (Oesterling and Adams, 1982). Thus, the gender differences noted in infestation rates could be explained by an inability of the barnacle to tolerate low salinity.

Adult blue crabs have great salinity tolerance with populations found in waters ranging from freshwater to hypersaline lagoons (Williams, 1984). The larval stages of *O. mülleri* have been reared successfully in the lab in 35 ppt water (Lang, 1976); barnacle larval stages would not be expected to survive in low salinity waters. Adult barnacles were unable to survive in 5 ppt water during brief (24 h) exposures (Figure 1). From the lethargy exhibited by the barnacles, it is likely that mortality would have increased in 15 ppt water if the exposure had been longer. This confirms low salinity intolerance as a factor in the distribution of *O. mülleri* on blue crabs.

Previous studies found minimal effects of *O. mülleri* on blue crab physiology. There were no differences in oxygen uptake or hemolymph lactate levels between infested and uninfested crabs (Gannon and Wheatly, 1992). Hemolymph pH, PO_2, CO_2 concentration and O_2 concentration were not greatly different between infested and uninfested crabs (Gannon and Wheatly, 1992; Gannon and Wheatly, 1995). The elevated heart and ventilation rates found in resting, infested crabs (Figure 2) presumably compensate for the presence of barnacles in the gill chamber partially occluding the ventilatory current. The barnacles may cause increased turbulence or create "shadows" of poorly ventilated areas in the gill chamber. Hyperventilation should compensate for both of these possibilities. Exercise, which normally stimulates hyperventilation, was expected to exacerbate the differences between infested and uninfested crabs. However, during exercise all crabs elevated f_{SC} and f_h to near-maximal levels, and there were no significant differences between uninfested and heavily infested crabs. There was increased variance in these rates during exercise and it was not possible to determine if all crabs were exercising equally. Previous studies on

swimming blue crabs (Booth et al., 1982; Booth et al., 1984) did not measure intensity of exercise but did find that blue crabs are highly resistant to fatigue during exercise sustained for as long as one hour. The minimal effect of the barnacle on the crab during exercise and recovery may have been due to a decrease in intensity of exercise in the infested crabs or to the great efficiency of the blue crab at aerobic exercise (Booth et al., 1982; Booth et al., 1984; Milligan et al., 1989).

In spite of the minimal observed effect of the barnacle on its host during exercise, there is evidence that infested crabs are affected by the barnacle. Greater mortality in blue crabs during transport was associated with infestation by the barnacle (Table 2). Several crabs with massive infestations did not survive the stress of being handled in the lab. During stressful periods the relatively minimal effect of the barnacle on its host may be magnified. The minimal effect that we measured suggests that brief (15 minutes) exercise may not be a great enough stress to cause adverse effects.

In conclusion, blue crab populations in higher salinity waters are likely to be commonly infested (c. 40%) by the stalked barnacle, *O. mülleri*, and may suffer mortality due to this ectocommensal during periods of environmental stress. Unstressed blue crab populations in low salinity waters would not be expected to exhibit detrimental effects from the barnacle.

Acknowledgements

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A Review of Blue Crab Predators

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Abstract. — The diverse life history stages, abundance, and wide distribution over a variety of habitats are attributes that expose blue crabs (*Callinectes sapidus* Rathbun) to numerous predators. An extensive literature search was undertaken on food habits of marine and estuarine invertebrate, and vertebrate species to identify predators of blue crab zoea, megalopae, and juvenile/adults. Ninety-three species, which included invertebrates, fish, reptiles, birds, and mammals, were documented to prey upon blue crabs. An additional 119 species had other crab species or brachyuran remains in their stomach contents. More fish species were identified as blue crab predators than any other taxonomic group (67), and 60 fish species were documented to prey upon unidentified crabs and/or brachyurans. The red drum was the highest ranked predator based upon a predation index of estuarine fish predators.

KEY WORDS: blue crab, predators, red drum

The distribution, life history, and biology of the blue crab (*Callinectes sapidus* Rathbun) make it a preferred prey item for a number of vertebrate and invertebrate predators. The blue crab is one of the most abundant estuarine macroinvertebrates, distributed throughout the Atlantic coast and Gulf of Mexico from Massachusetts to northern Argentina, including Bermuda and the Antilles (Williams, 1974). Life history stages of blue crabs include planktonic, nektonic, and benthic forms that occur throughout the estuarine and nearshore marine environments (Guillory et al., in review). Crab zoeae are found in oceanic and lower estuarine habitats, while megalopae are more widely distributed, occuring in both oceanic and nearshore habitats. Juvenile and adult blue crabs occur throughout the estuary, ranging from fresh/estuarine [from 305 km upstream in the Atchafalaya River in Louisiana (Gunter, 1938)] to shallow/oceanic waters [to depths of 90 m (Franks et al., 1972)].

Several factors contribute to the high diversity of species that utilize blue crabs as a food source. Morgan (1989) suggested that the zoeae of blue crabs are generally smaller with shorter spines than other estuarine crabs rendering them more vulnerable to small planktivorous fish and invertebrates. Energetically, blue crabs are less desirable than fish or shrimp (0.8 calories per gram wet weight) but more so than molluscs, ctenophores, or barnacles (Thayer et al., 1973). Finally, blue crabs are less able to escape predation than are other prey like fish and shrimp due to poor mobility.

Interspecific and intraspecific predation is recognized as a major source of natural mortality of blue crabs regulating abundances of early stage blue crabs. Orth and van Montfrans (1990) considered predator diversity and density to be important influences on the regional trends observed in juvenile blue crab populations. Several authors have documented extremely heavy predation pressure in tethering experiments (Smith, 1990; Ruiz et al., 1993; Dittel et al., 1995; Hines and Ruiz, 1995). Greater diversity of predators, fewer predation-free refuges, and year-round predation activity all contribute to high mortality of early crabs in the Gulf of Mexico (Heck and Coen, 1995).

While numerous species have been documented to utilize blue crab as prey (Norse, 1975; Van Engel, 1987; Steele and Perry, 1990), a comprehensive list of predators has not been compiled. In order of priority, the objectives of this paper are first to document known vertebrate and invertebrate predators of blue crabs (including zoea, megalopae, juveniles, and adults) and second to rank certain estuarine predators of juvenile blue crabs.

Blue Crab Predators

The occurrence of blue crabs in stomach contents of some predators has been well documented; however, for this report only one source was cited for each predator species. Literature from the Gulf of Mexico were emphasized, although other literature were also included to illustrate the diversity of potential predators. Ninety-three individual species, three genera, and two larger taxonomic groups were documented as predators of blue crab zoeae, megalopae, juveniles, or adults (Appendix 1), and an additional 119 species have been verified to prey upon other brachyurans or crabs (Appendix 2).

Six species have been verified to prey upon blue crab zoeae or megalopae (Appendix 1). While there are few specific reports of predation on blue crab larvae, several species or taxonomic groups have been alluded to as predators of larvae: plankters, fish, jellyfish and comb jellies (Van Engel, 1958); and various clupeids (McHugh, 1967; Millikin and Williams, 1984). Unidentified crab or brachyuran zoeae and megalopae were also identified in the stomachs of 51 species, including eight invertebrates, 39 fishes, one reptile, and one bird (Appendix 2).

A total of 88 species has been identified as predators of juvenile or adult blue crabs (Appendix 1) while 97 species have been reported to prey upon crabs, brachyurans or *Callinectes* (Appendix 2). Four species of invertebrate predators were documented (Appendix 1) and an additional twelve invertebrate predators had unidentified crab or brachyuran remains in their stomachs (Appendix 2). Sixty-seven species of fish were documented to prey upon blue crabs (Appendix 1) while an additional 60 fish species contained prey items categorized as crabs, crab remains, or *Callinectes* (Appendix 2).

Higher vertebrate species which specifically prey on blue crabs include three reptile species, eleven species and three genera of birds, and three mammal species (Appendix 1). In addition, four reptile, sixteen bird, and six mammal species reportedly preyed upon unidentified crabs or crabs in general (Appendix 2). Although not included in the appendices, Neill (1958) noted that freshwater or inland frogs and lizards, which are normally insectivorous, occasionally preyed upon crabs and other marine organisms in brackish, intertidal habitats.

Although our list of predators includes a taxonomically and ecologically diverse array of species, many other potential predators of blue crabs exist based upon their feeding behavior and co-occurrence with blue crabs. For example, all fish larvae are selective plankton feeders (Hunter, 1980) and could, therefore, prey upon blue crab larvae. In addition, the foraging habits of many marine species have yet to be determined suggesting a strong potential for additional blue crab predators not included on either list (Appendix 1 and 2).

Ranking of Predators

A quantitative ranking of all blue crab predators is not possible due to inadequate abundance and foraging data. Estuarine fish were selected that are important blue crab predators. The predation indices for these species were calculated from the product of the following variables: *abundance* (as calculated from Louisiana Department of Wildlife and Fisheries, LDWF fishery independent gill and trammel net samples); *average weight* (calculated from LDWF samples); and *frequency of occurrence in diets* (obtained from published literature). The average frequency of occurrence of blue crabs in the diet was <15% [with the exception of red drum, *Sciaenops ocellatus*, (32%) and sea catfish, *Arius felis*, (23%)] (Table 1). Red drum was clearly the dominant predator with a predation index 4.8 times greater than the next highest ranked species. Sea catfish, black drum (*Pogonias cromis*), sheepshead (*Archosargus probatocephalus*), and spotted seatrout (*Cynoscion nebulosus*) had the next highest predation indices.

Predation intensity varies with size and species of predator, its life history stage, feeding habits, residency in the estuary, and tolerance to environmental parameters (Van Engel, 1987). The higher ranked predators were epibenthic and common in the shallow estuarine habitats such as intertidal flats, bayous, and ponds in the interior marshes and the fringes of the larger bays and lakes where early juvenile blue crabs are most abundant. Several species of freshwater and marine fish with restricted areal distributions or low numerical abundance also prey heavily on blue crabs and may be locally important predators in some estuaries (Table 2).

TABLE 1. — Abundance index and average weight from Louisiana Department of Wildlife and Fisheries gill and trammel net samples, average percent frequency of blue crabs in stomachs, and predation index of selected fish. Abundance index = average percent by numbers; predation index = abundance index x average weight x percent frequency of occurrence of blue crabs [1=Arnoldi (1978), 2=Boothby and Avault (1971), 3=Darnell (1958), 4=Fontenot and Rogillio (1970), 5=Fox and White (1969), 6=Guillory and Prejean (2001), 7=Gunter (1945), 8=Kemp (1949), 9=Lambou (1961), 10=Levine (1980), 11=Lorio and Schafer (1966), 12=Miles (1949), 13=Overstreet and Heard (1978a), 14=Overstreet and Heard (1978b), 15=Overstreet and Heard (1982), 16=Rogillio (1975), 17=Seagle (1969), and 18=Stokes (1977)].

Species	Abundance Index	Average Weight	% Frequency (Literature)	Predation Index
red drum	9.9	1.72	32(2,4,6,7,10,13, 16)	545
sea catfish	12.6	0.38	23 (3,7,10)	110
black drum	9.0	0.53	7(3,4,7,8,10,15, 16)	33
sheepshead	4.0	0.94	7(3,4,7,10,12,16)	26
spotted seatrout	12.2	0.40	5(1,3,4,7,10,11, 15,16,17)	24
gafftopsail catfish	0.6	0.65	7 (8,10,12)	3
Atlantic croaker	3.4	0.12	4 (3,4,10,14,16)	2
southern flounder	1.3	0.36	3 (5,7,12,15,16)	1
silver perch	0.7	0.08	2 (3,10)	<

Smaller blue crabs are subject to higher predation rates than are larger blue crabs. Guillory and Prejean (2001) found that almost half of blue crabs consumed by red drum were between 10 mm CW and 29 mm CW, and 78% were <50 mm CW. Blue crabs are also highly cannibalistic, and in some size classes blue crabs comprise as much as 13% of the diet (Darnell, 1958). Mansour (1992) found that cannibalism was common and noted that its frequency increased with increasing crab size and rates were high during the period of juvenile recruitment. Con-specific predation during periods of high small crab abundance led Peery (1989) to suggest that the potential of larger crabs to cannibalize juveniles is great enough to produce strong density-dependent regulation of juveniles.

In summary, 67 fish species were identified as blue crab predators and comprised the largest taxonomic group. An additional 60 fish species were documented to prey upon unidentified crabs, and/or brachyurans. Numerous other species have the potential to be predators of blue crabs and are also listed. Clearly these lists are not comprehensive and additional species will be listed as more predators are documented.

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TABLE 2. — Occurrence of blue crabs in stomach contents of fishes with restricted areal distributions or low numerical abundance (%F=percent frequency of occurrence).

Species	Occurrence
Carcharhinus leucas, bullshark	%F = 15 (Kemp, 1949)
	Blue crabs most numerous prey in young (Sadowsky, 1971).
Carcharhinus plumbeus, sandbar shark	%F = 41 (Gunter, 1945)
	%F = 80 for pups and young juveniles (Stillwell and Kohler, 1992).
Galeocerdo cuvier, tiger shark	%F = 42 (Kemp, 1949).
Sphyrna tiburo, bonnethead	2.5 blue crabs/fish (Gunter, 1945)
	Callinectes spp. are the most important prey (Hoese and Moore, 1958).
Lepisosteus oculatus, spotted gar	%F = 31 (Darnell, 1958; Goodyear, 1967; Knapp, 1951)
Lepisosteus spatula, alligator gar	%F = 31 (Darnell, 1958; Gunter, 1945; Goodyear, 1967; Knapp, 1951)
Anguilla rostrata, American eel	68% by volume (Wenner and Musick, 1975).
Ictalurus furcatus, blue catfish	%F = 15 (Darnell, 1958;Lambou, 1961;Levine, 1980).
Ictalurus punctatus, channel catfish	%F = 10 (Levine, 1980).
Strongylura marina, Atlantic needlefish	%F = 36 (Schwartz and Dutcher, 1963).
Opsanus tau, oyster toadfish	%F = 36 (Schwartz and Dutcher, 1963).
Micropterous salmoides, largemouth bass	%F = 21 (Darnell, 1958;Lambou, 1961).
Morone mississippiensis, yellow bass	%F = 27 (Darnell, 1958;Lambou, 1961).
Morone saxatalis, striped bass	%F = 18 (Darnell, 1958).
Rachyantron canadum, cobia	%F = 42 (for *Callinectes* sp.) (Knapp, 1951).

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BLUE CRAB PREDATORS

APPENDIX 1. Documented predators of blue crabs [derived in part from Norse (1975), Van Engel (1987), and Steele and Perry (1990)].

INVERTEBRATES

Jellyfish (Van Engel, 1958) [larvae]
Comb jellies (Van Engel, 1958) [larvae]
Asterias forbesi - starfish (Auster and Degoursey, 1994)
Callinectes sapidus - blue crab (Darnell, 1958)
Crangon septemspinosa - sand shrimp (Olmi and Lipcius, 1991) [megalopae]
Menippe adina - western gulf stone crab (Powell and Gunter, 1968)
Mithrax spinosissiumus - Caribbean king crab (Winfree and Weinstein, 1989)
Palaemonetes pugio - grass shrimp (Olmi and Lipcius, 1991) [megalopae]

FISHES

Carcharhinus leucas - bull shark (Sadowsky, 1971)
Carcharhinus obscurus - dusky shark (Kemp, 1949).
Carcharhinus plumbeus - sandbar shark (Medved and Marshall, 1981)
Galeocerdo cuvier - tiger shark (Kemp, 1949)
Mustelus canis - smooth dogfish (Bigelow and Schroeder, 1953)
Sphyrna tiburo - bonnethead (Hoese and Moore, 1958)
Dasyatis americanus - southern stingray (Dahlberg and Heard, 1969)
Dasyatis centroura - roughtail stingray (Hess, 1961)
Dasyatis sabina - Atlantic stingray (Darnell, 1958)
Dasyatis sayi - bluntnose stingray (Hess, 1961)
Raja eglanteria - clearnose skate (Hildebrand and Schroeder, 1923)
Lepisosteus oculatus - spotted gar (Lambou, 1961)
Lepisosteus osseus - longnose gar (Suttkus, 1963)
Lepisosteus spatula - alligator gar (Darnell, 1958)
Brevoortia tyrannus - Atlantic menhaden (McHugh, 1967) [larvae only]
Elops saurus - ladyfish (Austin and Austin, 1971)
Megalops atlanticus - tarpon (Hildebrand, 1963)
Albula vulpes - bonefish (Bruger, 1974)
Anguilla rostrata - American eel (Wenner and Musick, 1975)
Arius felis - hardhead catfish (Gunter, 1945)
Arius bonillai - new granada sea catfish (Norse, 1975)
Bagre marinus - gafftopsail catfish (Gunter, 1945)
Ictalurus catus - white catfish (Heard, 1973)
Ictalurus furcatus - blue catfish (Lambou, 1961)
Ictalurus punctatus - channel catfish (Menzel, 1943)
Urophycis regius - spotted hake (Sikora and Heard, 1972)
Opsanus beta - gulf toadfish (Steele and Perry, 1990)
Opsanus tau - oyster toadfish (Schwartz and Dutcher, 1963)
Strongylura marina - Atlantic needlefish (Brooks et al., 1982)
Tylosurus acus - agujon (Brooks et al., 1982)
Fundulus diaphaneus - banded killifish (Stehlik et al., 1998)
Fundulus grandis - gulf killifish (Levine, 1980)
Fundulus heteroclitus, mummichog (Morgan, 1989) [larvae only]
Menidia beryllina - inland silverside (Levine, 1980)
Menidia menidia - Atlantic silverside (Morgan, 1989) [larvae only]
Prionotus tribulus - bighead searobin (Diener et al., 1974)
Morone americana - white perch (Brooks et al., 1982)

APPENDIX 1. Con't

Morone mississippiensis - yellow bass (Lambou, 1961)
Morone saxatilis - striped bass (Darnell, 1958)
Centropristes striatus - black sea bass (Brooks et al., 1982)
Centropristes philadelphica - rock sea bass (Ross et al., 1989)
Epinephelus itajara - jewfish (Kemp, 1949)
Micropterus salmoides - largemouth bass (Lambou, 1961)
Pomatomus saltatrix - bluefish (Brooks et al., 1982)
Rachycentron canadum - cobia (Gunter, 1950)
Caranx hippos - crevalle jack (Steele and Perry, 1990)
Lutjanus apodus - schoolmaster (Austin and Austin, 1971)
Lutjanus campechanus - red snapper (Felder, 1971)
Lutjanus griseus - gray snapper (Starck, 1971)
Lobotes surinamensis - tripletail (Gunter, 1945)
Archosargus probatocephalus - sheepshead (Gunter, 1945)
Lagodon rhomboides - pinfish (Darnell, 1958)
Aplodinotus grunniens - freshwater drum (Darnell, 1958)
Bairdiella chrysoura - silver perch (Darnell, 1958)
Cynoscion arenarius - sand seatrout (Kasprzak and Guillory, 1984)
Cynoscion nebulosus - spotted seatrout (Gunter, 1945)
Cynoscion regalis - weakfish (Lascara, 1981) [larvae also]
Leiostomus xanthurus - spot (Levine, 1980)
Micropogonias undulatus - Atlantic croaker (Darnell, 1958)
Sciaenops ocellatus - red drum (Guillory and Prejean, 2001)
Pogonias cromis - black drum (Gunter, 1945)
Tautoga onitis - tautog (Moody, 1994)
Scomberomorus cavalla - king mackerel (Kemp, 1949)
Ancylopsetta quadrocellata - ocellated flounder (Stickney et al., 1974)
Citharichthys spilopterus - bay whiff (Stickney et al., 1974)
Paralichthys albiguitta - gulf flounder (Stokes, 1977)
Paralichthys dentatus - summer flounder (Moody, 1994)
Paralichthys lethostigma - southern flounder (Darnell, 1958)
Sphoeroides maculatus - northern puffer (Van Engel, 1987)
Sphoeroides nephelus - southern puffer (Reid, 1954)

REPTILES

Alligator mississippiensis - American alligator (Valentine et al., 1972)
Caretta caretta - loggerhead sea turtle (Van Engel, 1987)
Lepidochelys kempi - Atlantic ridley (Van Engel, 1987)

BIRDS

Ardea herodias - great blue heron (Steele and Perry, 1990)
Articilla spp. - gulls (Day et al., 1973)
Casmerodius albus - great egret (Bailey, 1971)
Florida caerulea - little blue heron (Rogers, 1982)
Guana alba - white ibis (Hammatt, 1981)
Grus americana - sandhill crane (Stephenson and Griffith, 1946)
Larus articilla - laughing gull (Barass and Kitting, 1982)
Larus spp. - gulls (Day et al., 1973)
Lophodytes cucullatus - hooded merganser (Stieglitz, 1966)

APPENDIX 1. Con't

Mergus merganser - American merganser (Stieglitz, 1966)
Nycticorax nycticorax - black-crowned night heron (Allen, 1938)
Rallus longirostris - clapper rail (Bateman, 1965)
Somateria mollissima - American eider (Burnett and Snyder, 1954)
Sterna spp. - terns (Barass and Kitting, 1982)

MAMMALS

Canis rufus - red wolf (Bill Vermilliod, LDWF, personal communication)
Lutra canadensis - river otter (Chabreck et al., 1982)
Procyon lotor - racoon (Hedgpeth, 1950)

APPENDIX 2. Predators of zoeae, megalopae, or crabs (adopted in part from Van Engel, 1987).

INVERTEBRATES	
Alcyonium siderium - alcyonacean octocoral	crab zoeae (Sebens and Koehl, 1984)
Metridium senile - sea anemone	crab zoeae (Sebens and Koehl, 1984)
Chelyosoma productum - ascidian	zoeae (Bingham and Walters, 1989)
Pyura haustor - ascidian	zoeae (Bingham and Walters, 1989)
Boltenia villosa - ascidian	zoeae (Bingham and Walters, 1989)
Herdminia momus - ascidian	zoeae (Bingham and Walters, 1989)
Ascidia curvat - ascidian	zoeae (Bingham and Walters, 1989)
Callinectes bocourti - swimming crab	crabs (Stoner and Buchanan, 1990)
Callinectes danae - swimming crab	crabs (Stoner and Buchanan, 1990)
Callinectes ornatus - swimming crab	crabs (Stoner and Buchanan, 1990)
Callinectes similis - lesser blue crab	brachyuran remains (Hsueh et al., 1992)
Carcinus maenas - green crab	crabs (Ropes, 1989)
Carpilus sp. - xanthid crab	*Callinectes* (Norse, 1975)
Libinia emarginata - spider crab	crabs (Ropes, 1989)
Ovalipes ocellatus - lady crab	crabs (Ropes, 1989)
Neopanopeus texana - mud crab	crabs (Ropes, 1989)
Penaeus aztecus - brown shrimp	crabs (Hunter and Feller, 1987)
Penaeus setiferus - white shrimp	crabs (Hunter and Feller, 1987)
Chiropsalmus quadrumanus - sea wasps	crab zoeae and megalopae (Phillips et al., 1969)
Octopus joubini - pygmy octupus	crabs (Hanlon, 1983)
FISHES	
Carcharhinus limbatus - blacktip shark	crab remains (Clark and von Schmidt, 1965)
Mustelis norrisi - Florida smoothhound	crabs (Clark and von Schmidt, 1965)
Rhizoprionodon terranovae - Atlantic sharpnose shark	crabs (Linton, 1905)
Sphyrna mokarran - great hammerhead	crabs (Clark and von Schmidt, 1965)
Squalis acanthias - spiny dogfish	crabs (Hildebrand and Schroeder, 1923)
Gymnura micrura - butterfly ray	crabs (Hildebrand and Schroeder, 1923)
Amia calva - bowfin	crab (Stacy et al., 1970)
Elops saurus - ladyfish	crab zoeae (Harrington and Harrington, 1961)
Megalops atlanticus - tarpon	crab zoeae (Harrington and Harrington, 1961)
Echidna catenata - chain moray	crabs (Bohlke and Chaplin, 1971)
Anchoa mitchilli - bay anchovy	*Callinectes* spp. zoeae and megalopae (Johnson et al., 1990)
Harengula jaguana - scaled sardine	brachyuran zoeae, megalopae, and crabs (Modde, 1979)
Harengula pensacolae - scaled sardine	zoeae (Odum, 1971)
Opisthonema oglinum - Atlantic thread herring	crabs (Bebee and Tee-Van, 1973) megalopae (Carr and Adams, 1973)
Anchoa hepsetus - striped anchovy	brachyuran zoeae and megalopae (Modde, 1979)
Anchoa lyolepis - dusky anchovy	brachyuran zoeae, megalopae, and crabs (Modde, 1979)
Arius felis - hardhead catfish	crab larvae (Sheridan et al., 1984)
Urophycis floridana - southern hake	crabs (Divita et al., 1983)
Porichthys porosissimus - Atlantic midshipmen	*Callinectes* larvae and juveniles (Lane, 1967)
Synodus foetens - inshore lizardfish	crabs (Hildebrand and Schroeder, 1923)
Lepophidium brevibarbe - blackedge cusk-eel	crabs (Divita et al., 1983)

APPENDIX 2. Con't

Hyporhampus unifasciatus - halfbeak	megalopae (Linton, 1905)
	crabs (Subrahmanyam and Drake, 1975)
Cyprinodon variegatus - sheepshead topminnow	crab zoeae (Harrington and Harrington, 1961)
Fundulus confluentus - marsh killifish	crab zoeae (Harrington and Harrington, 1961)
Fundulus grandis - gulf killifish	crab zoeae (Harrington and Harrington, 1961)
Fundulus heteroclitus - mummichog	crabs (Knieb and Stiven, 1978)
Fundulus majalis - striped killifish	crabs (Knieb, 1976)
Fundulus similis - longnose killifish	crabs and crab larvae (Motta et al., 1995)
Floridichthys carpio - goldspotted killifish	crab parts (Motta et al., 1995)
Lucania parva - rainwater killifish	crab zoeae (Harrington and Harrington, 1961)
Gambusia affinis - mosquitofish	crab zoeae (Harrington and Harrington, 1961)
Poecilia latipinna - sailfin molly	crab zoeae (Harrington and Harrington, 1961)
Menidia beryllina - tidewater silverside	crab megalopae (Carr and Adams, 1973)
Menidia menidia - Atlantic silverside	crabs (Bayliff, 1950)
Menidia peninsulae - gulf silverside	brachyuran zoeae (Lucas, 1982)
Scorpaena calcarata - smoothhead scorpionfish	crabs (Divita et al., 1983)
Scorpaena grandicornis - plumed scorpionfish	*Callinectes* (Austin and Austin, 1971)
Prionotus carolinus - northern searobin	crabs (Hildebrand and Schroeder, 1923)
Prionotus rubio - blackwing searobin	crabs (Divita et al., 1983)
Prionotus scitulus - leopard searobin	crabs (Linton, 1905)
Centropomus undecimalis - snook	zoeae and crabs (McMichael et al., 1989)
Centropristis ocyurus - bank sea bass	crabs (Divita et al., 1983)
Diplectrum formosum - sand perch	crabs (Bortone, 1971)
Epinephelus morio - red grouper	crabs (Nelson and Bortone, 1996)
Rypticus maculatus - whitespotted soapfish	crabs (Bullock and Smith, 1991)
Serraniculus pumilio - pygmy sea bass	crabs and crab megalopae (Hastings, 1973)
Serranus atrobranchus - blackear bass	crabs (Divita et al., 1983)
Serranus subligarius - belted sandfish	crabs (Bullock and Smith, 1991)
Lepomis punctatus - spotted sunfish	crabs (Levine, 1980)
Priacanthus arenatus - bigeye	crabs (Divita et al., 1983)
Echeneis naucrates - sharksucker	crabs (Divita et al., 1983)
Trachinotus carolinensis - pompano	brachyuran megalopae and crabs (Modde, 1979)
Trachinotus falcatus - permit	crabs (Carr and Adams, 1973)
Coryphaena hippurus - dolphin	crabs (Kemp, 1949)
Lutjanus synagris - lane snapper	crabs (Divita et al., 1983)
Rhomboplites aurorubens - vermilion snapper	crabs (Grimes, 1979)
Diapterus plumieri - striped mojarra	crab zoeae (Harrington and Harrington, 1961)
Eucinostomus gula - silver jenny	crab parts (Motta et al., 1995)
Conodon nobilis - barred grunt	crabs (Divita et al., 1983)
Haemulon plumieri - white grunt	crabs (Carr and Adams, 1973)
Orthopristis chrysoptera - pigfish	crabs (Linton, 1905)
Diplodus holbrooki - spottail pinfish	crabs (Carr and Adams, 1972) and crab zoeae (Livingston, 1982)
Stenotomus caprinus - longspine porgy	crabs and crab larvae (Sheridan et al., 1984)
Bairdiella chrysoura - sand seatrout	crab zoeae and megalopae (Sheridan, 1979)
Cynoscion nothus - silver seatrout	crabs and crab larvae (Sheridan et al., 1984)
Larimus fasciatus - banded drum	zoeae and megalopae (Ross, 1989)
Leiostomus xanthurus - spot	brachyuran zoeae and megalopae (Stickney et al., 1975)
Menticirrhus americanus - southern kingfish	*Callinectes* sp., brachyuran megalopae (McMichael and Ross, 1987)
Menticirrhus littoralis - gulf kingfish	brachyuran zoeae and crabs (Modde, 1979)

APPENDIX 2. Con't

Menticirrhus saxatalis - northern kingfish	*Callinectes* sp., brachyuran megalopae (McMichael and Ross, 1987)
Micropogonias undulatus - Atlantic croaker	brachyuran megalopae (Stickney et al., 1975)
Stellifer lanceolatus - star drum	crabs (Welsh and Breder, 1923)
	brachyuran zoeae and megalopae (Stickney et al., 1975)
Abudefduf saxatalis - sergeant major	crab zoeae (Linton, 1905)
Mugil cephalus - striped mullet	crab zoeae (Harrington and Harrington, 1961)
Chasmodes saburrae - Florida blenny	crabs (Carr and Adams, 1973)
Paraclinus fasciatus - banded blenny	crabs (Livingston, 1982)
Trichiurus lepturus - Atlantic cutlassfish	crabs and crab larvae (Sheridan et al., 1984)
Katsuwonus pelamis - skipjack tuna	crab megalopae (Batts, 1972)
Scomberomorus maculatus - Spanish mackerel	crab (Saloman and Naughton, 1983)
Etropus crossotus - bay whiff	crabs (Stickney et al., 1974)
Monacanthus hispidus - planehead filefish	crabs (Nelson and Bortone, 1996)
Chilomyceterus schoephfi - striped burrfish	crabs (Linton, 1905)
REPTILES	
Caretta caretta - loggerhead	crab zoeae (Bjorndal, 1997)
Dermochelys coriacea - leatherback	crabs (Bjorndal, 1997)
Eretmochelys imbricata - hawksbill	crabs (Bjorndal, 1997)
Lepidochelys olivacea - olive ridley	crabs (Bjorndal, 1997)
BIRDS	
Ajaia ajaia - roseate spoonbill	*Callinectes* (Green, 1968)
Anas acuta - pintail	crabs (Bull and Farrand, 1977)
Ammospiza maritima - seaside sparrow	crabs (Bull and Farrand, 1977)
Branta canadensis - canada goose	crabs (Bent, 1925)
Calidris canutus - American knot	crabs (Bent, 1962a)
	crab larvae (Forbush, 1912)
Catoptrophorus semipalmatus - willet	crabs (Bent, 1962b)
Chaulelasmus streperus - egret	crabs (Bull and Farrand, 1977)
Mareca americana - widgeons	crabs (Day et al., 1973)
Megaceryle alcyon - belted kingfisher	crabs (Bull and Farrand, 1977)
Numenius americanus - long-billed curlew	crabs (Wickersham, 1902)
Nyctanassa violacea - yellow-crowned night heron	crabs (Audubon, 1840)
Oxyechus vociferus - killdeer	crabs (McAfee, 1912)
Plegadis falcinellus - glossy ibis	crabs (Bull and Farrand, 1977)
Squatarola squatarola - black-billed plover	crabs (Grinnel et al., 1918)
Sterna maxima - royal tern	crabs (Oberholser, 1974)
Sterna nilotica - gull-billed tern	crabs (Oberholser, 1974)
MAMMALS	
Logia breviceps - pygmy sperm whale	crabs (Handley, 1966)
Mustela vison - North American mink	crabs (Lowery, 1974)
Ondatra zibethicus - common muskrat	crabs (O'Neil, 1949)
Oryzomys palustris - marsh rice rat	crabs (Sharp, 1967)
Physeter catodon - sperm whale	crabs (Caldwell et al., 1966)
Tursiops truncatus - bottlenose dolphin	crabs (Kemp, 1949)

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Patterns of Predation on Juvenile Blue Crabs in Lower Chesapeake Bay: Size, Habitat and Seasonality

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Abstract. — Previous studies of blue crabs, *Callinectes sapidus*, in Chesapeake Bay have suggested that predation on juvenile crabs by adult conspecifics and demersal fish may determine population year-class strength. I measured predator-induced mortality rates of tethered juvenile blue crabs in shallow areas of the lower York River Estuary, a tributary of the Chesapeake Bay. Three size classes of crabs, between 10 and 70 mm in carapace width, were tethered in three different habitats (sea grass beds, unvegetated sand, and unvegetated mud) during summer months over a three-year period. Crabs were subject to consistently more predator-induced mortality in sand habitats than in grass or mud. Vulnerability to predation decreased almost linearly with increasing crab size, regardless of habitat or time of year. This trend effectively terminated in a size refuge from predation, roughly corresponding to one complete year of growth (70 to 90 mm carapace width). Mortality rates were also highly correlated with seasonal water temperature fluctuation, suggesting two likely sources of variation in predation pressure: temperature-dependent activity rhythms of predators, and seasonal-migration of transient predators. The combination of factors influencing vulnerability of juvenile crabs underscores the importance of both spatial and temporal recruitment variation in the determination of blue crab year-class strength.

KEY WORDS: predation, *Callinectes sapidus*, size, habitat, seasonality

In aquatic or marine environments, experiments assessing the impact of predation on prey populations have dealt primarily with sessile or sedentary prey that can be monitored periodically *in situ* for evidence of predator-induced mortality (Connell, 1972; Virnstein, 1977; Peterson, 1979; Menge, 1983). In contrast, studies dealing with mobile prey in these systems have been logistically constrained. In some notable instances, they have been based on events which resulted in the removal or introduction of predators (Brooks and Dodson, 1965; Zaret and Paine, 1973). Otherwise, they have depended on the creation of controlled environments such as field enclosures or laboratory tanks. In both types of experiments, dynamic variables related to the nature of the environment (numbers or types of predators, light, temperature, etc.) may be overlooked or held artificially in a static state. Understanding the nature of predictable changes in predation potential over time is a necessary step in determining the overall impact of predation on prey populations and associated communities (Black and Hairston, 1988; Thrush et al., 1994).

Blue crabs, *Callinectes sapidus*, are highly mobile, generalist foragers, playing key functional roles in a variety of estuarine and coastal habitats (Baird and Ulanowitcz, 1989; Hines et al., 1990). A great deal of research has been focused on the impact of blue crabs as predators on benthic infauna (Virnstein, 1977; Blundon and Kennedy, 1982; Arnold, 1984; Mansour and Lipcius, 1991; Eggleston et al., 1992), but the highly vagile nature of blue crabs has made it difficult to assess the role of predator-induced mortality in the ecology of this

species. Gut content analyses of epibenthic foragers have identified some likely predators of blue crabs, including conspecifics (Laughlin, 1982; Mansour, 1992) and several species of demersal fish (Manooch, 1973; Bass and Avault, 1975; Overstreet and Heard, 1978; Dittel et al., 1995; Pile et al., 1996). In Chesapeake Bay, predation on juvenile blue crabs has been implicated as a mechanism driving crab behaviors, including recruitment and migration (Heck and Orth, 1980; Wilson et al., 1987), ontogenetic habitat shifts and foraging dynamics (Orth and van Montfrans, 1990; Mansour, 1992; Pile et al., 1996), and ultimately determining overall population year-class strength (Hines et al., 1987; Lipcius and Van Engel, 1990). Unfortunately, direct evidence of predation is limited, and these data give little indication of the history or nature of apparent predation events.

As with many epibenthic species, mortality rates of blue crabs are highest during early life-history stages (Lipcius and Van Engel, 1990). High concentrations of small juvenile crabs found in sea grass beds and drift algae suggest that body size and habitat structure may both play important roles in determining predator-induced mortality rates (Orth and van Montfrans, 1987). In addition, periodic changes in biotic and abiotic environmental factors associated with seasonality may regulate predation pressure in shallow benthic habitats (Quammen, 1984; Hines and Ruiz, 1995). Here, I report the results of a tethering experiment designed to identify patterns in predation pressure on juvenile blue crabs in lower Chesapeake Bay as a function of crab size, habitat type, and month over three years.

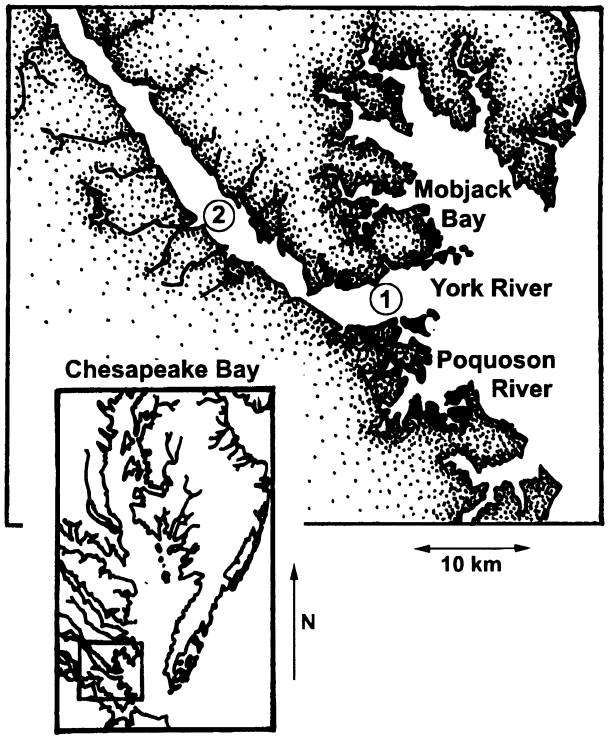

FIGURE 1. — Map of tethering locations on the lower York River Estuary, Chesapeake Bay. Dots at the mouth of the estuary represent Site 1, and those upstream represent Site 2. The sites are approximately 15 km apart. Site 1 contains three habitat types: unvegetated sand, unvegetated mud, and sea grass (SMG). Site 2 contains only the unvegetated habitats (SM). Each year x month x site x habitat treatment combination represents five replicate crabs in each of three size classes (total N = 750).

Methods

For this project, a tethering technique was used to characterize predation potential on juvenile blue crabs in the lower York River Estuary (Figure 1), Chesapeake Bay. The crabs were tethered on 20 cm lengths of steel fishing leader material. The tethers were flexible enough to allow the crabs to move freely within a limited area, but strong enough that they would not break, and rigid enough that they did not tangle. The line was looped around the carapace spines on the crab and closed tightly with a metal crimping band (Figure 2). In an initial experiment, performed in holding pens, 108 inter-molt crabs were tethered to submerged bricks for 24 hour periods using this technique. Four crabs died during these tests with their tethers intact, but none of the surviving crabs escaped from their tethers. Based on these observations, it was assumed during the field experiments that missing crabs were removed by predators.

The crabs were tethered to 10-m lengths of galvanized chain at 2-m intervals (5 crabs per chain) (Figure 2). The tethers were attached to the chains with small fishing swivels. At each end of each chain was a lead weight and a float on a 3-meter length of nylon line. The chains were deployed

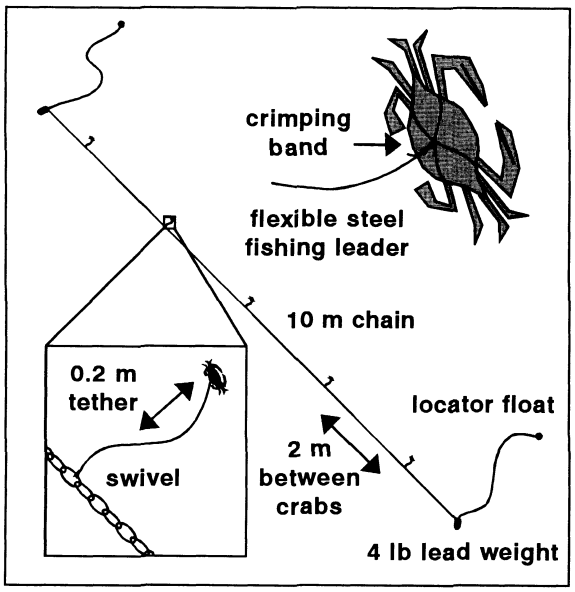

FIGURE 2. — Schematic diagram of field tethering technique.

from a small boat in approximately 2 to 3 meters of water. Visual transects (using a diving mask and snorkel) along recently deployed chains, showed that this method did not result in injury to the crabs or notable disturbance of the local environment.

The three major variables examined in this project were: crab body size (carapace width), habitat type, and time (year and month). During a typical experimental run, three chains were deployed, one in each of three habitat types. Five crabs in each of three size classes were assigned to the fifteen chain-positions in a systematic manner which gave each crab an equal initial probability of being at any position. The chains were retrieved after 24 hours, and numbers of missing and remaining crabs were recorded.

The crab specimens used in these experiments fell between 10 and 70 mm in carapace width from spine to spine. The growth rate of newly-recruited blue crabs is such that they reach the lower end of this size range in only 20 to 30 days (Churchill, 1921; Gray and Newcombe, 1938; Leffner, 1972). During the early benthic phase, they are found primarily in sea grass beds (Orth and van Montfrans, 1987; Heck and Thoman, 1984), but once they reach 10 mm, they begin to occupy other habitats (Pile et al., 1996). The upper size limit of 70 mm represents the minimum size at maturity (Millikin and Williams, 1984). The size range was sub-divided into three size classes for use in analysis: 11-29 mm, 31-49 mm, and 51-69 mm carapace width (Figure 3).

The habitats examined were chosen to represent broad functional variation in the natural environment where juvenile blue crabs are found in the lower Chesapeake Bay. Two major environmental variables that affect predation potential in soft-bottom estuarine habitats were considered: the presence or absence of vegetation and the nature of the sediment. The three habitat types tested were sea grass beds, unvegetated sand, and unvegetated mud. Sea grass beds were distinguished as areas with at least a 75% cover of vegetation, generally dominated by eelgrass, *Zostera marina*, but often containing other grasses and algae. Unvegetated areas contained less than a 25% cover of vegetation. These areas were characterized as mud habitats if more than half of a local surface sediment sample could be washed through a 100 µm sieve. Otherwise, they were characterized as sand habitats. Initially, a series of sites was chosen in areas on both sides of the

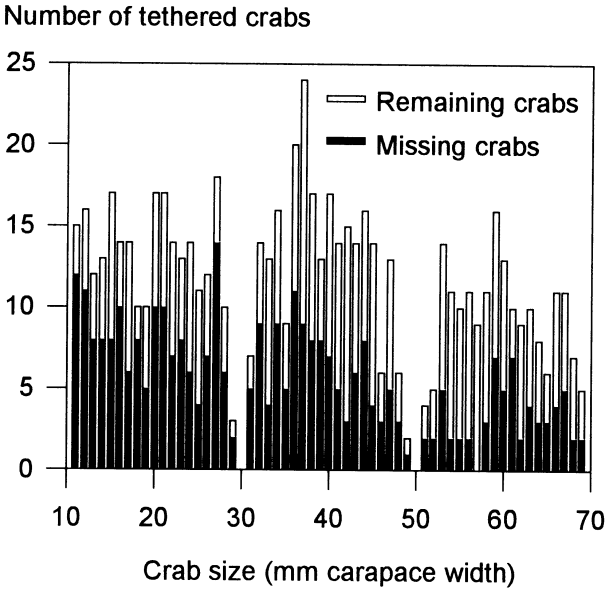

FIGURE 3. — Size frequency histogram of tethered juvenile blue crabs indicating relative numbers of surviving and missing crabs over 24 hrs.

TABLE 1a. — Schedule and location (Site 1 and Site 2, Figure 1) of crab tethering experiments.

Month	1990	1991	1992
May		1	
Jun		1	
Jul		1	1 and 2
Aug	1	1 and 2	1 and 2
Sep	1	1 and 2	1 and 2
Oct		1 and 2	
Nov		1 and 2	

lower York River Estuary (Figure 1), where each of these habitat types occurred. Later, additional unvegetated sites were examined approximately 15 km upstream from the original areas.

Experimental trials were replicated during summer months over three years in order to include both seasonal and inter-annual patterns in predation potential. Logistical constraints precluded a fully-balanced design across time and habitat conditions (Table 1a and b). Therefore, the data were compartmentalized and analyzed in multiple configurations. For example, inter-annual differences across all three years could only be assessed based on data from downstream sites during August and September, and month effects across the entire season could only be assessed based on data from 1991. Each data compartment was analyzed as a multi-dimensional contingency table using a hierarchical log-linear model (Norusis, 1990).

Results

Of the six data configurations tested (Table 1a and b), all contained habitat effects, five contained month effects, and four contained size effects (Table 2). No year effects, stream position effects, or interactions were detected at an α level of 0.05.

All of the size effects identified reflected lower vulnerability to predation for larger crabs. This pattern was characterized mathematically by pooling the compartments (Figure 4) and using a logistic regression procedure (Homer and Lemeshow, 1989) on the original data with weightings applied to account for unbalanced

TABLE 1b . — Balanced data compartments (a-f) of crab tethering experiments chosen for analysis (Site = location as defined in Figure 1, Habitat types include: S = unvegetated sand, M = unvegetated mud, G = sea grass).

Compartment	Years	Months	Sites	Habitats
a	'90 '91 '92	Aug - Sep	1	SMG
b	'91 '92	Jul - Sep	1	SMG
c	'91 '92	Aug - Sep	1 and 2	SM
d	'91	May - Nov	1	SMG
e	'91	Aug - Nov	1 and 2	SM
f	'92	Jul - Sep	1 and 2	SM

treatments. In this analysis, the actual sizes of the tethered crabs were used. The resulting regression equation,

$$\mu = 1/(1+e^{(-0.542 + 0.030S)})$$

in which μ represents the mortality rate of tethered crabs over 24 hours, and S represents crab size (mm carapace width), has an overall P-value less than 0.00005, with both the constant and the size coefficient contributing significantly.

The nature of the habitat effects in the data compartments which included three habitat types (a, b, and d) were determined using lower-level G-tests. All three of these compartments contained significantly higher mortality rates in the

TABLE 2. — Chi square values for main effects from hierarchical log-linear analyses (G-tests) of six saturated balanced compartments (a-f) in a data set consisting of the fates of 750 juvenile blue crabs tethered for 24 hours across year, month, site, habitat, and crab size treatments (see methods for treatment descriptions)(* $P < 0.05$, ** $P < 0.01$). "NA" indicates where results were not available.

Compartment	Year	Month	Site	Habitat	Size
a	1.52	6.99**	NA	16.07**	6.72*
b	1.02	6.89*	NA	13.69**	6.11*
c	1.36	6.30*	0.03	17.73**	4.73
d	NA	61.51**	NA	10.72**	11.35**
e	NA	32.94**	0.43	21.98**	8.28*
f	NA	4.15	0.00	9.60**	2.26

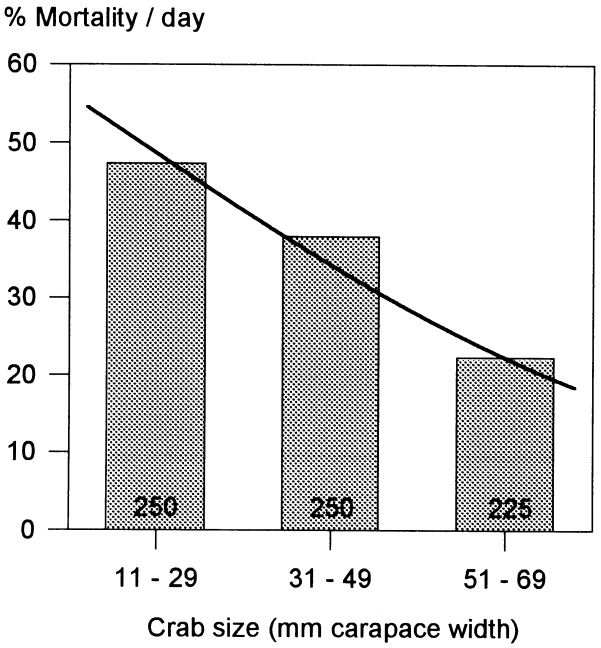

FIGURE 4. — Proportional mortality (24 hrs) of tethered juvenile blue crabs by size class. Data are pooled across year, month, and habitat treatments and weighted to balance the effects of those variables. The number at the base of each bar indicates the total number of tethered crabs contributing to the bar. The line is based on a logistic regression of the original data using the actual sizes.

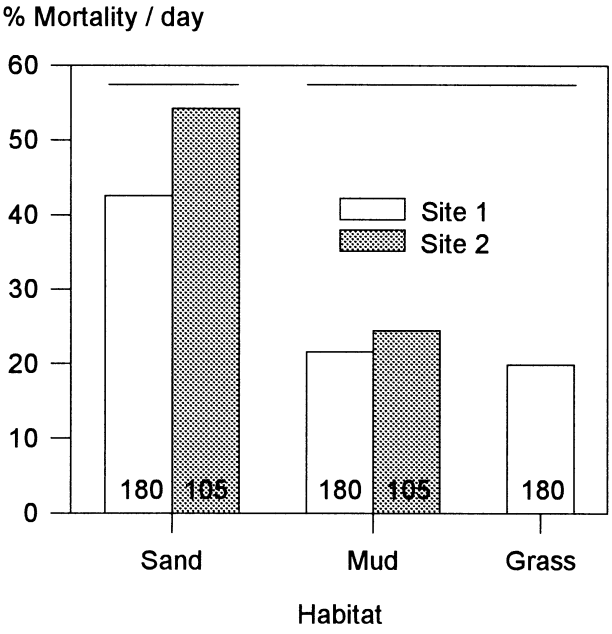

FIGURE 5. — Proportional mortality (24 hrs) of tethered juvenile blue crabs by habitat and river position. Data are pooled across year, month, and crab size treatments, and weighted in order to balance the effects of those variables. The number at the base of each bar indicates the total number of tethered crabs contributing to the bar. The horizontal lines at the top of the graph connect groups which are not statistically different at an α level of 0.05.

unvegetated sand habitats than in the other two types ($P<0.05$). The data configurations that included only two habitats (sand and mud) also contained significantly higher mortality rates in the sand ($P<0.05$).

These results consistently reflect a pattern in which tethered crabs were more vulnerable to predation in unvegetated sand than in mud or sea grass (Figure 5).

All five of the configurations which contained month effects reflected a seasonal pattern in predation potential with the highest values occurring in late summer. Configuration 4, which included the entire range of months followed a rise in mortality rates from near zero in May to a peak during August and a decline by November. The near-sinusoidal nature of this pattern allowed it to be paramaterized by transforming the month variable, t, into two components, $\cos(2\pi t/7)$, and $\sin(2\pi t/7)$ which could then be fitted together through a logistic regression procedure using all of the original data, pooled and weighted to account for unbalanced treatments (Figure 6). The resulting regression equation,

$$\mu = 1/(1+e^{(0.795 - 1.486\cos(2\pi t/7) - 0.526\sin(2\pi t/7))})$$

in which μ represents the mortality rate of tethered crabs over 24 hours, and t represents the month, had an overall P-value of .0452 with all three of the parameters contributing significantly.

Discussion

The use of tethering as a research technique for investigating the impacts of predation has been the subject of some scrutiny (Barshaw and Able, 1990; Zimmer-Faust et al., 1994). A point of concern is

that predation rates on tethered animals are likely to be inflated greatly over natural rates, particularly in cases of highly mobile prey. For this reason, interpretation of information from tethering experiments should be limited to consideration of the patterns apparent in the data, and not the actual predation rates.

Four of the six data configurations contained crab size effects which consistently reflected a decrease in predation potential with increasing carapace width. Given that juvenile crab growth occurs in a step-wise fashion, with size increases of 20 to 35% following ecdysis (Millikin and Williams, 1984), these results indicate that crabs may experience dramatic decreases in predation pressure with each molt cycle. An extrapolation of the logistic regression suggests that blue crabs in the habitats studied reach a 95% size refuge from predation at approximately 90 mm carapace width.

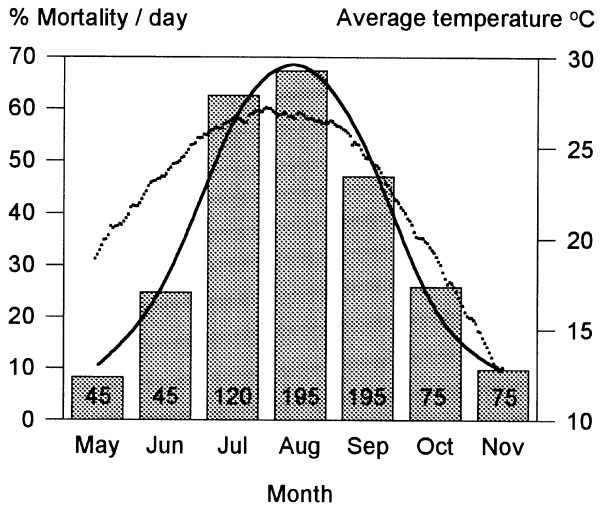

FIGURE 6. — Proportional mortality (24 hrs) of tethered juvenile blue crabs by month. Data are pooled across year, habitat, and crab size treatments, and weighted to balance the effects of those variables. The number at the base of each bar indicates the total number of tethered crabs contributing to the bar. The solid line is based on a logistic regression of the original data. The dotted line shows the daily averaged water temperature (right axis) at a 2 m depth measured at the Virginia Institute of Marine Science on the lower York River Estuary (1947-1992 pooled).

Since blue crabs in Chesapeake Bay reach an average size of 85 mm carapace width during their first year of growth (Van Engel, 1958; Millikin and Williams, 1984) and have generally reached reproductive maturity at this size, it appears that predation in these shallow habitats has little effect on adult crabs.

Habitat type accounted for the greatest amount of variation in the data for four of the six configurations tested. In all cases, mortality rates of tethered crabs were higher in unvegetated sand than in sea grass or unvegetated mud. The lack of site effects indicates that the absence of sea grass beds at the upstream site did not alter relative predation potential in the other two habitats. Therefore, it appears that both sea grass and mud habitats independently provided refuge from predation that was unavailable in sand.

While the refuge provided by the complex three-dimensional structure of aquatic vegetation is well known (Orth et al., 1984; Wilson et al., 1987; Gotceitas and Colgan, 1989; Heck and Crowder, 1991; Diehl, 1992), the mechanism of predator avoidance in mud is less clear. In areas where vegetation is sparse or absent, mobile organisms may avoid predators by burying, tunneling, or otherwise penetrating the sediment surface. Presumably, the nature of local sediments (e.g., sorting or grain sizes) may determine the relative effectiveness of this type of refuge by controlling the speed and depth of digging (Arnold, 1984; Lipcius and Hines, 1986). Another possible explanation for reduced predation pressure in mud habitats is that the important predators in this system may rely on chemical or visual cues which are less detectable in these areas due to suspended sediments (Aksnes and Giske, 1993; Weissburg and Zimmer-Faust, 1993).

Five of the six data configurations contained month effects indicating a seasonal pattern in predation potential. Data compartment d, which included all seven months of the season during which blue crabs are active in the Chesapeake Bay (Van Engel, 1958; Lipcius and Van Engel, 1990) contained the strongest effect (Table 2). In benthic macroinvertebrate communities, seasonal patterns in predation pressure have been attributed to timing in recruitment, migration, activity levels, and even

life history characteristics of predators (Coultas, 1980; Choat and Kingett, 1982; Nelson et al., 1982; Foreman, 1985; Hines et al., 1990; Prejs and Prejs, 1992). The nearly-sinusoidal seasonal pattern identified in this study closely resembles the annual water temperature fluctuation in the research area (Figure 6), suggesting that it may be due to physiological control of predator activity levels. Alternatively, this pattern may reflect migration of transient predator species such as red drum (Bass and Avault, 1975) or juvenile striped bass (Manooch, 1973) into the shallow waters of the lower bay during warmer months. Regardless of the cause; however, this strong seasonality is clearly a dynamic component of predation pressure in this system, and should be considered in future attempts to characterize blue crab population dynamics.

The statistical independence of the three primary variables in this study was unexpected. However, despite the lack of interaction effects identified here, there may be important relationships among these factors in nature. For example, the timing of recruitment may determine the size at which juvenile crabs experience seasonal periods of intense predation pressure. Also, the relative availability of habitat types may vary seasonally as a result of intraspecific competition or other density-dependant factors. While many experiments have dealt with the effects of body size and habitat (both singly and together) on predator-induced mortality rates, the relationships of these variables with possible seasonal dynamics must be explored in order to fully understand the impact of predation at the population and community levels.

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Red Drum Predation on Blue Crabs

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Abstract. – Historic and new data on predation of blue crabs (*Callinectes sapidus*) by red drum (*Sciaenops ocellatus*) and a brief review of general red drum food habits are presented. Percent frequency of occurrence of blue crabs in red drum stomachs averaged 30% in Louisiana studies and 24% in Texas studies. Approximately 1,200 red drum were collected from regular and 24-hour diel samples in the Terrebonne estuary of Louisiana. Blue crabs occurred in 31% of red drum stomachs and comprised 37% and 31% of the total diet by weight and number, respectively. The index of relative importance of blue crabs was 13.8 times greater than the next ranked species. Small juvenile blue crabs were usually consumed by red drum; almost half of blue crabs were from 10-29 mm carapace width. Depending on the approach used, blue crab food ration per kg of red drum was 1.86 or 1.92 /day (679 or 701/year).

KEY WORDS: blue crab, red drum, food habits, food ration

Red drum (*Sciaenops ocellatus*), a highly desirable recreational species, is one of the most abundant and largest estuarine fish predators in Gulf of Mexico estuaries (Guillory and Elliot, 2001). Similarly, the blue crab (*Callinectes sapidus*) is an abundant estuarine macroinvertebrate that also supports valuable commercial and recreational fisheries. Blue crab commercial landings declined during the mid-1990s coincident with increased red drum abundance. Some commercial crab fishermen and industry representatives have suggested that increased red drum predation has adversely impacted blue crab populations in Louisiana. These concerns were partly based on anecdotal reports and casual observations of the numbers of blue crabs in red drum stomachs and the assumption that reduced red drum predation would yield a proportionate increase in number of harvestable blue crabs. A similar controversy has developed in Chesapeake Bay concerning striped bass (*Morone saxatalis*) and blue crab (Booth and Gary, 1993; Goshorn and Casey, 1993; Mosca and Rudershausen, 1994).

Although there are data on red drum food habits in the South Atlantic and Gulf of Mexico, the focus of these investigations was not on blue crab consumption and results were usually reported qualitatively (Pearson, 1929; Gunter, 1945; Kemp, 1949; Knapp, 1950; Miles, 1950; Darnell, 1958; Simmons and Breuer, 1962; Yokel, 1966; Fontenot and Rogillio, 1970; Boothby and Avault, 1971; Odum, 1971; Heffernan, 1973; Bass and Avault, 1975; Rogillio, 1975; Overstreet and Heard, 1978; Matlock and Garcia, 1983; Steen and Laroche, 1983; Music and Pafford, 1984; Morales and Dardeau, 1987; Peters and McMichael, 1987; Levine, 1980; Soto et al., 1997; Lianso et al., 1998). Recognizing these limitations, a study was undertaken to obtain data on the blue crab component of the red drum diet. Our objectives are to: a) summarize available literature concerning red drum predation on blue crabs; b) analyze red drum food habit data to assess the relative importance of blue crab as a prey item of red drum; and, c) determine the blue crab food ration of red drum.

Review of Red Drum Food Habit Literature

A summary of red drum food habit studies with reference to blue crab predation is provided in Appendix 1. Literature was excluded that was outside the Gulf of Mexico, or that derived results from insufficient numbers of fish.

Red drum are opportunistic predators, and their diet is influenced by local and seasonal availability

TABLE 1a. – Frequency of occurrence of blue crabs in red drum stomachs based on predator size.

Author(s)	Red Drum Size (SL)	Frequency of Occurrence in Stomachs
Bass and Avault (1975)	<40 mm	0
	40-69 mm	≤ 1%
	70-149 mm	12%
	150-179 mm	32%
Miles (1950)	40-127 mm	5% portunid crabs and 7% unidentified crabs
Morales and Dardeau (1987)	< 30 mm	0
	40-70 mm	5-10%
	70-120 mm	12%
Odum (1971)	≤ 20 mm	ingested zoea.
Overstreet and Heard (1978) *	190-349 mm	49%
	350-499 mm	63%
	500-780 mm	54%
Peters and McMichael (1987)	<105 mm	crabs rare
	> 105 mm	crabs were a major prey
Simmons and Breuer (1962)	100-175 mm	blue crabs and mud crabs collectively are the dominant prey
Yokel (1966)	larger fish	proportionately more crabs

* for *Callinectes* spp.

of prey within the physical constraints associated with fish size. Juvenile red drum, <15 mm standard length (SL), feed on copepods and copepod nauplii. At approximately 15-75 mm SL they shift to mysid and caridean shrimp, followed by gammarid amphipods and polychaetes. Penaeid shrimp, small blue crabs, and fish are important dietary components of red drum from 75-100 mm SL. The diet of red drum >100 mm SL consists of crustaceans (portunid, xanthid, and grapsid crabs and penaeid shrimp) and fish, although the relative proportions of prey species and prey size vary with individual red drum size.

Red drum are very efficient predators. Increased turbidity levels, vegetation densities, and the availability of prey refuge (i.e., sand substrates for borrowing) did not reduce brown shrimp consumption in the studies of Minnello and Zimmerman (1983) and Minello et al. (1987). In laboratory studies, foraging was found to occur over a 24-hour period, with peaks at sunrise and sunset (Minello and Zimmerman, 1983). Nocturnal foraging by red drum has also been verified in the field (Bass and Avault, 1975). Nocturnal feeding and the ability to locate prey under conditions of high turbidity and dense vegetation suggest that red drum use olfactory and tactile mechanisms to locate prey in addition to visual feeding. Burrowed prey is located by rubbing the lower jaw along the substratum (Yokel, 1966).

Frequency of occurrences of blue crabs consumed by various size classes of red drum are summarized in Table 1a. Blue crabs first appear in the diets of 40 mm SL red drum, but become more common in fish ≥75 mm SL. Because blue crabs are more important in the diets of larger red drum, data were summarized for fish approximately 200 mm SL and larger (Table 1b). Percent frequency of occurrence of blue crabs in red drum stomachs averaged 30% (24-42%) in Louisiana studies and 24% (7-43%) in Texas studies (Table 1b). Occurrence of blue crabs in red drum diets was highest in spring and summer (Overstreet and Heard, 1978) and summer and fall (Boothby and Avault, 1971).

Guillory and Elliot (2001) ranked estuarine fish predators of blue crab based upon predator abundance and size, and occurrence of blue crabs in stomach contents, and concluded that red drum were the dominant predator of blue crabs. The predation index of red drum was 4.8 times greater than the next highest ranked species.

TABLE 1b. – Overall variation in frequency of occurrence of blue crabs in red drum stomachs.

State	Author(s)	Frequency of Occurrence in Stomachs
Louisiana	Boothby and Avault (1971)	42%
	Darnell (1958)	62% (blue and mud crabs)
	Fontenot and Rogillio (1970)	30% (plus unidentified portunids at 23%)
	Levine (1980)	50% (blue and mud crabs)
	Rogillio (1975)	24%
Texas	Gunter (1945)	37%
	Heffernan (1973)	6% (for *Callinectes* spp.)
	Kemp (1949)	2% (plus unidentified crabs at 11.1%)
	Knapp (1950)	43%
	Pearson (1929)	7%
Mississippi	Overstreet and Heard (1978)	17%
Florida	Yokel (1966)	55% (xanthid and portunid crabs)

Predation Study Methods

LDWF Finfish Monitoring Studies

Coast wide Louisiana Department of Wildlife and Fisheries (LDWF) gill and trammel net samples from 1986-1996 yielded a total of 6,948 red drum. The TL in mm was measured and converted to SL in mm by a TL-SL regression (Harrington et al., 1979). Occurrence of each prey item in each stomach was recorded. The Louisiana coast was divided into seven estuaries, or coastal study areas (CSAs): CSA I - Breton Sound estuary; CSA II - Chandeleur Sound estuary; CSA III - Barataria Bay estuary; CSA IV - Terrebonne/Timbalier Bay estuary; CSA V - Lake Mechant/Caillou Lake estuary; CSA VI - Vermilion Bay estuary; and, CSA VII - Calcasieu Lake estuary.

Terrebonne/Timbalier Study

Red drum were collected with a trammel net in the Terrebonne/Timbalier estuary of southeast Louisiana. Twenty-two regular sampling trips were made from 9 Sep 1994 to 11 Apr 1996. In addition, diel samples were made on:

7-8 Nov 1994,
6-7 Dec 1994,
26-27 Jan 1995,
29-30 Mar 1995,
30-31 May 1995,
26-27 Jul 1995,
25-26 Sep 1995,
13-14 Nov 1995.

In the diel surveys, samples were taken every six hours, beginning at either 0600 or 1200 and ending 18 hours later; where feasible, 15-20 red drum were examined from each sample. Supplemental data collected with each sample included water temperature, salinity, and tidal stage. Regular sampling and diurnal sampling yielded 615 and 605 red drum, respectively, for food habit analyses. All red drum were measured and stomach contents were enumerated and identified to the lowest recognizable taxon. All fish and larger invertebrate prey items were measured and blue crabs were measured for either carapace width (CW) or propodus length (PL) (if the former was broken). A PL-CW regression was developed to convert PL to CW.

The reconstructive approach was used to determine weight of prey items. Weights of ingested blue crabs were calculated from a CW-weight regression model developed by Guillory and Hein (1997). Weights for some larger prey items were calculated from published length-weight regressions whereas weights for some small prey species were obtained from their average weight in LDWF seine or trawl samples or from published literature.

Food Ration Determination

The daily consumption of blue crabs by red drum was determined in two different ways. The first method used metabolic requirements and the gravimetric contribution of blue crabs to overall

diet to determine the total and blue crab food rations. Although quantitative food requirements have not been adequately defined for red drum, some estimates of daily food consumption of other fish are available. Daily food consumption (measured as percent of body weight) was estimated at 3% for moderately active fish (Gerking, 1967) and 1-2% for cold water marine fish (Tyler and Dunn, 1976; Cohen et al., 1982; Francis, 1983). Daily feeding rates of red drum in culture experiments ranged from 0.98%-2.86% (Tucker et al., 1997) while Davis (1990) and Robinson (1990) recommended feeding rates of 2% and 3%, respectively. Red drum were assumed to consume 2% of body weight per day or 7.3 times their body weight each year.

The second approach involved determination of the daily blue crab consumption by red drum from the series of 24-hour diel samples. This method assumes that prey consumed in one sampling interval have cleared the stomach by the next sampling interval. This method is a conservative approach because gastric evacuation occurs continuously and stomach contents at the end of a sampling period underestimate the actual amount consumed (Elliott and Persson, 1978). Additionally, Minnello et al. (1989) estimated evacuation times of southern flounder (*Paralichthys lethostigma*), another northern Gulf of Mexico predator, of 4 h.

Results and Discussion

LDWF Finfish Monitoring Data

The blue crab was the most frequently encountered species in the diet of red drum across the Louisiana coast, occurring in 24% of examined stomachs. Fishes (all species), penaeid shrimp, grass shrimp, and mud crabs occurred in 21%, 8%, 4%, and 3%, respectively, of red drum stomachs. Empty stomachs occurred in 34% of red drum. The percentage of empty stomachs declined with fish size; 57% for <300 mm, 34% for 300-499 mm, and 25% $\geq$500 mm SL red drum. Percent of empty stomachs was lowest in fall (23%) and spring (18%) and highest in winter (38%) and summer (39%).

The effect of fish size, season, area, and habitat sampled on occurrence of blue crabs in red drum diets was also examined. Blue crabs, as prey, increased in importance with fish size; the percent frequency of occurrence of blue crabs was 11% in fish <300 mm, 22% in fish 300-399 mm, 28% for fish 400-499 mm, 34% for fish 500-699 mm, and 31% in fish $\geq$ 700 mm SL. The occurrence of blue crabs in red drum stomachs was lowest in winter (21%) and summer (23%) and highest in spring (30%) and fall (26%). The percent frequency of occurrence of blue crabs was lowest in CSA VII - Calcasieu Lake estuary (15%) and highest in CSA II - Chandeleur Sound estuary (59%) and ranged from 18-38% in the remaining CSAs. The percent frequency of occurrence of blue crabs was similar (19-24%) in four different habitats (barrier island, lower estuary, middle estuary, upper estuary) in the Terrebonne/Timbalier Bay estuary.

Terrebonne/Timbalier Study

The importance of several species groupings (crabs, fishes, large crustaceans, small crustaceans, insects) as prey of red drum was assessed (Table 2) with an index of relative importance (IRI) calculated according to Armstrong et al. (1995):

IRI = (% number + % weight) x (%freq. of occurrence).

Crabs included blue crabs, mud crabs, and fiddler crabs; whereas, 39 different species were included in the fishes category. The crabs category had the highest IRI value. Crabs ranked first in frequency of occurrence, second to small crustaceans in number, and second to fishes in weight. Numbers of small crustaceans and insects were inflated because of the consumption of large numbers of mysid shrimp and chironomid larvae by a few small fish.

Blue crabs were a major prey item of red drum, occurring in 30.8% of stomachs and comprising 37% and 31% of the total diet by weight and number, respectively. By species or lowest identified taxonomic group, blue crabs ranked first in frequency of occurrence and weight and second, after mysid shrimp, in number of prey items in red drum stomachs. The importance of mysid shrimp as a food item was overestimated because of large numbers in a few small red drum. According to the IRI, blue crabs ranked first, followed by striped mullet (*Mugil cephalus*), grass shrimp

TABLE 2. – Percent number (% No), weight (% Wt), frequency of occurrence (% Freq), and index of relative importance (IRI) (Armstrong et al., 1995) of major prey categories in red drum stomachs, Terrebonne/Timbalier Bay, 1994-1996.

Prey Category	% No	% Wt	% Freq	IRI
Crabs (blue crab, hermit crab, mud fiddler, and mud crab)	20	43	43	2,782
Fishes (39 different species)	18	46	34	2,209
Small crustaceans (mysid shrimp, grass shrimp, and amphipod)	48	7	11	618
Large crustaceans (brown shrimp, white shrimp, pink shrimp, pistol shrimp, burrowing shrimp, and crayfish species)	2	3	9	52
Insects (damselfly larvae, dragonfly larvae, chironomid larvae, water beetle, and backswimmers)	10	0.1	2	21

(*Palaemonetes* spp.), rainwater killifish (*Lucania parva*), sheepshead minnow (*Cyprinodon variegatus*), and sailfin molly (*Poecilia latipinna*) (Table 3). The IRI of blue crab was 13.8 times greater than the next most important single item.

Size composition of blue crabs from stomach contents indicates that small juvenile crabs were usually consumed by red drum, although the mean size of blue crabs increased with fish size. Almost half (48%) of the blue crabs consumed by red drum ranged between 10-29 mm CW, with 78% less than 50 mm CW (Figure 1). Overall mean size and weight of blue crabs was 35 mm CW and 8 g, respectively. The mean size of blue crabs increased from 18 mm CW in 200-249 mm SL red drum to 70 mm CW in >650 mm SL red drum (Figure 2).

Consumption of blue crabs by red drum varied with fish size, season, and time of day. Blue crabs were more common as prey in medium-sized (350-649 mm SL) red drum than in smaller or larger fish (Table 4). The percent by number of blue crabs consumed was highest in the summer and fall whereas the percent by weight was substantially higher in the spring (Table 4). However, it should be noted that the percent frequency of occurrence of blue crabs was fairly consistent across seasons.

Diel food habit data indicated that consumption of blue crabs by red drum was highest in the morning: number and weight of ingested blue crabs was highest at 0600 and 1200 and lowest at 1800 and midnight (Table 5).

TABLE 3. – Index of relative importance (IRI) (Armstrong et al., 1995) of major prey items in red drum stomachs, Terrebonne/Timbalier Bay, 1994-1996.

Prey Item	IRI	Prey Item	IRI
Blue crab	1,679	Mud fiddler	22
Striped mullet	122	Mysid shrimp	22
Grass shrimp	118	White shrimp	10
Sheepshead minnow	53	Chironomid larvae	5
Sailfin molly	33	Gulf killifish	5
Amphipods	32	Brown shrimp	3
Rainwater killifish	27		

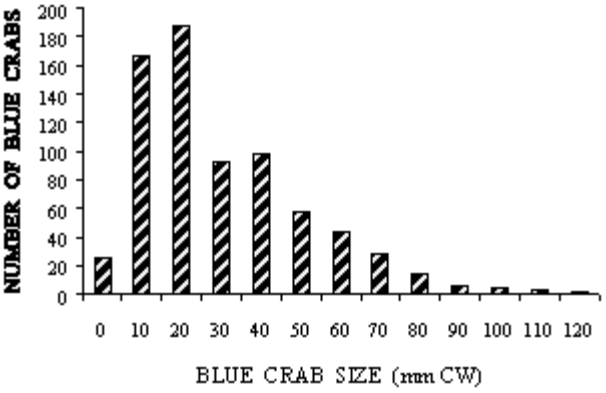

FIGURE 1. – Width (mm CW) frequency distribution of blue crabs consumed by red drum.

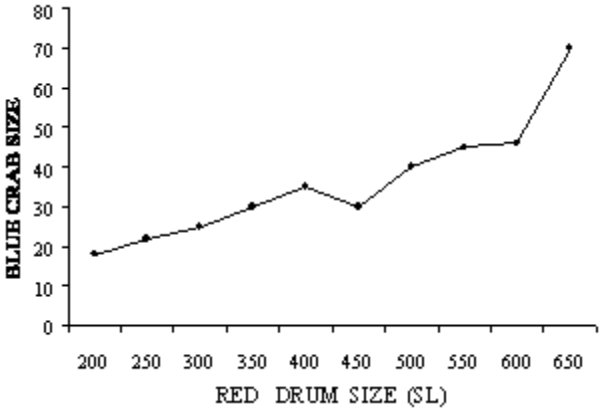

Figure 2. – Average size (mm CW) of blue crabs consumed by various sizes of red drum.

The daily blue crab food ration was determined from metabolic and diel food habit data. Assuming an overall 2% daily consumption rate and using the contribution (37%) by weight of blue crabs and the average weight (3.9 g) of blue crabs examined in red drum stomachs from diel samples, each red drum consumed 1.92 blue crabs per kg of fish daily; this value can be extrapolated to an annual food ration of 701 blue crabs per kg of red drum. Based upon the quantity of blue crabs ingested over the series of four diel samples, red drum consumed an average of 1.86 blue crabs weighing 7.56 g per kg per day (Table 5), which equates to an annual ration of 679 blue crabs or 2.76 kg per kg of fish. The total daily food ration of red drum was 23.7g/kg (Table 6); blue crabs by weight comprised 2.37% of the total diet.

The metabolic and diel sample approaches yielded similar results; the estimated daily food ration of blue crabs as a percentage of red drum weight was 2% in the former and 2.37% in the latter. Likewise, estimates of the annual consumption of blue crabs (679 or 701 blue crabs per kg of red drum) were fairly close.

The red drum is one of the more abundant species by weight in estuarine marsh habitats. Standing crop estimates for inshore Louisiana red drum based upon rotenone block-net samples ranged from 30-120 kg/ha and comprised from 10-32% of the total catch (Kilgen et al., 1973; Adkins and Bowman, 1976; Perry, 1976). The number of age 1-3 red drum from 1990 to 1995 were obtained using Virtual Population Analysis (VPA) data on Louisiana red drum (Joseph Shepard, LDWF, unpublished data). Age-0 and age-3+ were excluded because small age-0 red drum are not significant predators of blue crab and older fish migrate offshore. The number of age 1-3 red drum averaged 16.0 million from 1990 to 1995. However, the population level blue crab food ration was not calculated because trophic interrelationships are complex and the simple expansion of predator abundance and feeding rate data are not recommended (Robichaud et al., 1991).

TABLE 4. – Percent number (% No), percent weight (% Wt), and frequency of occurrence (% Freq) of blue crabs in red drum stomachs by fish size and season, Terrebonne/Timbalier Bay, 1994-1996.

	% No	% Wt	% Freq
Fish Size (SL)			
<350 mm	6	23	22
350-649 mm	26	42	35
>650 mm	18	15	26
Season			
Winter	19	27	27
Spring	12	63	38
Summer	28	36	30
Fall	27	34	31

TABLE 5. – Diel variability in number (No) and weight (Wt) of blue crab prey per individual or kilogram (Kg) of red drum, Terrebonne/Timbalier Bay, 1994-1995.

	Per Fish		Per Kg	
Time	No	Wt	No	Wt
0000	0.36	2.11	0.29	1.71
0600	0.76	2.63	0.38	1.32
1200	1.15	4.22	0.76	2.77
1800	0.52	2.14	0.43	1.76
Total	2.79	11.10	1.86	7.56

TABLE 6. – Number (No) and weight (Wt) in grams of all food items per individual or kilogram (Kg) of red drum, Terrebonne/Timbalier Bay, 1994-1995.

	Per Fish		Per Kg	
Time	No	Wt	No	Wt
0000	8.6	4.4	6.9	3.6
0600	17.2	18.0	8.6	9.0
1200	13.8	10.6	9.1	7.0
1800	3.9	5.0	3.2	4.1
Total	43.5	38.0	27.9	23.7

However, the total number of blue crabs consumed by the Louisiana red drum population is undoubtedly very high.

In conclusion, although red drum are opportunistic predators whose diet is influenced by local and seasonal availability of prey within the physical constraints associated with fish size, blue crabs are the most important single food item. Red drum are the dominant estuarine fish predator of blue crabs (Guillory and Elliot, 2001). The individual level consumption of blue crabs by red drum and the overall abundance of both species in the estuary suggests that population level consumption would be very high.

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APPENDIX 1. — Summary of red drum food habit studies. Food occurrence is expressed as frequency of occurrence unless otherwise noted.

Author	Location and Specimen Data	Study Results
Bass and Avault 1975	Caminada Bay, LA [568 age-0 fish (8-183 mm SL), winter of 1971-72]	Empty = 5.1%. Food items varied by size: copepods and copepod nauplii were dominant in 0-9 mm fish; mysid shrimp were most important in 10-49 mm fish, where they constituted 70-100% of total; fish averaged approximately 50% by volume in 20-180 mm fish; caridean shrimp, mostly grass shrimp (*Palaemonetes pugio*), first appeared in 20-29 mm fish, peaked in 60-99 mm fish (17% by volume), and then declined in importance; blue crabs first appeared in 40-49 mm fish and became important in 70-79 mm and larger fish (5-40% by volume); penaeid shrimp first appeared in 70-79 mm fish and in ≥90 mm fish constituted 15-25% of the diet; polychaetes occurred in 30-139 mm fish but were important only in 60-79 mm fish (15% by volume).
Boothby and Avault 1971	Hopedale, LA [349 fish (250-932 mm SL), Oct 1967-Oct 1968]	Empty = 18%. Crustaceans (mostly shrimp and crabs) were the primary food items -- 75.5% by frequency and 57.5% by volume. The most important single species was blue crab -- 41.9% by frequency of occurrence and 25.9% by volume. Fish (74.1% by frequency and 35.3% by volume) and *Penaeus* spp. (48.9% by frequency and 22.6% by volume) were prominent. Occurrences of these three major groups varied little in 250-932 mm fish, although smaller fish ate smaller-sized items. Seasonal occurrences of blue crabs were 22.2% in winter, 12.5% in spring, 45.5% in summer, and 53.4% in fall. Fish were more prevalent in the diet during winter and spring while crustaceans became important during late spring. Almost 70% of stomachs contained a combination of two or more food items.
Fontenot and Rogillio 1970	Biloxi Marsh, LA [141 fish (355-508 mm), 1960 to 1968]	Empty = 21.8%. Food = blue crab (30.5%), unidentified portunids (appeared to be partially digested blue crabs) (22.6%), penaeid shrimp (9.8%), fish (10.6%), and grass shrimp (5.7%).
Gunter 1945	Copano and Aransas Bay, TX and Gulf of Mexico [237 fish (245-745 mm TL), March 1941- June 1942]	Empty = 16%. The blue crab exceeded any other species in both frequency of occurrence and volume in stomachs. Food = brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*) (40.1%), blue crab (36.7%), grass shrimp (*Palaemonetes vulgaris*) (13.1%), fish (8.4%) oyster crab (*Panopeus herbstii*) and mud crab (*Neopanope texana*) (8.4%). In 16.8% of the fish, blue crabs were the only food items.
Heffernan 1973	Cedar Bayou Pass, TX (surf zone) [109 fish, 1973]	Empty = 48.6%. Food items = fish (22%) and *Callinectes* spp. (6.4%).
Kemp 1949	Port Aransas-Rockport, TX [442 fish from, June-Aug. 1949]	Empty = 18.5%. Food = penaeid shrimp (63.3%), fish (23.7%), unidentified crabs (11.1%), lesser blue crab (5.9%), and blue crab (2.0%)
Knapp 1950	Galveston, Cedar Bayou, Rockport, and Port Aransas, TX [754 fish from, June-Aug. 1948]	Food = penaeid shrimp (63.5%), blue crab (43.0%), and fish (18.8%).
Levine 1980	Lake Pontchartrain, LA [19 fish]	Crabs (*Callinectes* spp. and *R. harrisii*) occurred in 50% of red drum stomachs.
Matlock and Garcia 1983	Texas bays [140 fish (25-305 mm SL), Nov. 1975-July 1976]	Food = arthropods (70%), miscellaneous (30%), fish (25%), annelids (20%), and molluscs (5%). Crabs were not identified by species.
Miles 1950	Port Aransas to San Antonio Bay, TX [130 fish (40-127 mm SL), Sept 1949-Aug 1950]	Empty = 5.4%. Food = unidentified shrimp (39.2%), penaeid shrimp (24.6%), fish (20.0%), *Palaemonetes* spp. (11.5%), unidentified crabs (7.6%) and portunid crabs (4.6%). Shrimp alone occurred in 51% of fish, mixed organisms in 15.4%, fish alone in 6.9%, and crabs alone in 3.8%.

APPENDIX 1. — Continued

Author	Location and Specimen Data	Study Results
Morales and Dardeau 1987	Alabama waters [200 fish (10-120 mm SL), June 1985-May 1986]	Dominant food items were crustaceans (primarily shrimp and crabs) and fish remains with overall percentages by weight of 52.8% and 28.8%, respectively. Crab remains included brachyurans and fiddler crabs; the genus *Uca* predominated. The most numerous identified crustacean was grass shrimp (*P. pugio*), which accounted for 22.3% of all food by weight. Crab remains were insignificant in fish <30 mm, in low numbers (5-10% by weight) in 30-39 mm fish, and most abundant (12-50% by weight) in 70-120 mm fish. Major food items by fish size were identified: 10-40 mm -- copepods and mysid shrimp; 40-60 mm -- caridean shrimp; and, >60 mm -- larger crustaceans and fish. Polychaetes were important in 30-49 mm fish.
Music and Pafford 1984	Glynn County, GA [94 fish (100-1100 mm TL)]	Empty = 23.3%. Fish <300 mm preferred crustaceans, with penaeid shrimp, grass shrimp, and mud crabs being most common. Fish >300 mm incorporated more fish into their diets, although crustaceans remained the staple. Blue crabs occurred in 5.6% of fish. Seasonal and areal variations in food habits were identified. Feeding activity was lowest in winter (35% empty) and highest in spring and fall (7% empty).
Odum 1971	North River, FL [47 fish (<50 mm SL)]	Fish <20 mm ingested planktonic copepods, crustacean zoea stages, and larval fish while 20-50 mm fish preyed upon mysids, amphipods, caridean shrimp, and possibly postlarval penaeid shrimp.
Overstreet and Heard 1978	Mississippi waters [107 fish (190-780mm), May 1976 - Aug 1977]	Empty = 1%. Food = other decapods (57.7%), fish (43%), penaeid shrimp (40.4%), lesser blue crab (36.5%), and blue crab (17.3%). Seasonal occurrence of *Callinectes* spp. = winter - 36.7%; spring - 70.6%; summer - 65.4%; and, fall - 35.7%. Occurrence of *Callinectes* spp. by fish size = 190-349 mm - 48.8%; 350-499 mm - 62.9%; and 500-780 mm - 53.8%. As a group *Penaeus* species occurred in 38.3% of red drum.
Pearson 1929	Texas coast [236 fish (60-680 mm FL), April 1926 - June 1927]	Food = penaeid shrimp (61.4%), fish (13.1%), and blue crab (6.8%). Mixed food (a combination of shrimp, fish, and crabs) was found in 28.4% of stomachs. Occurrence of blue crabs by fish size: 470-680 mm - 50%; 60-460 mm - 2-10%.
Peters and McMichael 1987	Tampa Bay, FL [863 fish (<8-300 mm SL)]	Empty = 30.2%; highest percentages of empty stomachs in smallest fish. Food habits by fish size were: <9 mm -- copepods and copepod nauplii; 10-75 mm -- mysid shrimp in <45 mm fish and amphipods and polychaetes in >30 mm fish; >75-100 mm fish -- food items predominating in 10-75 mm fish declined and major food groups of larger fish begin to appear; and, >100 mm -- shrimp and crabs were the major prey, with fish also important. Crabs occurred almost exclusively in fish >105 mm.
Rogillio 1975	Breton Sound marsh, LA [168 fish from the, July 1968 - June 1973]	Empty = 60%. Food = blue crab (24.4%), fish (16.6%), and penaeid shrimp (8.3%). Found blue crab in stomachs during all months. Suggested that blue crabs were the preferred prey even though penaeid shrimp were more abundant locally.
Simmons and Breuer 1962	Laguna Madre, TX	Major prey of red drum were: copepods, amphipods, and palaemonetid shrimp for <100 mm fish; small penaeid shrimp, palaemonetid shrimp, small crabs and small fish for 100-175 mm fish. Blue crabs and mud crabs (*Neopanope texana*) collectively were the dominant prey.
Soto et al. 1997	Aransas and Redfish Bay, TX [274 fish (4-20 mm SL)]	Calanoid copepods, mysid shrimp, and harpacticoid copepods were the most numerous prey consumed by red drum. Calanoid copepods were important in red drum <10 mm SL red drum while mysid shrimp were most important in 10-20 mm SL red drum. A total of 20 taxonomic groups were identified.

APPENDIX 1. — Continued

Author	Location and Specimen Data	Study Results
Steen and Laroche 1983	Mississippi Sound and Gulf of Mexico [222 fish (18-176 mm SL), Sept-Oct 1980]	Copepods and crustacean nauplii were dominant food items. Crustacean eggs and decapod post-larvae were also important.
Yokel 1966	Florida and Whitewater Bays, and Ten Thousand Islands, FL [585 fish (100-500 mm)]	Food (percent volume) = xanthid and portunid crabs - 55%; penaeid shrimp - 15%. Red drum ate proportionately more crabs with size, with fish diminishing in importance. Crabs were the most numerous prey item in winter, spring, and fall.

Brouwer, M. University of Southern Mississippi, Institute of Marine Sciences, Department of Coastal Sciences, 703 East Beach Drive, Ocean Springs, Mississippi 39564. EFFECTS OF ENVIRONMENTAL CONTAMINANTS ON THE BLUE CRAB *CALLINECTES SAPIDUS*.

A variety of organic and inorganic contaminants, including polycyclic aromatic hydrocarbons (PAHs), organohalogens, pesticides, organometallics and heavy metals, can be present in the blue crab's estuarine environment. Our knowledge of the effects of these contaminants on blue crabs decreases from the molecular, cellular, organismal to the population level. For example, much has been learned about the molecular and cellular mechanisms used by the blue crab to detoxify organic contaminants and heavy metals. In addition, the mechanisms underlying the toxicity and sublethal effects of some classes of contaminants are known. Recent studies have shown that PAHs enhance ecdysone (molt hormone)-dependent gene transcription and cell proliferation. At the organismal level PAHs inhibit growth and molting of juvenile blue crabs, suggesting that PAHs act as endocrine disrupters in the crab. Tributyltin inhibits growth of blue crab oocytes and reduces hatching success of embryos. Heavy metals such as mercury, copper and cadmium inhibit hatching of blue crab embryos and reduce survival of megalopa and juvenile crabs. Most studies on the effects of contaminants on crabs have been carried out in the laboratory under conditions that may not be environmentally relevant. Little is known about the effects of contaminants on crabs at the population level. A few studies suggest that decreases in populations of blue crabs and grass shrimp have occurred in estuarine creeks impacted by agricultural insecticide runoff.

Gannon, A.T. Department of Biology, Birmingham-Southern College, Birmingham, Alabama 35254. THE HOST DISTRIBUTION OF THE ECTOCOMMENSAL GILL BARNACLE (*OCTOLASMIS MUELLEN*) AND ITS IMPACT ON BLUE CRAB HOST MORTALITY.

The gooseneck barnacle, *Octolasmis muelleri*, is found only in the gill chamber of crabs. Blue crabs, *Callinectes sapidus*, from the Chesapeake Bay, and the Gulf Coast of Texas and Louisiana have infestation rates of about 40% of adult crabs. In a two year survey of 1294 blue crabs from the Gulf coast of Florida, we found a 38% infestation rate. The number of barnacles per crab averaged 26.0 and ranged as high as 610. The barnacles aggregate in the best ventilated site in the gill chambers of their presumed optimal host - previously infested adults. The bias in sex ratios of infested crabs that we found, coupled with the known migrations of the crabs, suggests that the barnacle is not likely to be found on crabs in low salinity waters. Our lab studies confirm that the adult barnacles do not survive in low salinity waters. The physiological effects of the gill barnacle on its crab hosts are minimal in most infestations. The infested crabs have significantly increased ventilation rates (1.8X) and have a significantly elevated heart rate (1.4X). This leads to increased cardiac output and ventilation volume, which probably compensates for the presence of the barnacles in the crabs' ventilatory stream. Even when the crabs exercise moderately for short periods, the effect of the barnacles is minimal, presumably due to the crab's well developed aerobic exercise capacity. However, infested crabs were more likely to die during the stress of emersion and high temperature exposure. Therefore, only in heavily infested crabs during exposure to environmental stresses could the barnacle pose a mortality threat to the blue crab.

Guillory V. Louisiana Department of Wildlife and Fisheries, PO Box 189, Bourg, Louisiana 70343. RELATIONSHIP BETWEEN JUVENILE RED DRUM (*SCIAENOPS OCELLATUS*) ABUNDANCE AND BLUE CRAB (*CALLINECTES SAPIDUS*) MORTALITY AND ABUNDANCE.

The red drum (*Sciaenops ocellatus*) - blue crab (*Callinectes sapidus*) predator-prey relationship has become a controversial fisheries' issue in Louisiana. Red drum are probably the dominant estuarine fish predator of blue crabs. Various red drum and blue crab abundance indices and commercial blue crab fishing effort were obtained from available fishery independent and fishery dependent data. Red drum trammel net catch per unit effort (CPUE) was significantly correlated with commercial harvest per blue crab fisherman. Blue crab annual instantaneous mortality rates were calculated with fishery independent trawl data using Hoenig's (1987) length-based mortality model. Blue crab mortality was significantly correlated with indices of red drum abundance (trammel net CPUE, recreational harvest, and age 1-3 Virtual Population Analysis estimates) and blue crab commercial fishing effort (numbers of trap licenses and traps). Blue crab mortality had a significant long-term upward trend but also displayed considerable interannual variability. Single and multiple regression predictive equations for blue crab mortality rates were generated. There was considerable supportive evidence for the negative effects of red drum predation on blue crab abundance; caution, however, was advised before attributing interannual fluctuations in blue crab populations and mortality primarily to red drum predation because of the potential of spurious relationships, the complexity of estuarine predatory-prey interactions, and the influence of other unmeasured mortality factors.

Guillory, V. and P. Prejean. Louisiana Department of Wildlife and Fisheries, PO Box 189, Bourg, Louisiana 70343.
RED DRUM PREDATION ON BLUE CRABS.

Historic and new data on predation of blue crabs (*Callinectes sapidus*) by red drum (*Sciaenops ocellatus*) and a brief review of general red drum food habits are presented. Percent frequency of occurrence of blue crabs in red drum stomachs averaged 30% in Louisiana studies and 24% in Texas studies. Approximately 1,200 red drum were collected from regular and 24-hour diel samples in the Terrebonne estuary of Louisiana. Blue crabs occurred in 31% of red drum stomachs and comprised 37% and 31% of the total diet by weight and number, respectively. The index of relative importance of blue crabs was 13.8 times greater than the next ranked species. Small juvenile blue crabs were usually consumed by red drum; almost half of blue crabs were from 10-29 mm CW. Depending on the approach used, blue crab food ration per kg of red drum was 1.86 or 1.92 /day (679 or 701 /year).

Heck, Jr., K.L. and P.M. Spitzer. Dauphin Island Sea Lab/University of South Alabama, Dauphin Island, Alabama 36528.
POST-SETTLEMENT MORTALITY OF JUVENILE BLUE CRABS IN NURSERY HABITATS: PATTERNS AND PROCESSES.

While more than a decade of observations indicates that post-larval supply is usually greater in Gulf of Mexico than Atlantic coast estuaries (often by 10x or more), young-of-the-year (YOY) abundances are usually of the same order of magnitude in both geographical locations. This has been explained by hypothesizing higher rates of post-settlement predation losses in Gulf locations, which was subsequently found to be supported by the existing experimental evidence. To reevaluate, we comprehensively review both older and recently available data sets. We still find general support for an Atlantic-Gulf gradient in increasing YOY loss rates, with losses in the Gulf sometimes approaching 100%, although the measured seasonal and annual variability in predation rates among Gulf and Atlantic locations is large enough to reach opposite conclusions, depending on the timing of the study. In addition, recent data on cannibalism rates among the earliest crab instars indicate that predation by conspecifics can constitute a large portion of the density dependent mortality experienced by YOY crabs.

Helser, T. and D. Kahn. Delaware Division of Fish and Wildlife, PO Box 330, Little Creek, Delaware 19961.
APPLICATION OF A SIZE-STRUCTURED POPULATION DYNAMICS MODEL TO ESTIMATE ABUNDANCE AND MORTALITY OF DELAWARE BAY BLUE CRAB (*CALLINECTES SAPIDUS*).

We applied a size-structured population dynamics model to estimate abundance and fishing mortality rates of Delaware Bay blue crab from 1979-1997. This model used fishery catch in numbers and research survey indices of abundance and predicts the fully-recruited stock size at the beginning of the year ($N_{o,y+1}$) from the fully-recruited stock size in the previous year ($N_{o,y}$), plus recruitment in the previous year ($R_{o,y}$), minus the catch (C_y), all discounted for natural mortality, M. Implementation of the model within a nonlinear least squares framework with incorporation of a bootstrap procedure provides full statistical evaluation of goodness of fit, validation of assumptions and uncertainty. The model provided a good statistical fit to the Delaware blue crab data; coefficients of variation (CV) of model parameter estimates on stock sizes ranged from 16% to 31%, and standardized residuals (ranging –1.0 and 1.0) revealed no significant annual patterns. In addition, scatter plots of abundance indices on estimated stock sizes were randomly distributed about a solid line confirming the model's linear catchability assumption. Exploited blue crab stock biomass ranged from 6.3 million to 28 million pounds, with an average biomass of 13.5 million pounds over the 1979-1997 period. Overall, blue crab stock biomass has trended upward over time since 1979, but has appeared to stabilize at about 18-20 million pounds since 1990. Fishing mortality rates on fully-recruited blue crabs ranged from 0.20 to 1.45, with an average of 0.83 over the 1979-1997 period. Average terminal F in recent years (1995-1997) for fully-recruited blue crabs was 0.93 with 80% confidence intervals ranging from 0.78 to 1.40.

Kahn, D. and T. Helser. Delaware Division of Fish and Wildlife, PO Box 330, Little Creek, Delaware 19961.
REPLACEMENT FISHING MORTALITY RATE FOR THE DELAWARE BAY BLUE CRAB (*CALLINECTES SAPIDUS*) STOCK.

We developed a size-structure yield and spawning stock biomass (SSB) per recruit model and coupled this with a research survey index-based stock and recruitment model to estimate the replacement fishing mortality rate for Delaware Bay blue crab. This analysis is based on the concept that under a given fishing pattern (F and recruitment to the fishery) the value of SSB/R from yield per recruit analysis can be superimposed as a line on the standard stock-recruitment plot which has a slope equal to the inverse of SSB/R and an intercept of zero. A common reference point from this analysis is F_{REP}, which defines the fishing pattern for which adequate recruitment will be generated to replace the stock biomass lost due to all sources of mortality; therefore, stock biomass and recruitment theoretically stabilize. Biological reference points calculated from the yield-per-recruit model were: $F_{0.1}$=0.6, F_{MAX}=1.0 and $F_{20\%}$=1.1, while F_{REP} calculated from SSB-per-recruit coupled with the S-R model was 1.3. The replacement fishing mortality (F_{REP}) may serve as an appropriate recruitment overfishing threshold as fishing mortality rates in excess of this value would increase the

likelihood of recruitment failure. Based on yield and SSB-per-recruit considerations, a fishing target somewhere between $F_{0.1}$=0.6 and F_{MAX}=1.0 may also be appropriate. Given the shape of the yield-per-recruit response to fishing mortality, there would be little yield to gain by fishing above F_{MAX} (=1.0), while the potential consequences of a fishing target above that level could result in depleting spawning biomass.

Lawrence, M.L., A. Woodard, T.D. Sherman, E.J. Boone, and **J.J. O'Brien**. Dept. of Biological Sciences, Univ. of South Alabama, Mobile, Alabama 36688-0002. MOLECULAR INVESTIGATIONS OF THE ASSOCIATION BETWEEN THE RHIZOCEPHALAN BARNACLE, *LOXOTHYLACUS TEXANUS* AND ITS BLUE CRAB HOST.

Loxothylacus parasitizes portunid crabs in the Gulf of Mexico. Hosts are castrated and do not attain harvestable size. Accurate estimates of fishery losses are unavailable due to a lack of information about how, when and where crabs are parasitized. We report here preliminary results from ongoing investigations that address this need. Previous work has indicated that small post-molt (metecdysial) crabs are vulnerable to infective parasite larvae. Efforts are underway to determine whether infective parasite larvae can be induced to settle upon either SDS PAGE gels or nitrocellulose that contain proteins extracted from the exoskeleton of metecdysial crabs. We have developed an assay using PCR that can detect parasite DNA in either hepatopancreas or claw muscle within a few days of infection in the laboratory. This assay is being used to determine whether there is a refuge size for host crabs, i.e., whether there is a threshold above which crabs are invulnerable to infection.

McConaugha, J.R. Department of Ocean, Earth and Atmospheric Sciences, Old Dominion University, Norfolk, Virginia 23529. BIOCHEMICAL AGE DETERMINATION IN BLUE CRABS A TOOL FOR ESTIMATING MORTALITY.

Modern fisheries management techniques such as life table analysis require accurate estimates of vital rates, growth, mortality and reproduction schedules. Estimates of these rates require precise estimates of age. Age determination of crustaceans is particularly difficult since they lack a growth record stored in a permanent hard structure. The accumulation of lipofuscin, a complex lipoprotein produced in all cells, can be used as a measure of metabolic and chronological age. Histological sections through the olfactory lobe of the brain reveal a high concentration of lipofuscin granules. Using image analysis techniques, lipofuscin is quantified by calculating the percentage covered by lipofuscin granules. Using the accumulation of lipofuscin in the olfactory lobe in the brains of laboratory reared animals, we have demonstrated a significant correlation between age and lipofuscin concentration. Calibrations of the effects of temperature and salinity on accumulation of lipofuscin have also been conducted. Based on these laboratory studies and data from field collected animals, this technique has the potential to improve our ability to estimate the age structure of blue crab population and consequently improve our estimates of both natural and fishing mortality.

Messick, G. National Ocean Service, Cooperative Oxford Laboratory, Oxford, Maryland 21654-9724. INFLUENCE OF HOST AND PHYSICAL PARAMETERS ON *HEMATODINIUM* SP. INFECTIONS IN BLUE CRABS.

Hematodinium sp. infections in blue crabs *Callinectes sapidus* are found along the Atlantic and Gulf coasts of the United States with associated mortalities reported in some areas. In Maryland coastal bays, prevalence fluctuates greatly and follows a seasonal pattern with up to 90% of crabs infected during early winter. In Maryland coastal bays, associated mortalities in adults are reported during summer months. Data collected from over 7,000 crabs from the Atlantic and Gulf coasts of the United States indicate crab size, molt, water salinity, temperature, and depth influence infection prevalence. Experiments conducted to assay salinity and temperature effects on parasite proliferation and crab mortality found infected crabs held at 9°C. Presumably uninfected crabs collected from an endemic area which were held at 22°C in 23% seawater presented infections after 14 d. The influence these host and environmental factors have on the prevalence and intensity of *Hematodinium* sp. infections in blue crabs will be discussed.

Overstreet, R.M. and J.J. O'Brien. Institute of Marine Sciences, The University of Southern Mississippi, Ocean Springs, Mississippi, 39566-7000, and Department of Biology, University of South Alabama, Mobile, Alabama, 36688-0002. *LOXOTHYLACUS TEXANUS*, BLUE CRAB MORTALITY, AND THE BLUE CRAB FISHERY.

The parasitic rhizocephalan *Loxothylacus texanus* probably has an intermittent major impact on the blue crab fishery. We hypothesize that it affects the stocks in different ways. Based on preliminary experimental evidence, the parasite can kill a recently infected individual. Apparently, only young, postmolt softshelled crabs can be parasitized by the female cyprid, and such an infection may be as or more important to overall mortality of young crabs as predation. Important for the successful individual infection is the seasonal combined availability of threshold numbers of both infective female cyprid larvae and molting, young crabs, along with relatively high salinity, relatively high temperature, and appropriate water clarity. Consequently, infections exhibit seasonal and yearly variations. Moreover, surviving infected crabs may present a much more influential role in regulating the relative abundance of commercial sized crabs than mortality of individuals. Assuming the infected crabs have adequate food and the environmental conditions are

conducive to infection by the male cyprid parasite and continued growth by the parasites, we believe these infected crabs, both with and without manifest externae, compete with non-infected individuals and thereby reduce the number of crabs available for harvest and reproduction. In the northern Gulf of Mexico, infections are restricted to *Callinectes sapidus*, and observed as manifest externae only in small, stunted, 3- to 8-cm wide, individuals. In Florida and further south, infected *C. sapidus* and other related species are typically larger. This larger size can be explained by higher water temperatures and more growth between molts. Funded in part by USDA, CSREES, Award No. 98-38808-6019 and USARC 3-61415, 3-61429, and 3-61519.

Perry, H.M., C.F. Rakocinski, K.M. Larsen, C. Trigg, and J. Warren. Gulf Coast Research Laboratory, Institute of Marine Sciences, University of Southern Mississippi, Ocean Springs, Mississippi, 39566-7000. POST-SETTLEMENT MORTALITY OF BLUE CRABS IN THE NORTHERN GULF OF MEXICO.

Blue crab megalopal settlement has been monitored at selected sites in Mississippi since 1991. While settlement is highly variable between years, numbers of megalopae recruiting to northern Gulf estuaries suggest that the fishery is not recruitment limited, but influenced by post-settlement process affecting juvenile survival. Significant coherence was found between abundances of megalopae from settlement collectors and abundances of early crabs from nearby soft sediment habitats. However, from monitoring surveys, there appears to be little relationship between initial abundance of these early crab stages and subsequent numbers of late stage juveniles; high levels of recruits do not translate into proportionally elevated numbers of late stage juveniles. Quantity and quality of essential blue crab habitat and mortality of juveniles associated with non-directed fishing activities are the important determinants of year-class strength. Predation on early crab stages is high. In addition to predation, substantial numbers of larger juvenile blue crabs are taken as bycatch in the shrimp fishery. Over 20 million pounds of sub-legal crabs are taken in trawls in Louisiana and 40 to 100 million blue crabs are captured by the Texas shrimp fleet. Reduction of non-directed fishing mortality and protection of essential habitat must be an integral part of any management strategy to maintain current harvest levels of blue crabs in the Gulf of Mexico.

Stickle, W.B., Jr. Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, 70808. EFFECTS OF ENVIRONMENTAL FACTOR GRADIENTS ON JUVENILE *CALLINECTES SAPIDUS*.

Larval *Callinectes sapidus* immigrate to coastal estuaries where juveniles grow to reproductive adults. Environmental factor gradients affect their tolerance and physiological adaptations. Juvenile blue crabs are very intolerant of hypoxia. Their hypoxia tolerance varied inversely with salinity at 30°C but directly with salinity at 20°C. Juvenile blue crabs tolerated a 100% -25%-100% diurnal pattern of percent saturation of dissolved oxygen without mortality over 28 days exposure. Juvenile blue crabs are extremely tolerant of salinity gradients exhibiting a 21 day LC_{50} range of 0-56.0%S for a brackish water population and 0.5-66.5%S for a hypersaline population. Juvenile crabs are extremely tolerant of 28 days exposure to cadmium; LC_{50} values were an order of magnitude lower in crabs maintained at 2.5%S than at 25%S. Juvenile blue crabs exhibited a 21 day LC_{50} of 3927ppb South Louisiana crude oil and maintained a positive energy budget at aromatic hydrogen concentrations up to 2504ppb. Juvenile blue crabs feeding on TBT contaminated grass shrimp catabolized the TBT thereby increasing their tolerance of TBT. Juvenile *Callinectes sapidus* are particularly sensitive to exposure to hypoxic water. We lack an understanding of the effects of seasonal change in water temperature on the tolerance, physiology and growth of juvenile blue crabs.

About the Artist – After living in Washington, D.C. and New Orleans, Susan Carranza settled in Ocean Springs, MS where she continues to work as a professional artist. She does photography at the Gulf Coast Research Laboratory, College of Marine Sciences and teaches art at Spiral Studio. Susan works in a variety of mediums including papermaking and bookmaking.

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