# Incorporating Toxic Disturbance Effects into a Population Model of a Crustacean Fishery

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#### ABSTRACT

Population models have been used to describe and predict changes in population structures through time. In fishery applications these models (utilizing such factors as growth, recruitment, fishing mortality and natural mortality) are used to manage and regulate fishing activities. As our waters are increasingly impacted by both point and non-point source pollution theparameter of "natural mortality" must be examined in greater detail. Toxicological studies based on both commercially important species and proxy species have shown a variety of physiological effects that have not been addressed in practical applications of modeling. Stage specific mortality, altered rates of development and reduced growth have been reported. These effects were documented in a xanthid crab exposed to sub-lethal concentrations of the mosquito larvicide, methoprene, and have been incorporated into a crustacean fishery model. Impacts on survival and fecundity produce a much different picture for long term population growth that needs to be considered in the application of population models. Multi-species tropical fisheries will tend to magnify the effects demonstrated on prey species through complex tropho-dynamic linkages. Design and placement of marine protected areas or attempts to rehabilitate degraded habitats must consider the effects of xenobiotics in the aquatic habitat and provide for restrictions of terrestrial inputs as part of their overall management strategy.

KEY WORDS: Crustacea, Eurypanopeus depressus, fisheries, methoprene, modeling, toxicity

#### INTRODUCTION

A large volume of toxicity data exists that is of considerable importance and should be of considerable interest to ecologists, fishery scientists and natural resource managers. Unfortunately much of the information is in a format that is not readily accessible for those who are not practicing organic- or bio-chemists. Often only the cursory information is disseminated. As the impacts of these exogenous products continue to impact our coastal systems, it will become increasingly important for effective cross-over studies to interpret these findings with respect to anticipated population effects for a larger, more diverse audience.

The lethal and sub-lethal effects should be incorporated into population models, if the models are to accurately reflect observed effects on important fishery species, particularly those of coastal crustaceans.

Crustaceans are represented in estuaries, coastal wetlands, and seagrass areas by species of both commercial and ecological importance. Commercial shrimp and crab species comprise a majority, up to 97% by weight, of the seafood harvest in the Gulf of Mexico (Duke and Kruczynski (and sources therein), 1990; McHugh, 1977). All these harvested species are estuarine dependent, at least during a portion of their life cycles (Boesch and Turner, 1984; Weinstein, 1979).

Throughout the Caribbean, crustacea, such as the spiny lobster (Panulirus argus), represent an extremely valuable portion of the fishery catch (Richards and Bohnsack, 1990). As arthropods, crustaceans are closely related both phylogenetically and physiologically to the target pests of insecticidal treatments (Williams and Duke, 1979). As species that are tied to estuarine/coastal areas, these invertebrates are exposed to point and non-point source pollutants at critical times during their development. These exposures create the potential for ecological disruptions.

Ecologically, both commercial and non-commercial crustaceans play critical roles in estuarine and other wetland ecosystems (Epifanio and Dittel, 1984; McDonald, 1977). They participate in the planktonic and detrital food webs with diverse feeding habits. Estuarine crustaceans provide the critical link between these more basic energy resources and organisms feeding at higher trophic levels (Closs and Lake, 1994; Mauchline, 1980; Welsh, 1975). Substantial reductions in their populations would adversely impact trophic couplings within the estuarine or coastal environment (Markle and Grant, 1970; Smith et al., 1984).

Many of the commercially important crustaceans have been difficult to maintain in the laboratory for extensive evaluations of toxic responses so alternate species have been used as proxies to represent the Crustacea in toxicological screenings: This paper reports on the effects of the pesticide methoprene on Eurypanopeus depressus (Smith), a xanthid mud crab likely to undergo incidental exposure in an estuarine setting during surface water run-off or pesticide spraying events. Laboratory exposure parameters were chosen to mimic natural exposure conditions and bracket chemical concentrations recommended for field application. Ontogenetic variations in physiological and biochemical responses were documented throughout the larval development. The impacts of the pesticide on individual organisms has been extrapolated to some likely consequences at higher levels of organization. To relate the effects to fishery or ecological science, this paper compares the sub-lethal responses of E. depressus to other published studies documenting toxic effects to commercially and ecologically important species. It, further, suggests ecological effects that

are likely to show up in fisheries as direct toxic effects and through disruption of trophic dynamics. These effects are significant enough that they should be considered when placing marine protected areas or setting goals for habitat restoration in impacted coastal zones.

#### METHODS AND MATERIALS

Primary study

Eurypanopeus depressus (Smith) is one of the more numerous xanthid crabs found as juveniles in estuarine plankton (Walton and Williams, 1971) and as adults inhabiting oyster reefs (McDermott, 1060; McDonald, 1977). As a full time resident of estuaries, it is subject to coastal pollutants throughout its entire life cycle. To obtain larva with known backgrounds of chemical exposures, a breeding stock was maintained in a flow-through sea water system in the Environmental Research Laboratory (U.S. Environmental Protection Agency's Sabine Island facility) in Gulf Breeze, Florida. Randomly selected E. depressus larvae were exposed to the single isomer (S)-methoprene (isopropyl [2E, 4E, 7S]-methoxy-3, 7, 11-trimethyl-2, 4-dodecadienoate), in a dynamic, flow-through system in nominal concentrations of 64, 32, 16, 8, 4, and 2 μg/l and compared against control (0 μg/l) exposures. Methoprene, a highly specific pesticide, is an analogue of a naturally occurring juvenile hormone. It is classed as an insect growth regulator. Complete details of the pesticide exposures were reported by Hill (1995).

Stage-specific survival and intermolt duration were monitored for each of the four zoeal stages (ZI - ZIV) through the metamorphosis of the megalopae (Meg) to the postlarval first crab (C-1) stage. Subsamples of each stage and all surviving crabs were weighed and dried to determine ash weights and elemental compositions of carbon, hydrogen, and nitrogen (CHN). CHN analyses were performed on a Perkin Elmer PE 2400 CHN Elemental Analyzer. Using published conversion factors/equations, the elemental contents were converted to "equivalent contents" as carbohydrates, proteins, lipids and energy (joules) (Donnelly et al., 1993; Salonen et al., 1976). These comparisons provided <indications of bioenergetic alterations attributable to the exposures to the juvenile hormone analog.

Results were analyzed with the Statistical Analysis System (SAS Institute, Inc., 1989) on the VAX 4000-500 using the General Linear Models procedure. Analysis of variance (ANOVA) was used to test for significant differences at  $\alpha = 0.05$ . Duncan's multiple-range test was used to test for significant differences between treatment means. Dunnett's test was used to compare dose-response values against control treatments (Zar, 1984).

# Comparative species examinations

The current literature identifies a variety of toxicity studies that have examined both commercially important species and those that are either ecologically important or proxy species. Test procedures and results that compared toxic responses between a commercially important species and the more commonly used test animals were evaluated to investigate the validity of using the primary test results, above, to infer general population responses.

## Model investigation.

A review of the more common population or fishery models investigated the use of natural mortality as a model variable or parameter. Population growth models frequently use mortality as their primary indicator of future population directions. More complex models, such as virtual population analysis, use either "assumed constant" or size-specific mortality values and often gloss over the importance of natural mortality since it is difficult to verify. The confounding effects of lethal and sub-lethal responses can be well illustrated using an exponential decay model, so it is presented here to demonstrate model effects.

## RESULTS AND DISCUSSION

## Toxicity studies

Various measurements have been used to assess the impact of pesticides on target and non-target species, as reviewed by Giesy and Graney (1989). Effects can range from gross effects on the individual or the population to more subtle impacts at the cellular-biochemical level (Capuzzo et al. 1988). Acute toxicity tests have been used to investigate total mortality rates and lethal dosage levels (Christiansen et al., 1978, Tyler-Schroeder, 1979; Wilson and Costlow, 1987), and continue to provide guidelines for maximum concentrations of various toxicants allowed into the environment (Capuzzo et al., 1988). Targeting of particularly sensitive stages such as crustacean larval stages, in either acute or chronic tests, helps to reveal minimum chemical concentrations that might impact an organism or population (Giesy and Graney, 1989).

These primary test results were derived from chronic exposure tests that examined the effects of sub-lethal concentrations of the juvenile hormone mimic (S)-methoprene on the non-target estuarine species, Eurypanopeus depressus. Larval development was monitored from egg hatching through metamorphosis to first-crab (C-1) at concentrations of 0, 2, 4, 8, 16, 32, and 64  $\mu$ g/l. Mortality occurred most frequently during ecdysis. Exposure to 32 and 64  $\mu$ g/l greatly increased mean larval mortality (from hatch to C-1), 63% (p = 0.06, n.s.) and

75% (p < 0.0187), respectively. Stage-specific mortality, resulting from exposures to 32 and 64  $\mu$ g/l methoprene, showed greatest impacts in the early zoeal stages, Z<sup>1</sup> to Z<sup>III</sup>. At 64  $\mu$ g/l, an secondary drop in survival rates, during the metamorphic molt from Meg to C-1, reflected increased sensitivity to higher levels of methoprene during metamorphosis (Hill, 1995). Similar results in natural estuarine population would result in altered abundances of all zoeal stages, megalopae and crabs.

Toxic effects on growth rates and growth efficiencies have routinely been quantified by recording changes in body weights, respiration rates and ammonia excretion rates (Capuzzo and Lancaster, 1982; Laughlin and Neff, 1981; McKenney, 1985; McKenney and Celestial, 1993). E. depressus larvae exposed to methoprene demonstrated dose-dependent effects that were measured as changes in mean dry weight. The effects were most evident in the Meg.

Exposure to 2  $\mu$ g/l caused a reduction in mean dry weight of 28.3%; the greatest decrease was after exposure to 64  $\mu$ g/l which showed a 35.2% mean reduction in dry weights (p < 0.002) compared to the control. In the post-metamorphic first crabs 64  $\mu$ g/l again produced the most significant reductions in mean growth (31.5%; p < 0.008). Smaller sized individuals are typically subject to increased mortality due to predation and display decreased reproductive potentials, e.g., spawning frequency, fecundity, hatching success, and  $F_1$  generation mating (Tyler-Schroeder, 1979).

These variations in growth and scope for growth can be traced to biochemical and cellular abnormalities in metabolic demands and energetic utilizations (Amsler and George, 1984b). The analysis of elemental (CHN) composition can be used to construct energy budgets (Mootz and Epifanio, 1974; Levine and Sulkin, 1979). Mathematical conversion of the elemental contents to energy, protein, carbohydrates and proteins (Donnelly et al., 1993; Salonen et al., 1974) provided indications of bioenergetic alterations attributable to the exposures to the juvenile hormone analog.

This study showed altered patterns of carbohydrate, lipid and protein utilization and storage (Hill, 1995). As a result of those biochemical alterations and the reductions in growth, energy content (joules/individual) of all larval stages was reduced. Megalopa showed significant reductions in energy contentresulting from all methoprene concentrations. The most severe reduction in mean energy content, to 71% of the control animals, resulted from the 32 µg/l exposure. The effect persisted into the juvenile crab stage with energy reduced from 54 - 74% (Hill, 1995). For the population this can mean reduced fecundity and hatching success, due to depleted energy reserves; and, ecologically this translates into less energy transfer per feeding foray for predators of these species.

# Comparative species studies

Previous investigations have addressed the effects of hormonal pollutants on a variety of small crustacean species (crabs, shrimp, zooplankton, and lobsters) that are ecologically important in estuaries: Rhithropanopeus harrisii (Celestial and McKenney, 1994; Christiansen et al., 1977a; 1977b; Forward and Costlow, 1978), Palaemonetes pugio (McKenney and Celestial, 1993; McKenney and Matthews, 1990b; Touart, 1989; Wilson and Costlow, 1986), Mysidopsis bahia (McKenney and Matthews, 1990a; Nimmo et al., 1980), and copepods (Bircher and Ruber, 1988). Unfortunately, other than Homarus americanus larvae (Hertz and Chang, 1986), little has been reported for commercial species that can be used to directly compare the results of the primary study.

In earlier test with other types of pesticides there have been some comparative studies that can be used to compare interspecific effects. In acute studies with Mirex, Bookhout et al. (1972) reported comparable effects for the xanthid crabs, Rhithropanopeus harissi, and Menippe mercenaria and the portunid crab, Callinectes sapidus. Concentrations of 0.01 and 0.1 µg/l were sub-lethal but caused delays in development either by extending intermolt duration or by producing extra zoeal stages. Concentration of 1.0 and 10.0 µg/l proved lethal to all three species with greatest sensitivity found in the earlier zoeal stages, and in the megalopae. Both M. mercenaria and C. sapidus support sizable fisheries.

The organophosphate, Malathion, has shown variable results in acute studies comparing *R. harrisii* with *C. sapidus*. *C. sapidus* was 3 - 4 times more tolerant of Malathion than *R. harrisii* before lethal effects were observed. Sub-lethal effects however, were similar between the two species (Bookhout and Monroe, 1977). Similarities of responses support the hypothesis that trends can be deduced from comparative studies although the exact magnitudes of effect may vary. The reported effects on impacted populations may logically lead to ecological comparisons.

## Ecological concerns.

Many of the effects that have been demonstrated on crustaceans from both lethal and sub-lethal pesticide exposures result in net reduction of the population size and/or fitness and can be assumed to produce alterations in relative abundances within the community. Reduced abundances of these crustacean species may be assumed to produce three rather obvious ecological consequences:

- i) reduced interspecific competition resulting in altered species diversities;
- ii) reduced nutrient cycling (the shredding and processing) of detrital nutrients and.
- iii) reduced availability as a prey item requiring changes in feeding behaviors or reducing feeding efficiencies in the predators that feed on these crustaceans.

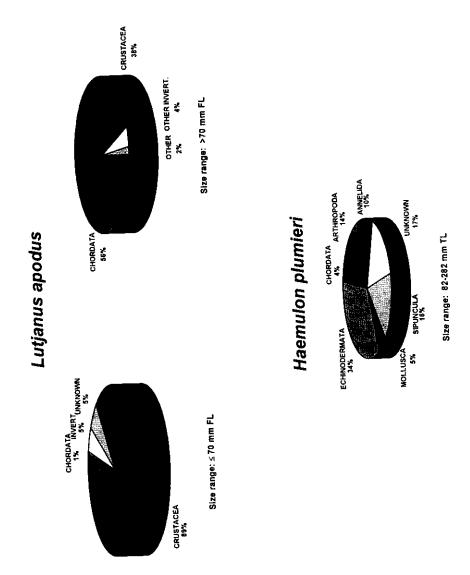
According to the studies referenced above, these effects would be manifest in all exposed populations of crustaceans, including crabs, lobsters, zooplankton, and shrimp. Trophic effects have been documented in laboratory studies using contaminated food items that multiply effects through bioaccumulation as they are passed up the food chain (Bookout and Costlow, 1970)

Crustacea are a major direct source of food for many of the important commercial species of the Gulf and Caribbean region. Many of these species (e.g., snappers and grunts) that prey on crustaceans have been in steady decline over the last decade or so (Appeldoorn and Meyers, 1993). Dennis (1992) analyzed the diet of several haemulid species from Puerto Rico (Figure 1). The species of greatest commercial interest, *Haemulon plumieri* (size range: 82 - 282 mm TL), utilizes crustacean species as 14% of their diet; at smaller sizes the bulk of their diet consists of zooplankton (personal observation). Small *Lutjanus apodus* (70mm FL) use crustaceans for 89% of their diet; this percentage drops to 38% for fish larger than 70 mm FL (Figure 1) (Rooker, 1991). Significant reductions in these prey populations or shifts in abundances could be contributing to the decline of these reef associated species, as well as other guilds of benthic feeders or zooplanktivores.

## Modeling effects.

Fisheries models can include those as simple as Growth Models, such as von Bertalanfy and Gompertz (Sparre et al. 1989). The obvious effects on growth as a result of toxicosis will have serious effects, altering rates of growth (K) and asymptotic length ( $L_{\infty}$ ). Increases in rates of predation and reductions in fecundity as a result of smaller size at age are well known for crustaceans and fish.

Models of mortality for highly fecund fast growing species, such as shrimp, have frequently been characterized using exponential decay curves where population size is dependent on the interaction between  $N_{(t)}$ , population at a previous time and the instantaneous mortality rates (Ricker 1975). Z, the total mortality rate is composed of F, the instantaneous mortality rate due to fishing efforts, and M, the instantaneous rate of mortality due to all other causes (predation, disease, emigration, parasitism, etc.) An increase of annual mortality rate of 58% as seen in E. depressus (Hill, 1995) is equivalent to a drop in Z of 0.55. Using the equation  $N_t = N_0 \ e^{-Zt}$ , this amounts to a reduction of 40% in the expected population after only one (1) time interval. After three (3) time intervals this difference has been magnified to a 78% decrease in the population (Figure 2). To further examine the consequences on fishery production, the historical catch data from the Cuban shrimp fishery are plotted in Figure 3 (Baisre, 1993). Cuban coastal waters are subject to run-off and riverine inputs,



**Figure 1.** Dietary compositions for *L. apodus* (Rooker, 1991) and *H. plumieri* (Dennis, 1992).

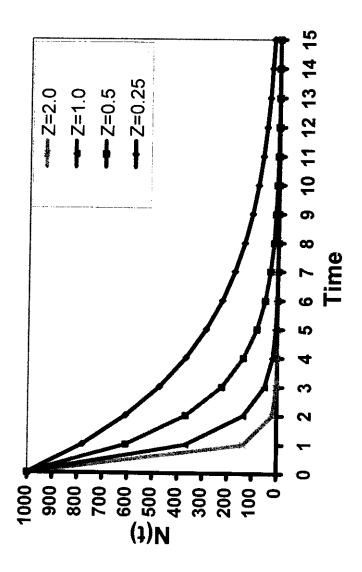


Figure 2. Exponential population decline for various values of Z, total mortality.

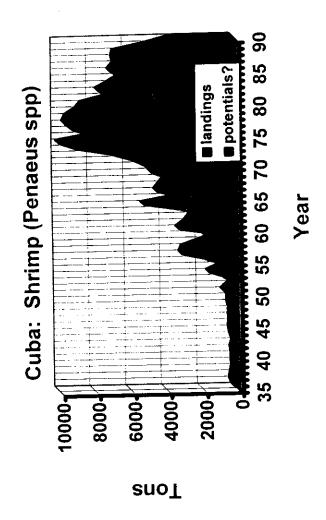


Figure 3. Speculation of the potential yields from the Cuban shrimp fishery, under the assumption that populations are currently depressed because of the influence of pesticide exposure. (Baisre 1993.)

likely to contain pesticide residues from agricultural practices. These exogenous inputs are likely to affect wetland species such as the penaeid shrimp. The secondary curve in Figure 3 assumes that impacts were similar to those reported above and speculatively predicts the potential yields that may have been available if the stocks were not impacted. Stocks that were not depressed through toxicosis would also be expected to be more resilient to fishing pressure.

## CONCLUSIONS

Numerous studies have shown lethal and sub-lethal concentrations of xenobiotics to affect a wide variety of organismic responses, beyond those cited here. Particularly important is alteration of an organism's physiological ability to osmoregulate or to manage environmental stresses such as the cycling of temperature and/or salinity (Christiansen et al., 1977a; 1977b; Laughlin and Neff, 1981; McKenney and Hamaker, 1984; Shirley and McKenney, 1987; Voyer and Modica, 1990). The ability to tolerate regular changes of temperature and salinity is an essential aspect of an estuarine animal's life (McKenney, 1986).

Chemically induced alterations in behaviors, such as phototaxic response (Wilson et al., 1985) and swimming speed (Forward and Costlow, 1976; 1978), have been documented, suggesting increased rates of predation and/or the loss of animals from suitable habitats by countering the naturally-selected mechanisms for predator avoidance and for estuarine retention. As with direct reduction in population survival, growth and fitness, these induced behavioral changes can be assumed to reduce recruitment and therefore abundances of local populations (Farr, 1977; Sulkin, 1984). These "unnatural" sources of mortality can considerably affect population dynamics that should be addressed in models of populations or fisheries.

Vetter (1988) reviewed the techniques for assigning M for various populations: (1) assume that M is relative to some population (life history) parameter K,  $L_{\infty}$ , or r (Gunderson, 1980); (2) analyze catch data; (3) estimate deaths from predation. From just this preliminary analysis of some of the toxic responses that can be impacting important crustacean fishery species, it is likely that our estimates of M are lacking in their consideration of exogenous inputs into our coastal systems. These concerns must be addressed in fishery management, whether it is in stock assessments or design of marine protected areas (MPA). Stock characteristics from one geographical region may not be reflective of life history traits in another if one of the stocks is impacted from pesticide run-off or over-spray. Similarly an MPA placed in an estuary or marine catchment basin that is subject to agricultural run-off is not likely to produce the same results as one located in a more isolated habitat. Capuzzo and Leavitt (1988) have demonstrated that energy resources, in a crab and a shellfish,

marine catchment basin that is subject to agricultural run-off is not likely to produce the same results as one located in a more isolated habitat. Capuzzo and Leavitt (1988) have demonstrated that energy resources, in a crab and a shellfish, will vary as a direct result of pollutant gradients. Attention to coastal details and maintenance or restoration of coastal wetlands will provide natural barriers and enhance conditions for protection of coastal fishery resources.

## LITERATURE CITED

- Amsler, M.O., and R.Y. George. 1984a. The effects of temperature on the oxygen consumption and developmental rate of the embryos of Callinectes sapidus Rathburn. J. Exp. Mar. Biol. Ecol. 82:221 229.
- Amsler, M.O., and R.Y. George. 1984b. Seasonal variation in the biochemical composition of the embryos of Callinectes sapidus Rathburn. J. Crustacean Biol. 4(4):546 553.
- Appeldoorn, R.S., and S. Meyers. 1993. Puerto Rico and Hispañiola. Pages
   99 158 In: Marine fishery resources of the Antilles: Lesser Antilles,
   Puerto Rico and Hispaniola, Jamaica, Cuba. FAO Fisheries Technical
   Paper. No. 326. Rome, FAO.
- Baisre, J., 1993. Cuba. Pages 181 235 in: Marine fishery resources of the
   Antilles: Lesser Antilles, Puerto Rico and Hispaniola, Jamaica, Cuba.
   FAO Fisheries Technical Paper. No. 326. Rome, FAO.
- Bircher, L., and E. Ruber. 1988. Toxicity of methoprene to all stages of the salt marsh copepod, *Apocyclops spartinus* (Cyclopoida). *J. Amer. Mosq. Control Assoc.* 4(4):520 523.
- Boesch, D.F., and R.E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7:460 468.
- Bookhout, C.G., and J.D. Costlow, Jr. 1970. Nutritional effects of Artemia from different locations on larval evelopment of crabs. Helgolander wiss. Meeresunters 20:435 442.
- Bookhout, C.G., and R. Monroe. 1977. Effects of Malathion on the development of crabs. Pages 3 19 in: F.J. Vernberg et al., (eds.) Physiological Responses of Marine Biota to Pollutants. Academic Press, New York.
- Bookhout, C.G., A.J. Wilson, Jr., T.W. Duke, and J.I. Lowe. 1972. Effects of mirex on the larval development of two crabs. Water, Air, Soil Pollut.
  1: 165 180.
- Capuzzo, J.M., and B.A. Lancaster. 1982. Physiological effects of petroleum hydrocarbons on larval lobsters (*Homarus americanus*): Hydrocarbon accumulation and interference with lipid metabolism. Pages 477 501 in: W.B. Vernberg, A. Calabrese, F.P. Thurberg, and F.J. Vernberg,

- (eds.), Physiological Mechanisms of Marine Pollution Toxicity. Academic Press, New York.
- Capuzzo, J.M., and D.F. Leavitt. 1988. Lipid composition of the digestive glands of *Mytilus edulis* and *Carcinus maenas* in response to pollutant gradients. *Mar. Ecol. Prog. Ser.* 46:139 145.
- Capuzzo, J.M., M.N. Moore and J. Widdows. 1988. Effects of toxic chemicals in the marine environment: Predictions of impacts from laboratory studies. Aq. Tox. 11:303 311.
- Celestial, D.M., and C.L. McKenney, Jr. 1994. The influence of an insect growth regulator on the larval development of the mud crab *Rhithropanopeus harrisii. Env. Poll.* 85:169 173.
- Christiansen, M.E., J.D. Costlow, Jr. and R.J. Monroe. 1977a. Effects of the juvenile hormone mimic ZR-512 (Altozar®) on larval development of the mud-crab *Rhithropanopeus harrisii* at various cyclic temperatures. *Mar. Biol.* 39:281 288.
- Christiansen, M.E., J.D. Costlow, Jr. and R.J. Monroe. 1977b. Effects of the juvenile hormone mimic ZR-515 (Altosid®) on larval development of the mud-crab *Rhithropanopeus harrisii* in various salinities and cyclic temperatures. *Mar. Biol.* 39:269 279.
- Christiansen, M.E., J.D. Costlow, Jr. and R.J. Monroe. 1978. Effects of the insect growth regulator Dimilin (TH 6040) on larval development of two estuarine crabs. *Mar. Biol.* 39:269 279.
- Closs, G.P., and P.S. Lake. 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecol. Monog.* **64**(1):1 21.
- Dennis, G.D., III. 1992. Resource Utilization by Members of a Guild of Benthic Feed Reef Fish. PhD. Dissertation. Univ. Of Puerto Rico. Mayagüez, PR. 224 pp.
- Donnelly, J., D.G. Stickney, and J.J. Torres. 1993. Proximate and elemental eomposition and energy content of mesopelagic crustaceans from the eastern Gulf of Mexico. *Mar. Biol.* 115:469 480.
- Duke, T.W., and W.L. Kruczynski. 1990. A summary of the report: Status and trends of emergent and submerged vegetated habitats of the Gulf of Mexico, USA, Proc. First Biennial Meeting on the Environmental and Economic Status of the Gulf of Mexico (Gulf of Mexico Program) Gulf of Mexico Program Office, U.S. Dept. of Interior.
- Epifanio, C.E., and A.I. Dittel. 1984. Seasonal abundance of brachyuran crab larvae in a tropical estuary: Gulf of Nicoya, Costa Rica, Central America. *Estuaries* 7:501 505.
- Farr, J.A. 1977. Impairment of antipredator behavior in *Palaemonetes pugio* by exposure to sublethal doses of parathion. *Trans. Amer. Fish. Soc.*

- 106:287 290.
- Forward, R.B., Jr. and J.D. Costlow, Jr. 1976. Crustacean larval behavior as an indicator of sublethal effects of an insect juvenile hormone mimic. Pages 279 289 in: M. Wiley (ed.) Estuarine Processes, vol. 1. Academic Press, Inc., New York.
- Forward, R.B., Jr. and J.D. Costlow Jr. 1978. Sublethal effects of insect growth regulators upon crab larval behavior. Water, Air, and Soil Poll. 9:227 238.
- Giesy, J.P., and R.L. Graney. 1989. Recent developments in and intercomparisons of acute and chronic bioassays and bioindicators.

  Hydrobiologia 188/189:21 60.
- Gunderson, D.R. 1980. Using r-K selection theory to predict natural mortality. Can. J. Fish. Aquat. Sci. 37(12):2266 - 2271.
  - Hertz, W.A., and E.S. Chang. 1986. Juvenile hormone effects on metamorphosis of lobster larvae. *Intl. J. Inv. Rep. Dev.* 10: 71 77.
  - Hill, R.L. 1995. Changes in larval development and elemental composition
    (C, H, N) of an estuarine xanthid crab, Eurypanopeus depressus
    (Decapoda: Brachyura) in response to sub-lethal concentrations of the juvenile growth hormone mimic, Methoprene. MS thesis, University of West Florida, Pensacola. 62 p.
  - Laughlin, R.B., Jr. and J.M. Neff. 1981. Ontogeny of respiratory and growth responses of larval mud crabs *Rhithropanopeus harrisii* exposed to different temperatures, salinities, and naphthalene concentrations. *Mar. Ecol. Prog. Ser.* 5:319 332.
- Levine, D.M. and S.D. Sulkin. 1979. Partitioning and utilization of energy during the larval development of the xanthid crab, *Rhithropanopeus harrisii* (Gould). *J. Exp. Mar. Biol.* 40:247 257.
- Markle, D.F., and G.C. Grant. 1970. The summer food of young-of -the-year striped bass in three Virginia rivers. *Chesapeake Sci.* 11:50 54.
- Mauchline, J. 1980. The biology of mysids. Adv. Mar. Biol. 18:1 369.
- McDermott, J.J. 1960. The predation of oysters and barnacles by crabs of the family Xanthidae. *Proc. Pa. Acad. Sci.* 34:199 211.
- McDonald, H.J.J. 1977. The comparative intertidal ecology and niche relations of the sympatric mud crabs Panopeus herbstii (Milne-Edwards) and Eurypanopeus depressus (Smith) at North Inlet, South Carolina, U.S.A. (Decapoda: Brachyura: Xanthidae). Ph.D. Dissertation. University of South Carolina, Columbia.
- McHugh, J.L. 1977. Estuarine fisheries: are they doomed? Pages 15-27 In: M. L. Wiley (ed.) Estuarine processes, Uses, Stress and Adaptation to the Estuary, Vol. 1. Academic Press, New York.

- McKenney, C.L., Jr. 1985. Associations between physiological alterations and population changes in an estuarine mysid during chronic exposure to a pesticide. Marine Pollution and Physiology: Recent Advances. 397 418.
- McKenney, C.L., Jr. 1986. Critical responses of populations of crustacea to toxicants. EPA Environmental Research Brief: EPA/600/M-86/004.
- McKenney, C.L., Jr. and D.M. Celestial. 1993. Variations in larval growth and metabolism of an estuarine shrimp *Palaemonetes pugio* during toxicosis by an insect growth regulator. *Comp. Biochem. Physiol.* 105C(2):239 245.
- McKenney, C.L., Jr and D.B. Hamaker. 1984. Effects of fenvalerate on larval development of *Palaemonetes pugio* (Holthuis) and on larval metabolism during osmotic stress. Aq. Tox. 5:343 355.
- McKenney, C.L., Jr. and E. Matthews. 1990a. Alterations in energy metabolism of an estuarine mysid (Mysidopsis bahia) as indicators of stress from chronic pesticide exposure. Mar. Environ. Res. 30:1 19.
- McKenney, C.L., Jr. and E. Matthews. 1990b. Influence of an insect growth regulator on the larval development of an estuarine shrimp. *Env. Poll.* 64: 1 10.
- Mootz, C.A., and C.E. Epifanio. 1974. An energy budget for *Menippe mercenaria* larvae fed Artemia nauplii. *Biol. Bull.* 146:44 55.
- Nimmo, D.R., T.L. Hamaker, J.C. Moore, and R.A. Wood. 1980. Acute and Chronic Effects of Dimilin on Survival and Reproduction of *Mysidopsis bahia*. In: J.G. Eaton, P.R. Parrish, and A.C. Hendricks (eds.) *Aquatic Toxiclogy, ASTM STP 707*, American Society for Testing and Materials. 366 376.
- Richards, W.J., and J.A. Bohnsack. 1990. The Caribbean Sea: A large marine ecosystem in crisis. Pages 44 53 in: K. Sherman, L.M. Alexander, and B.D. Gold (eds.) Large Marine Ecosystems: Patterns, Processes, and Yields. American Association for the Advancement of Science. Washington, D.C.
- Ricker, W.E. 1975. Computation and Interpretation of Biological Statistics of Fish Populations. *Bull.Fish.Res.Board Can.* 191: 382 p.
- Rooker, J.R. 1991. Ontogenetic patterns in the feeding ecology of the Schoolmaster Snapper (*Lutjanus apodus*). MS thesis. Univ. of Puerto Rico, Mayagüez. 63 p.
- Salonen, K., J. Sarvala, I. Hakala, and M. Viljanen. 1976. The relation of energy and organic carbon in aquatic invertebrates. *Lim. Ocean* 21:724 - 730.
- Shirley, M.A., and C.L. McKenney, Jr. 1987. Influence of Lindane on survival and osmoregulatory/metabolic responses of the larvae and adults of the

- estuarine crab, Eurypanopeus depressus. Pages 275 297 In: W.B. Vernberg, A. Calabrese, F.P. Thurberg and F.J. Verberg (eds.) Pollution Physiology of Estuarine Organisms. University of South Carolina Press, Columbia, South Carolina.
- Smith, S.M., J.G. Hoff, S.P. O'Neil and M.P. Weinstein. 1984. Community and trophic organization of nekton utilizing shallow marsh habitats, York River, Virginia. Fish. Bull. 82:455 467.
- Sparre, P., E. Ursin, and S.C. Venema. 1989. Introduction to tropical fish stock assessment. Part 1. Manual. FAO Fisheries Technical Paper. No. 306.1. Rome, FAO. 337 p.
- Sulkin, S.D. 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Mar. Ecol. Prog. Ser.* 15:181 205.
- Touart, L.W., Jr. 1989. Effects of selected insect growth regulators on ecdysteroid titers in the grass shrimp, Palaemonetes pugio. Ph.D. Dissertation. George Mason University, Fairfax, VA.
- Tyler-Schroeder, D.B. 1979. Use of the Grass Shrimp (*Palaemonetes pugio*) in a life-cycle toxicity test. Pages 159-170 in: L.L. Marking and R.A. Kimerle (eds.) *Aquatic Toxicology ASTM STP 667*, American Society for Testing and Materials. Philadelphia, PA.
- Vetter, E.F. 1987. Estimation of natural mortality in fish stocks: A review. Fish. Bull. 86(1):25 43.
- Voyer, R.A., and G. Modica. 1990. Influence of salinity and temperature on acute toxicity of cadmium to *Mysidopsis bahia* Molenock. *Arch. Environ. Contam. Toxicol.* 19: 124 131.
- Walton, E., and A. B. Williams. 1971. Reef populations of mud crabs and snapping shrimp. Pages 205 238 In: E. J. Kuenzler and A. J. Chestnut (eds.) Structure and Functioning of Estuarine Ecosystems Exposed to Treated Sewage, Ann. Rep. for 1970-1971, Sea Grant No. GH 103, Proj. UNC-10. University of North Carolina, Chapel Hill.
- Weinstein, M.P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. Bull. 77(2):339 357.
- Welsh, B. L. 1975. The role of grass shrimp, *Palaemonetes pugio*, in a tidal marsh ecosystem. *Ecology* **56:** 513 -530.
- Williams, A.B., and T.W. Duke. 1979. Crabs (Arthropoda: Crustacea: Decapoda: Brachyura). Pages 171 233 in: C.W. Hart, Jr. and S. L. H. Fuller (eds.) Pollution Ecology of Estuarine Invertebrates. Academic Press, Inc. New York.
- Wilson, J.E.H., and J.D. Costlow. 1986. Comparative toxicity of two dimilin formulations to the grass shrimp, *Palaemonetes pugio*. Bull. Environ.

- Contam. Toxicol. 36:858 865.
- Wilson, J.E.H., and J.D. Costlow. 1987. Acute toxicity of diflubenzeron (DFB) to various life stages of the grass shrimp, *Palaemonetes pugio*. Water, Air, and Soil Poll.. 33:411 417.
- Wilson, J.E., R.B. Forward, Jr. and J.D. Costlow. 1985. Effects of embryonic exposure to sublethal concentrations of Dimilin on the photobehavior of grass shrimp larvae. *Marine Pollution and Physiology: Recent Advances*. 377 396.
- Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inc. Englewood Cliffs, NJ.