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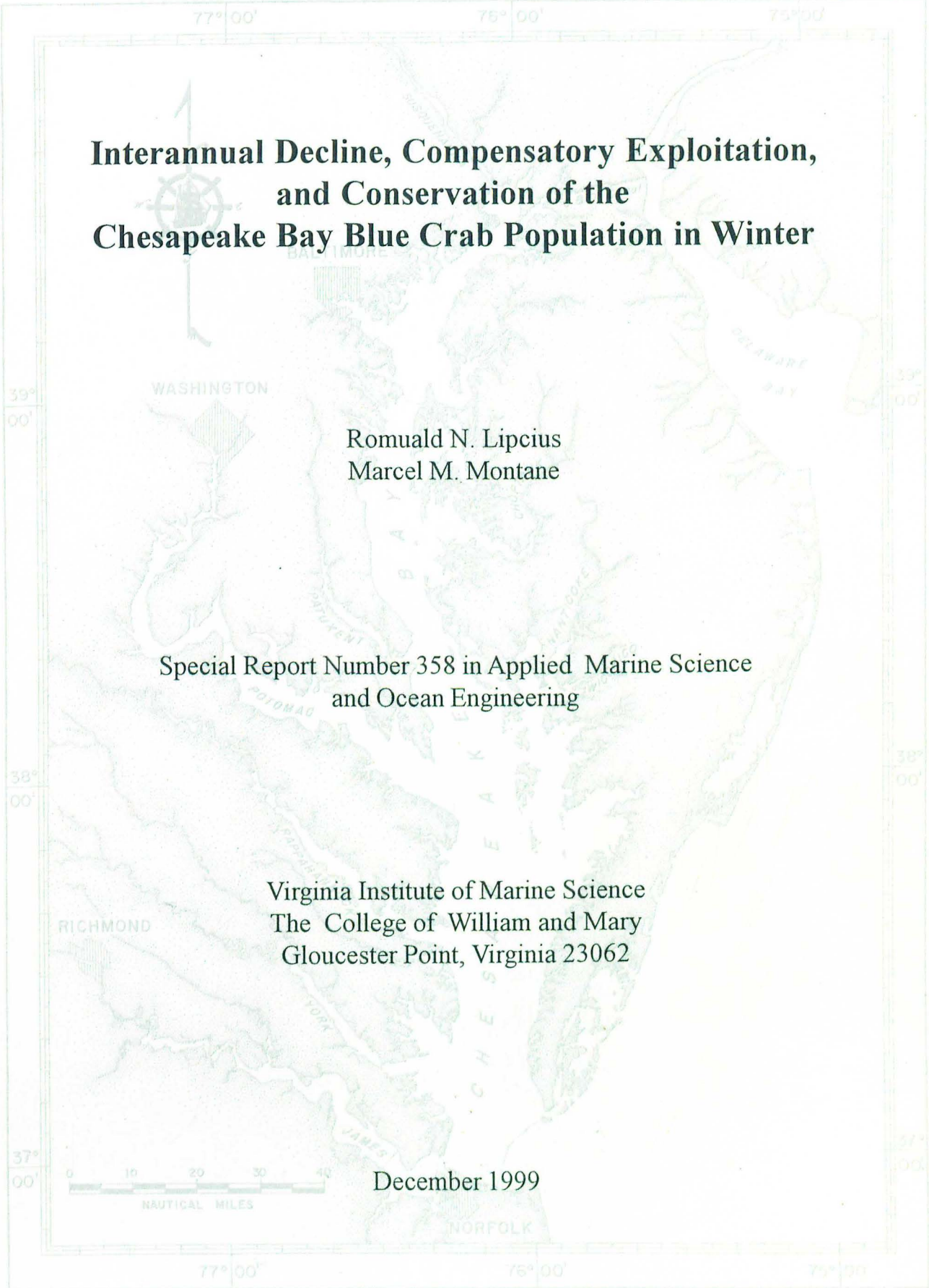
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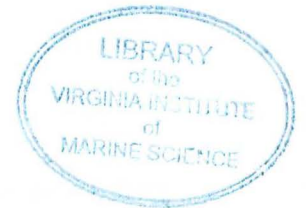
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**Interannual Decline, Compensatory Exploitation, and Conservation of the  
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**Abstract.**-Conservation of exploited species requires knowledge of the relationships between exploitation rate or fishing mortality and population abundance. This investigation with the Chesapeake Bay blue crab population in winter (i) quantified interannual population variation, (ii) measured exploitation and fishing mortality rates due to the winter dredge fishery, (iii) related the rates to population abundance and fishing mortality due to all fisheries, and (iv) examined characteristics of the winter dredge fishery with regard to conservation and sustainable exploitation. Key findings included: (i) the baywide population declined substantially from 1991 to 1999 on the order of 70 %; (ii) exploitation rates by the winter dredge fishery were proportional to crab abundance in lower Chesapeake Bay, as well as to the percentage of the crab population residing there, a pattern that typifies compensatory exploitation; (iii) the fraction of the population exploited by the winter dredge fishery was nearly always less than the proportion of crabs susceptible to the fishery; (iv) fishing mortality rates due to the winter dredge fishery did not vary systematically from 1991-1999, in contrast to rising fishing mortality rates due to all blue crab fisheries ( $F$ ), which increased concurrently with the decline in baywide crab abundance; and, (v) there were either declines or no trends in annual estimates of winter dredge fishery removal of crabs, licenses and landings. The collective evidence is consistent with a hypothesis of compensatory exploitation by the winter dredge fishery, and indicates that the decline in the baywide crab population is not due to that fishery. The characteristics of the winter dredge fishery are compatible with effective conservation and sustainable exploitation of the blue crab in Chesapeake Bay. In contrast, exploitation rates by the remaining fisheries in Chesapeake Bay appear to be depensatory; these fisheries should be scrutinized to prevent overexploitation and population collapse of the blue crab.



## Introduction

Conservation of exploited species requires an intimate understanding of the relationships between levels of exploitation (i.e., exploitation rate [ $u$ ] or fishing mortality [ $F$ ]), fishing effort [ $f$ ], catchability of the exploitable segment of the population [ $q$ ], and population size ( $N$ ). In particular, effective utilization of effort controls (e.g., area closures or gear restrictions) to prevent overexploitation requires that  $F$  is proportional to  $f$  in the relationship:

$$F = q \cdot f$$

where the catchability coefficient  $q$  (fraction of fish removed per unit of  $f$ ) is independent of  $N$  (Gulland, 1964; Garrod, 1964; Crecco and Savoy, 1985). If this assumption is invalid, then  $N$  and  $F$  may be over- or under-estimated, depending on the functional relationship between  $q$  and  $N$ , which potentially leads to recruitment overfishing, population collapse or inefficient exploitation (Crecco and Savoy, 1985; Crecco and Overholtz, 1990).

The dynamics between fishers and their exploited species are often comparable to those characterizing predator-prey interactions such that their exploitation patterns depend significantly on  $N$ , thereby causing density-dependent [= compensatory (Neave, 1953)] or inversely density-dependent [= depensatory (Neave, 1953)] relationships between  $q$  or  $F$  and  $N$ . Whereas Van Winkle et al. (1978) modeled  $F$  as a compensatory function of  $N$ , Paloheimo and Dickie (1964) theorized that  $q$ , and therefore  $F$  when  $f$  is constant, should vary inversely with  $N$  due to nonrandom searching behavior of fishers coupled with strong schooling behavior by fish. In most empirical cases, a depensatory relationship between  $q$  (or  $f$  in some cases) and  $N$  has characterized exploitation patterns, such as in Pacific sardine *Sardinops sagax caerulea* (MacCall, 1976), Norwegian herring *Clupea harengus* (Dragesund et al., 1980), North Sea cod *Gadus morhua* (Houghton and Flatman, 1980), Lake Whitefish *Coregonus clupeaformis* (Henderson et

al., 1983), American shad *Alosa sapidissima* (Crecco and Savoy, 1985), and Georges Bank haddock *Melanogrammus aeglefinus* (Crecco and Overholtz, 1990). Such a depensatory relationship between  $F$  and  $N$  may be the general pattern for exploited species (Condrey, 1984; Winters and Wheeler, 1985; Crecco and Overholtz, 1990). Where exploitation is depensatory, a population may be driven to extinction due to the lack of a population refuge at low population densities (Hassell, 1978).

In contrast, there are few cases of a compensatory relationship between  $q$  or  $F$  and  $N$ . Exploitation of Lake Whitefish is characterized by a depensatory relationship between  $q$  and  $N$ , yet  $F$  is a compensatory function of  $N$  due to a substantial increase of  $f$  with  $N$  (Henderson et al., 1983). In Pacific salmon (*Oncorhynchus* spp.),  $q$  and  $F$  are compensatory functions of local population size, likely due to intraspecific facilitation of feeding by salmon at high local densities (Shardlow, 1993). Furthermore, prey switching by fishers from sparse to abundant species appears to promote a compensatory relationship between  $F$  and  $N$  in scallops *Notovola meridionalis* (Olsen, 1955). When exploitation is compensatory, a fished population may persist at low levels even under relatively heavy exploitation (Hilborn and Walters, 1992), thereby reducing the likelihood of population collapse or localized extinction.

In this investigation, we present empirical evidence that  $F$  and  $u$  for the winter dredge fishery ( $F_{WD}$  and  $u_{WD}$ ) vary positively with  $N$  for the blue crab, *Callinectes sapidus*, population in Chesapeake Bay, despite an inverse relationship between  $F$  and  $N$  over all fisheries combined (Miller and Houde, 1998). The findings are consistent with the hypothesis that  $q_{WD}$  or  $f_{WD}$  are compensatory functions of  $N$ , thereby promoting the conservation and sustainable exploitation of the blue crab by the winter dredge fishery. Our specific objectives with the Chesapeake Bay blue crab population were to: (i) quantify interannual variation of the population in winter; (ii)



measure  $u_{WD}$  and  $F_{WD}$  from population abundances before and after the winter dredge fishery; (iii) relate the annual estimates of  $u_{WD}$  and  $F_{WD}$  to  $N$  and  $F$ , and (iv) relate characteristics of the winter dredge fishery to conservation and interannual variation of the blue crab population.

### **Relevant aspects of the blue crab life history**

After a terminal maturity molt (Mangum and Towle, 1977) and mating in the oligohaline and mesohaline portions of Chesapeake Bay, adult females migrate to the lower Chesapeake Bay to spawn in the summer, or overwinter and then spawn the following spring and summer (Van Engel, 1958; Tagatz, 1968). Crabs overwinter by burying in sand and becoming inactive (Mangum and Towle, 1977). During winter, crabs in the lower Chesapeake Bay are mainly (85-98%) adult females (Van Engel, 1962; Schaffner and Diaz, 1988). When temperatures rise above 10° C in spring, crabs emerge from the sediment and resume normal activity, among the first of which is spawning (Mangum and Towle, 1977), which peaks between June and September (Jones et al., 1990).

### **Winter dredge fishery for the blue crab in Chesapeake Bay**

Blue crabs are relatively inactive and not vulnerable to traps when water temperature falls below 11-13 °C (Stehlik et al., 1998), and instead overwinter in bottom sediments from December to March (Schaffner and Diaz, 1988). Consequently, the only means of exploiting crabs during winter is by dredge. Winter crab dredging began in Chesapeake Bay before 1903 (as early as 1900) to support the hard-crab canning industry, and licenses to dredge were first issued during the winter of 1902-1903 (Bowdoin et al., 1903 as reported by Van Engel, 1999). The dredge fishery season runs from 1 December to 31 March, which began in 1936 (Van Engel, 1999).

The impact of the winter dredge fishery on the Chesapeake Bay blue crab population is poorly understood. The dredge fishery is concentrated in the lower Chesapeake Bay and chiefly targets adult females which have mated and migrated towards the Chesapeake Bay mouth (Schaffner and Diaz, 1988; Van Engel, 1962). The dredge fishery has long been criticized as a key factor in the decline of the blue crab population in Chesapeake Bay due to its exploitation of adult females (Van Engel, 1999), despite any convincing evidence. However, on average more than 80 % of Chesapeake Bay blue crab landings are derived from other fisheries, such as the soft- and hard-crab trap fisheries, which also impact the potential spawning stock (i.e., maturing and adult females). In the past decade, winter dredge landings have accounted for 5.5-23.9 % of the Virginia harvest and 4.1-11.1 % of the baywide harvest<sup>1</sup> (O'Reilly).

## Methods

### Population abundance

We sample the blue crab population in winter by a baywide winter dredge survey from 1991-1999<sup>2</sup> using a stratified random design, which divides Chesapeake Bay into three geographic strata (Fig. 1). The advantages of sampling in winter over summer are: (i) blue crabs are not exploited in most areas of Chesapeake Bay during the winter, except in the lower Chesapeake Bay by the winter dredge fishery, and (ii) blue crabs bury in the sediments during the winter, thereby sharply restricting their movement, which justifies the assumption of negligible

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<sup>1</sup> R. O'Reilly, Virginia Marine Resources Commission, Pers. Comm.

<sup>2</sup> 1991 refers to the 1990-1991 winter season, 1992 to the 1991-1992 winter season, etc.



immigration and emigration in the estimation of mortality.

Each year, 1500 sites were selected randomly, and apportioned by the area of each stratum. The Upper Bay Stratum includes the tributaries, creeks, and upper mainstem of Chesapeake Bay, which are characterized by oligohaline to mesohaline salinities, except near the mouths of tributaries in lower Chesapeake Bay. The Middle Bay Stratum encompasses the middle mainstem of Chesapeake Bay, whereas the Lower Bay Stratum circumscribes the major area of operation of the dredge fishery (Fig. 1). All sampling locations were deeper than 1.5 m, which limited accurate measurement of population abundance to the 1+ year classes<sup>3</sup>, since 0+ juvenile crabs are concentrated in shallower waters.

Survey vessels and sampling personnel were contracted through the Virginia Institute of Marine Science (VIMS), the Chesapeake Biological Laboratory (CBL) and the Maryland Department of Natural Resources (MDNR). The sampling gears were identical standard "Virginia crab dredges" (width 1.83 m) lined with hexagonal mesh (12.7 mm). The gear exhibited "knife-edged" selectivity for crabs greater than or equal to 15 mm carapace width (cw), although crabs smaller than 10 mm cw were routinely captured. At each sampling site, the vessel sampled for 1 min at a constant speed of ~ 3 nautical miles h<sup>-1</sup>. LORAN or GPS coordinates were recorded at tow start and end points. Each crab was measured (mm cw), and the sex, maturity, and overall condition recorded. At each sampling site depth, salinity, water temperature, and dissolved oxygen were recorded and a sediment sample was collected.

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<sup>3</sup> Year classes were designated as 0+ for crabs < 60 mm cw (Fig. 2), and as 1+ for all other crabs > 60 mm cw. The 1+ year class designation therefore includes crabs 1 year of age and older.

The stratified random survey was implemented following standard methods (Cochran, 1977). Stratum surface areas ( $A_h$ ) were determined from navigational charts by counting the number of 0.1-min squares contained in each stratum. The area covered by each tow was calculated by computing the least linear distance traversed and multiplying this quantity by the dredge width. The total possible stratum samples,  $N_h$ , is computed by dividing the stratum area by the stratum average tow area,  $T_h$ :

$$N_h = A_h / T_h$$

A given stratum weight,  $W_h$ , is then determined as

$$W_h = N_h / N_T$$

where  $N_T$  is the total possible sample size for all strata. Efficiency experiments were conducted annually to provide catchability coefficients used in calculations of absolute abundance (Lipcius and Montane, 1997).

### **Exploitation and fishing mortality rates**

Whereas the Upper Bay and Middle Bay strata were sampled only once from December through March, the Lower Bay was sampled intensively (approximately 50 tows  $\text{mon}^{-1}$ ) immediately prior to the start of the dredge fishery in December through its duration (i.e., late November through March) to estimate  $F_{WD}$  (=  $F$  due to the dredge fishery) and  $u_{WD}$  (=  $u$  due to the dredge fishery). Data from November through February was used, and not March, because crabs become active in March, thereby invalidating the assumption of negligible immigration and emigration required to measure mortality. Little exploitation occurs in March, so that the estimates of  $u_{WD}$  and  $F_{WD}$  are not impacted significantly by this exception (Lipcius and Montane, 1997). Estimates of  $u_{WD}$  and  $F_{WD}$  were calculated as follows:



1. The February and November baywide abundances provided measures of  $N_0$  (November abundance, prior to exploitation by the dredge fishery) and  $N_1$  (February abundance, after exploitation by the dredge fishery). Baywide abundance in November ( $N_0$ ) was calculated as:

$$N_0 = N_{UB} + N_{MB} + N_{LB,Nov}$$

where  $N_{UB}$  and  $N_{MB}$  are abundances in the Upper Bay and Middle Bay strata, and  $N_{LB,Nov}$  is abundance in the Lower Bay stratum in November. Baywide abundance in February ( $N_1$ ) was calculated similarly, but with  $N_{LB,Feb}$  (= abundance in the Lower Bay stratum in February) replacing  $N_{LB,Nov}$  and  $N_1$  replacing  $N_0$ .

2. Exploitation rates were calculated as:

$$u_{WD} = (N_0 - N_1) / N_0,$$

which were used to calculate  $s_{WD}$ , the survival rate of the population in winter as:

$$s_{WD} = 1 - u_{WD}.$$

3. Fishing mortality due to the dredge fishery,  $F_{WD}$ , was calculated from the relationship:

$$N_1 = N_0 \cdot e^{-F_{WD}}$$

such that:

$$s = \frac{N_1}{N_0} = e^{-F_{WD}}$$

and

$$F_{WD} = \ln(s).$$

Wintertime natural mortality was negligible in most years (< 1 % in the Lower Bay). In the only year (1996) when mortality rates were substantial in the Lower Bay (10.5 %),  $u_{WD}$  and  $F_{WD}$  were adjusted to eliminate the bias in  $u_{WD}$  and  $F_{WD}$  due to the relatively high natural mortality. In our analyses, we made the same assumptions as those of Index Removal Methods

(Hoenig et al., 1998): (i) population is closed except for removals; (ii) all crabs have the same probability of capture and this probability does not vary from survey to survey; and (iii) sampling is with replacement, or the fraction taken in the survey is negligible.

## **Results**

### **Size structure**

Males and females were distributed heterogeneously throughout Chesapeake Bay in winter (Fig. 2). Most adult females concentrated in the Lower Bay, with additional substantial densities in the Middle Bay. Relatively few adult females inhabited the Upper Bay and tributaries in winter. In contrast, males and juvenile females were most abundant in the Upper Bay, Middle Bay and tributaries. Hence, the winter dredge fishery had the greatest impact on adult and maturing females in the Lower Bay.

### **Interannual variation in population abundance**

The baywide blue crab population declined sharply and significantly from 1991 to 1999, both in November before the onset of the winter dredge fishery (Fig. 3A, C, E) and in February towards the terminus of the dredge fishery (Fig. 3B, D, F). Reductions in abundance were substantial and similar for all 1+ crabs, for 1+ females, and for 1+ males, and ranged on the order of 70 %.

In contrast, abundance of crabs in the Lower Bay during November did not display similar reductions over time (Fig. 4A, C, E). After dredge fishery exploitation, however, all 1+ crabs (Fig. 4B) and 1+ females (Fig. 4D) also decreased significantly from 1991-1999, whereas 1+ male abundance remained virtually unchanged (Fig. 4E, F). The pattern in 1+ females and all



1+ crabs was likely attributable to compensatory exploitation, whereas that for males was due to the relative scarcity of exploitable 1+ males in the Lower Bay fishing grounds (Fig. 2).

### **Exploitation rates in relation to crab abundance**

Exploitation rates of 1+ females by the winter dredge fishery ranged from 15.4-60.8 % (Fig. 5), and were proportional to the abundance of 1+ females in the Lower Bay (Fig. 5B), as well as to the percentage of baywide 1+ females residing in the Lower Bay (Fig. 5A). This pattern is typical of that observed under compensatory exploitation where exploitation rates are positively related to population abundance. Moreover, exploitation rates of 1+ females by the winter dredge fishery were always lower than the fraction of 1+ females residing in the Lower Bay (compare dotted line with observed values in Fig. 5A). Exploitation rates of 1+ females were not correlated with baywide abundance of 1+ females (Fig. 5C), probably due to the low exploitation rates of 1+ females in the Middle Bay, Upper Bay and tributaries.

Exploitation rates of all 1+ crabs by the winter dredge fishery ranged from 10.2-47.0 % (Fig. 6), and were significantly correlated with the fraction of baywide 1+ crabs residing in the Lower Bay (Fig. 6A), and nearly but not significantly so with the abundance of 1+ females in the Lower Bay (Fig. 6B). As above, this pattern is consistent with the hypothesis of compensatory exploitation by the winter dredge fishery. Similarly to that for 1+ females, the fraction of 1+ crabs exploited by the winter dredge fishery was always less than the fraction of 1+ crabs residing in the Lower Bay (Fig. 6A). Exploitation rates of 1+ crabs did not correlate with baywide abundance of 1+ crabs (Fig. 6C), as with 1+ females.

### **Fishing mortality rates**

Fishing mortality rates due to the winter dredge fishery did not exhibit a significant temporal trend from 1991-1999, both for 1+ females (Fig. 7A) and for all 1+ crabs (Fig. 7B). In contrast, fishing mortality rates due to all blue crab fisheries (Miller and Houde, 1998) increased significantly and substantially from 1991-1999 (Fig. 7C, D), in conjunction with the sharp reductions in baywide crab abundance (Fig. 3).

### **$F_{WD}$ in relation to $F$ and crab abundance in the Lower Bay**

Whether using VIMS or Calvert Cliffs data to estimate  $F$  (Miller and Houde, 1998), the fraction of  $F$  due to the winter dredge fishery ( $F_{WD}$ ) was in all but one case less than the fraction of the crab population available to the winter dredge fishery in the Lower Bay (Fig. 8). Moreover, if we adopt a recommended  $F$  of 1.0 for sustainable exploitation (Miller and Houde, 1998), and compare the proportion that  $F_{WD}$  comprises of  $F = 1$  with the fraction of the baywide population that inhabits the Lower Bay and is susceptible to the winter dredge fishery, then the former has exceeded the latter only once from 1991-1999 (Fig. 9). Hence, the winter dredge fishery is exploiting the crab population at levels equal to or less than the relative abundance of the crab population available to the winter dredge fishery for exploitation.

### **Winter dredge fishery removal, landings and licenses**

In contrast to the increases in fishing mortality rates for all Chesapeake Bay fisheries (Fig. 7C, D) and licenses in the hard-crab and soft-crab fisheries<sup>1</sup> (O'Reilly) from 1991-1999, there was either no trend or a slight decline in the estimates of fishery removal of crabs by our winter dredge survey (Fig. 10A), as well as in landings (Fig. 10B) and licenses (Fig. 10C) of the winter dredge fishery. Thus, the various characteristics of the winter dredge fishery are inconsistent



with the hypothesis that the winter dredge fishery is driving the reductions in the crab population from 1991-1999.



### **Winter dredge survey as a predictor of landings in the winter dredge fishery**

Our winter dredge survey estimates of 1+ crab removal by the winter dredge fishery correlated positively and significantly with landings in the fishery (Fig. 11). Hence, the winter dredge survey tracks interannual variation in crab exploitation by the winter dredge fishery.

### **Discussion**

The major findings of this investigation were that (i) the baywide blue crab population (1+ males and females) declined significantly from 1991 to 1999, with reductions generally ranging on the order of 70 %; (ii) exploitation rates of 1+ crabs and 1+ females by the winter dredge fishery ranged from 10.2-47.0 % and 15.4-60.8 % , respectively, and were proportional to crab abundance in the Lower Bay; (iii) the pattern in exploitation as a function of annual population abundance is typical of that associated with compensatory exploitation; (iv) the fraction of 1+ females or crabs exploited by the winter dredge fishery was always lower than the percentage of crabs residing in the Lower Bay and susceptible to the fishery; (v) fishing mortality rates due to the winter dredge fishery did not vary systematically from 1991-1999, in contrast to fishing mortality rates due to all blue crab fisheries, which increased concurrently with the decline in baywide crab abundance; (vi) the fraction of  $F$  due to the winter dredge fishery was nearly always lower than the proportion of the crab population available to the fishery; (vii) there were either declines or no trends in annual estimates of fishery removal of crabs, in licenses, and in

landings; and (viii) winter dredge survey estimates of fishery depletion of crabs correlated significantly with crab landings. Hence, the various characteristics of the winter dredge fishery are inconsistent with the hypothesis that the winter dredge fishery mediated the reductions in the crab population from 1991-1999. The collective evidence is consistent with a hypothesis of compensatory exploitation in the winter dredge fishery, and indicates that the decline in the baywide crab population is not due to that fishery. Rather, the characteristics of the fishery are compatible with effective conservation and sustainable exploitation of the blue crab in Chesapeake Bay. Furthermore, the remaining fisheries (e.g., trap and soft-crab fisheries) should be scrutinized for their role in the population decline.

#### **Interannual decline in population abundance**

The baywide decline of the blue crab in Chesapeake Bay from 1991-1999 was apparent in both males and females of the 1+ segment of the population. Reductions in abundance were substantial and similar for all 1+ crabs, whether female or male, generally averaging near 70 %. For instance, the 1991 estimate of baywide abundance for 1+ crabs was about 350 million crabs, and only approximately 100 million crabs in 1999. This pattern is comparable to the approximate 70 % reduction of spawning stock biomass in Chesapeake Bay from 1991-1999, but which was derived from an independent trawl survey within the Lower Bay spawning grounds during the reproductive period<sup>4</sup> (Lipcius and Stockhausen). Moreover, fishing mortality rates have concurrently increased, often at extremely high levels indicative of overexploitation (Miller and Houde, 1998). The lowering of the population is not necessarily a progressive reduction, but

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<sup>4</sup> R. Lipcius and W. Stockhausen, Unpublished manuscript.



may reflect a shift from a higher population level in 1990-1993 to a significantly lower level from 1994-1999<sup>4</sup> (Lipcius and Stockhausen). Although crab abundance is highly variable (Lipcius and Van Engel, 1990; Abbe and Stagg, 1996; Rugolo et al., 1998), the extended decrease of both the baywide population and the spawning stock from 1991-1999, in concert with the increased exploitation rates by all fisheries, is troubling and symptomatic of fisheries that may be on the verge of collapse (Hilborn and Walters, 1992). Hence, scrutiny of exploitation rates by all fisheries for the blue crab in Chesapeake Bay is warranted and necessary to assure the long-term viability of the population.

#### **Exploitation rates relative to crab abundance: compensatory exploitation?**

Exploitation rates of 1+ females and all 1+ crabs by the winter dredge fishery were proportional to crab abundance in the Lower Bay, as well as to the fraction of the baywide population residing in the Lower Bay. This pattern is typical of that observed under compensatory exploitation where exploitation rates (or fishing mortality rates) are proportional to population abundance (Van Winkle et al., 1978; Shardlow, 1993). If the observed covariation in exploitation rates and population abundance reflects compensatory mortality, then this is one of only a few demonstrated cases where fishery exploitation is compensatory (Henderson et al., 1983; Shardlow, 1993), and the first for an exploited marine crustacean. Moreover, it represents only the second demonstration where both compensatory and depensatory exploitation operate in a single exploited population. In the prior example with Lake Whitefish, there was a depensatory relationship between  $q$  and  $N$ , yet  $F$  was a compensatory function of  $N$  due to a substantial increase of  $f$  with  $N$  (Henderson et al., 1983). The reverse situation appears to characterize the blue crab fisheries such that exploitation is compensatory for a single fishery—the winter dredge

fishery—yet depensatory over all fisheries. The demonstrations of compensatory exploitation contrast the general rule for fisheries where fishery mortality is depensatory (see theoretical treatment and reviews by Paloheimo and Dickie, 1964; Condrey, 1984; Winters and Wheeler, 1985; Crecco and Savoy, 1985; Crecco and Overholtz, 1990).

The impact of compensatory (= density-dependent) exploitation upon population dynamics of exploited species has only been examined in a limited fashion (Van Winkle et al., 1978; Hilborn and Walters, 1992; Shardlow, 1993), probably due to the rarity of its documentation (Winters and Wheeler, 1985; Crecco and Overholtz, 1990). In contrast, density-dependent predation and its consequences to population dynamics have been examined in depth theoretically (e.g., Hassell, 1978) and empirically for various invertebrates (e.g., Lipcius and Hines, 1986; Eggleston, 1990; Eggleston et al., 1992; Hines et al., 1997; Moksnes et al., 1997; Barbeau and Scheibling, 1998) and fish (e.g., MacPherson and Gordo, 1994; Forrester, 1995; Rangeley and Kraner, 1998; Hixon, 1997; Steele, 1997, 1998). In general, the major benefit of compensatory mortality for a population exposed to intense predation or exploitation is a refuge from predation or exploitation at low population densities (Hassell, 1978; Hilborn and Walters, 1992). Hence, a heavily exploited population can persist indefinitely at relatively low levels and thereby prevent local extinction, barring catastrophic mortality. In contrast, depensatory (= inversely density-dependent) exploitation exacts a proportionally higher mortality at low population densities, which increases the likelihood of local extinction and population collapse (Hassell, 1978; Hilborn and Walters, 1992).

The potential mechanisms underlying the positive covariation between exploitation rates by the winter dredge fishery and crab abundance are diverse, and are most likely related to either catchability of crabs or effort by crabbers. First, the individual crabber may reduce search rates



or leave dredging altogether when crab encounter rates (and catchability) are so low that the benefits of exploitation outweigh the costs (i.e., poor economic return from the meager landings). Second, the crabber may switch to a more profitable prey (e.g., the oyster in past decades) at low crab densities, even when crabbing might still be profitable. Hence, effort on crabs is reduced at relatively low crab densities. Third, crabs may change their spatial distribution and be sparse when population densities are low, such that catchability is low whereby successful detection by the crabbers is effectively precluded. In contrast, if crabs were to remain aggregated and detectable at low population sizes, then catchability in specific locations would be high and crabbing would remain profitable, if only for a shorter time. Such is the case with many vertebrate fisheries, whereby schooling by fish in combination with nonrandom, effective search by fishers leads to depensatory mortality at low population densities (MacCall, 1976; Dragesund et al., 1980; Crecco and Savoy, 1985), and potentially to population collapse or local extinction. The preceding mechanisms of positive covariation between exploitation rates and crab abundance are feasible for the crabber-crab interaction, and if active, would be indicative of compensatory exploitation since they involve the relationship between catchability of the prey (crab) and behavior or effort by the predator (crabber).

An alternative mechanism for the covariation between exploitation rates and crab abundance involves circumstances whereby the pattern is unrelated to crab density, and therefore not representative of compensatory exploitation. For instance, the number of licenses in the winter dredge fishery has been somewhat lowered from 1991-1999 due to the imposition of a limited entry system in this decade. If effort in the fishery is proportional to the number of licenses, then the reduced exploitation rates at low population sizes might simply be due to concurrent decreases in licenses and the corresponding effort. However, the number of licenses

in the winter dredge fishery (i) did not decrease significantly from 1991-1999, and (ii) was not correlated with exploitation rate. Instead, the covariation between fishing mortality or exploitation rates and population abundance was apparently due to the relationship between exploitation rates and crab abundance within the area of operation of the winter dredge fishery (Lower Bay). Hence, a mechanism related to regulation of the number of licenses was not likely to be a major cause of the variation in exploitation rates by the winter dredge fishery, and we therefore conclude that the positive association between exploitation rates and crab density reflects compensatory exploitation.

#### **Fishing mortality rates, population decline, and conservation of the blue crab population**

Fishing mortality rates due to the winter dredge fishery did not exhibit a significant temporal trend from 1991-1999, in contrast to fishing mortality rates due to all blue crab fisheries (Miller and Houde, 1998) which increased significantly and substantially from 1991-1999 in conjunction with the sharp reductions in baywide crab abundance. Moreover, the fraction of  $F$  due to the winter dredge fishery ( $F_{WD}$ ) was nearly always lower than the fraction of the crab population available to the winter dredge fishery in the Lower Bay. The winter dredge fishery is evidently exploiting the crab population at levels equal to or less than the relative abundance of the crab population available to the winter dredge fishery for exploitation. Whereas exploitation and fishing mortality rates due to the winter dredge fishery were apparently compensatory, those due to the remaining fisheries were symptomatic of depensatory mortality (i.e., inverse association between  $F$  and crab abundance), which if unchecked would ultimately lead to population collapse (Hilborn and Walters, 1992). Hence, we conclude that this pattern justifies intense scrutiny of the remaining fisheries regarding their role in the baywide population decline.



## Acknowledgments

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## Figure Legends

**Figure 1.** Representative sampling stations by the winter dredge survey in Chesapeake Bay for the 1990-1991 winter season. The sampling strata include the (i) Upper Bay mainstem and all tributaries, (ii) Middle Bay mainstem, and (iii) Lower Bay mainstem. The Lower Bay stratum was sampled monthly from November, before the onset of the winter dredge fishery, through the fishery's closing in March; approximately 50 stations were sampled each month. Strata are divided by the solid horizontal lines slicing Chesapeake Bay. Typically 1500 stations were sampled annually.

**Figure 2.** Representative size structure of the blue crab population in the 1990-1991 winter season. Analyses were conducted with the 1+ segment of the population, which includes crabs 1 year of age and older.

**Figure 3.** Interannual abundance of the 1+ segment of the blue crab population throughout Chesapeake Bay in winter. Differences in baywide abundance between November and February were due to reductions in crab abundance in the Lower Bay stratum, which was the only stratum sampled through the dredge fishery season. Regression degrees of freedom = 1, 7.

**Figure 4.** Interannual abundance of the 1+ segment of the blue crab population within the Lower Bay stratum in winter. Differences in abundance between November and February in the Lower Bay were due to reductions in crab abundance within the stratum by the dredge fishery and 10.5 % natural mortality in 1996. Regression degrees of freedom = 1, 7.

**Figure 5.** Annual exploitation rate of 1+ females as a function of (A) % Lower Bay abundance (i.e., the fraction of all 1+ females residing in the Lower Bay), (B) Lower Bay abundance of 1+ females, and (C) baywide abundance of 1+ females. The dotted line in (A) indicates equality

between exploitation rate and % Lower Bay abundance. Power functions were fit to the relationships, as straight lines were characterized by non-random residuals and poor fits to the data. Regression degrees of freedom = 1, 7.

**Figure 6.** Annual exploitation rate of all 1+ crabs as a function of (A) % Lower Bay abundance (i.e., the fraction of all 1+ crabs residing in the Lower Bay), (B) Lower Bay abundance of 1+ crabs, and (C) baywide abundance of 1+ crabs. The dotted line in (A) indicates equality between exploitation rate and % Lower Bay abundance. Power functions were fit to the relationships, as straight lines were characterized by non-random residuals and poor fits to the data. Regression degrees of freedom = 1, 7.

**Figure 7.** Annual fishing mortality rates due to the winter dredge fishery for (A) 1+ females and (B) 1+ crabs, and due to all crab fisheries in Chesapeake Bay, calculated from (C) Lower Bay VIMS trawl survey data and (D) Middle Bay Calvert Cliffs crab trap data. Rates for (C and D) extracted from Miller and Houde (1998). Regression degrees of freedom = 1, 7 for (A) and (B) and 1, 5 for (C) and (D).

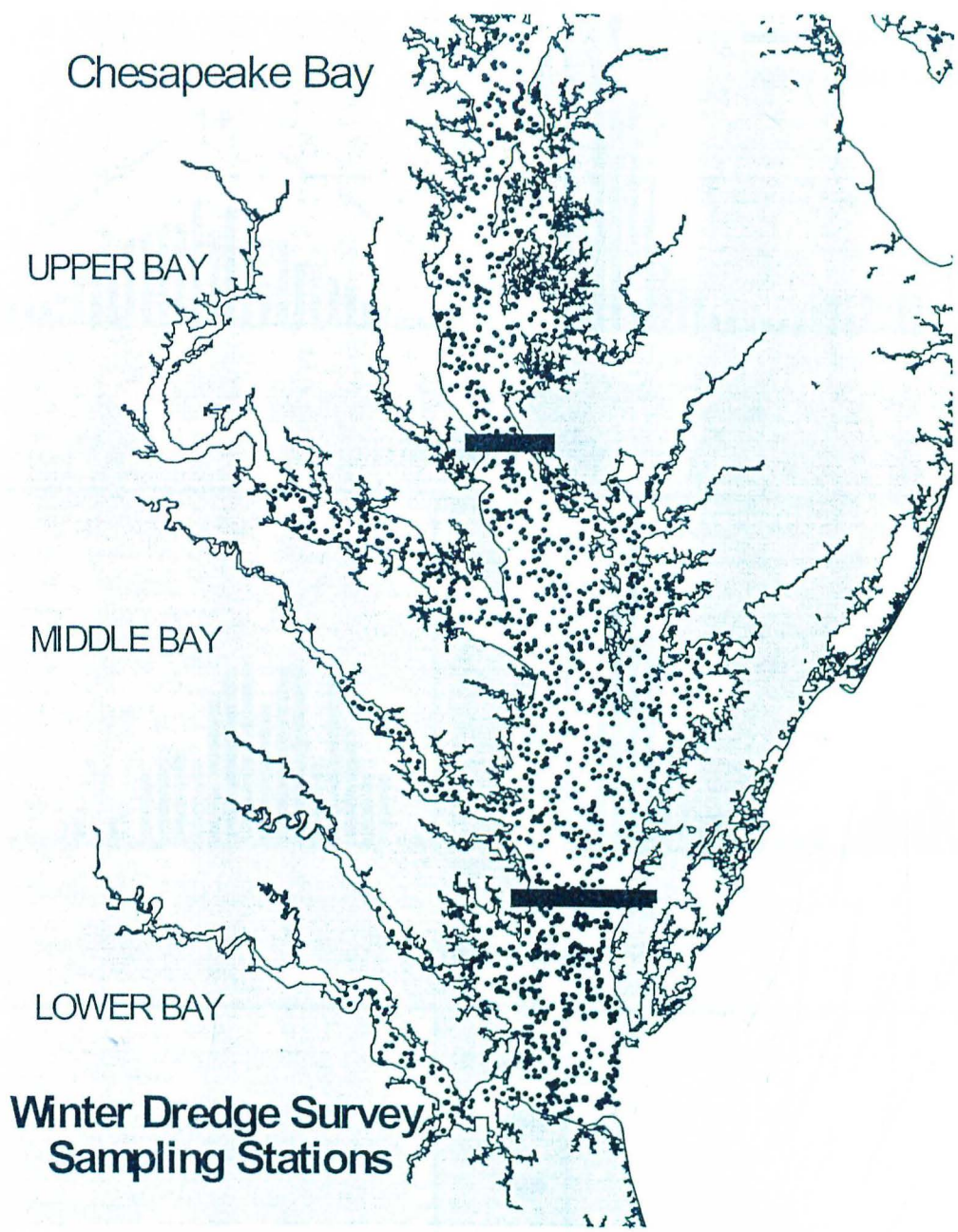
**Figure 8.** Comparisons of the (i) annual proportion of the baywide 1+ segment of the crab population residing in the Lower Bay with (ii) the fraction of annual fishing mortality from all fisheries ( $F$ ) due to the winter dredge fishery ( $F_{WD} = F_{WD}/F$ ), as calculated with (A) Lower Bay VIMS trawl survey data and (B) Middle Bay Calvert Cliffs crab trap data. Fishing mortality rates due to all fisheries ( $F$ ) were extracted from Miller and Houde (1998).

**Figure 9.** Comparison of the (i) annual proportion of the baywide 1+ segment of the crab population residing in the Lower Bay with (ii) the fraction of annual fishing mortality from all fisheries ( $F$ ) due to the winter dredge fishery ( $F_{WD} = F_{WD}/F$  assuming  $F = 1$ , as recommended by Miller and Houde (1998) for sustainable exploitation.



**Figure 10.** Interannual patterns in (A) the winter dredge survey estimated removal of crabs by the winter dredge fishery, (B) reported landings, and (C) the number of licenses. Data for (B) and (C) were provided by R. O'Reilly, Virginia Marine Resources Commission. None of the correlations were significant over time ( $P \gg .05$ ).

**Figure 11.** Comparison of (i) the winter dredge survey estimate of crab removal by the winter dredge fishery with (ii) reported landings provided by R. O'Reilly, Virginia Marine Resources Commission.

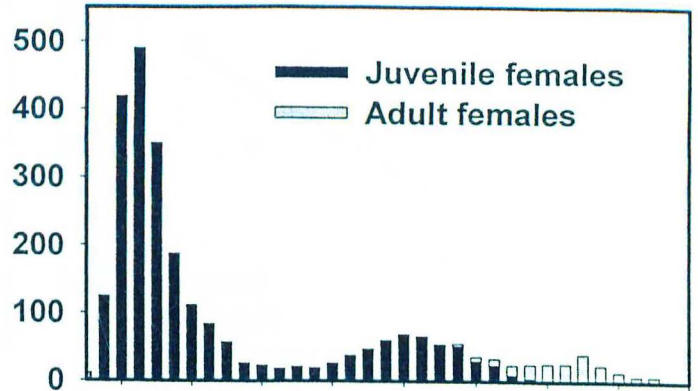
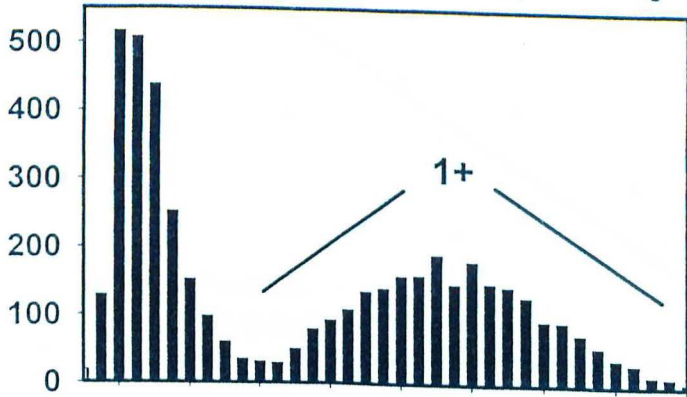




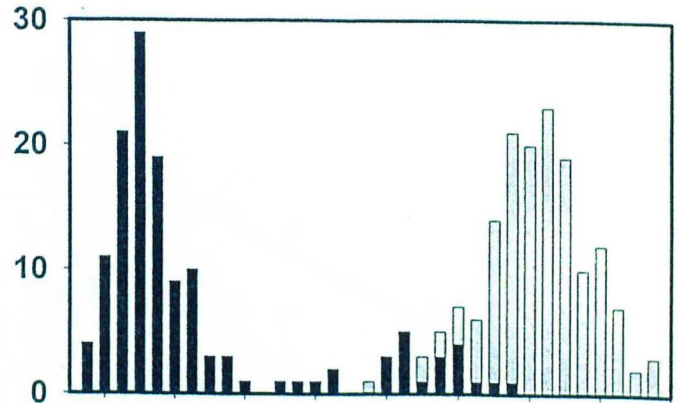
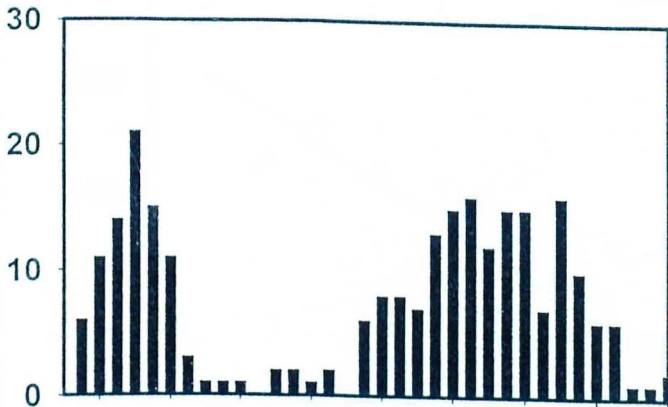
Males

Females

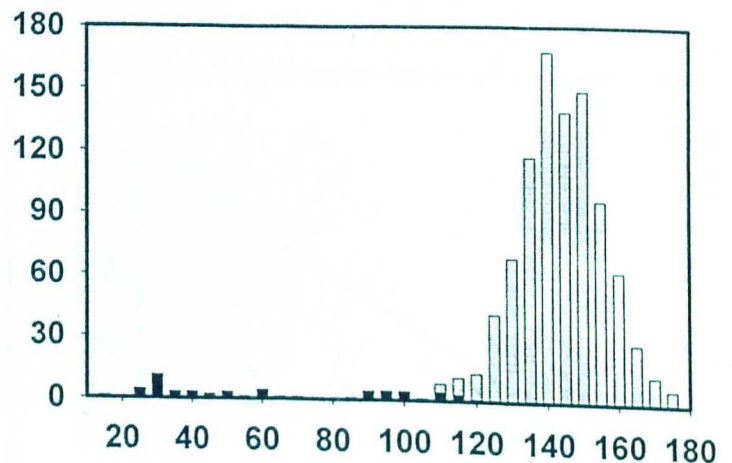
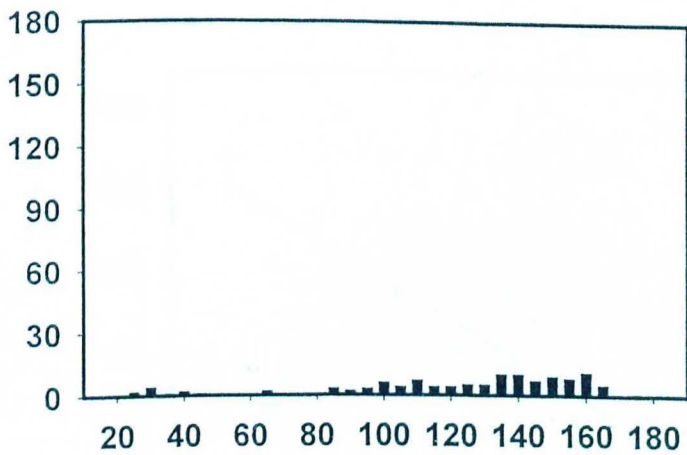
*Upper Bay and Tributaries*



*Middle Bay*



*Lower Bay*



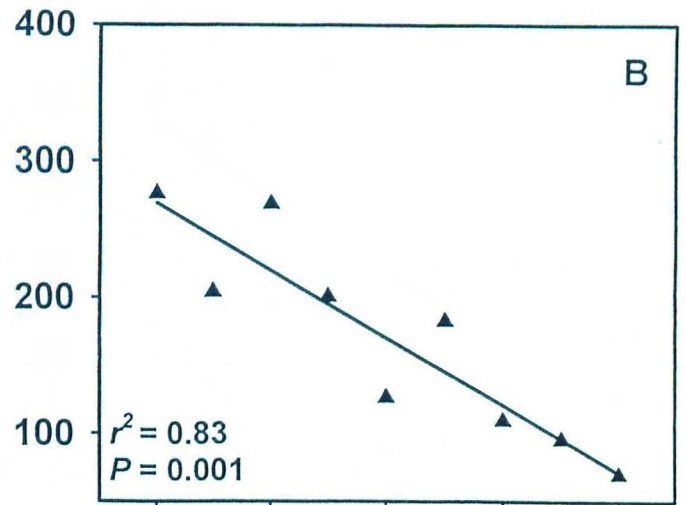
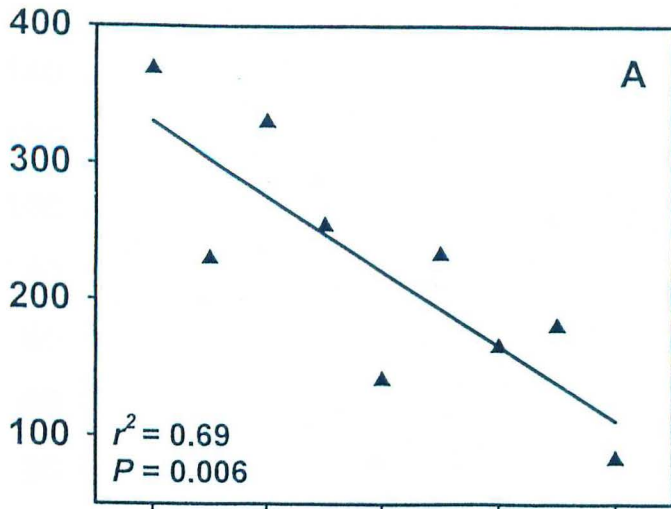
Carapace width (mm)

Abundance (millions of crabs)

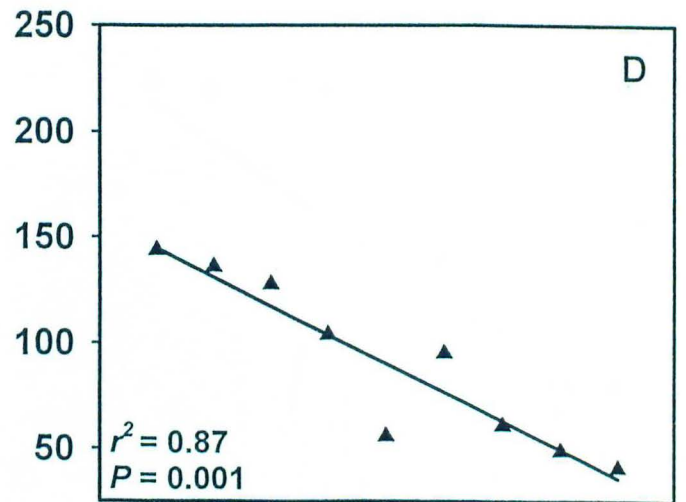
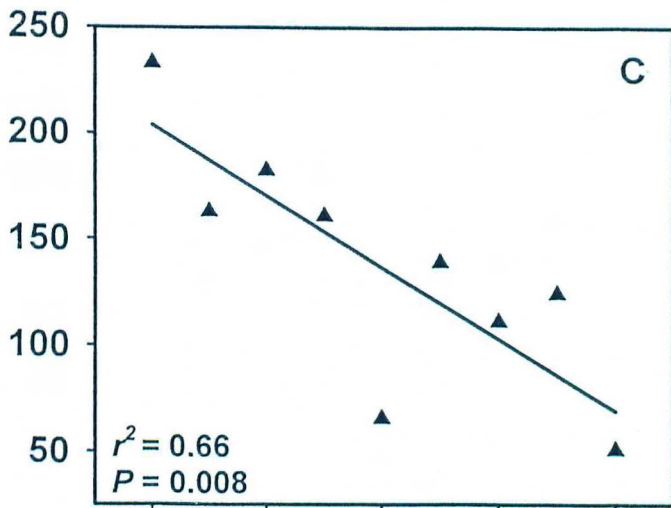
November

1+ Crabs

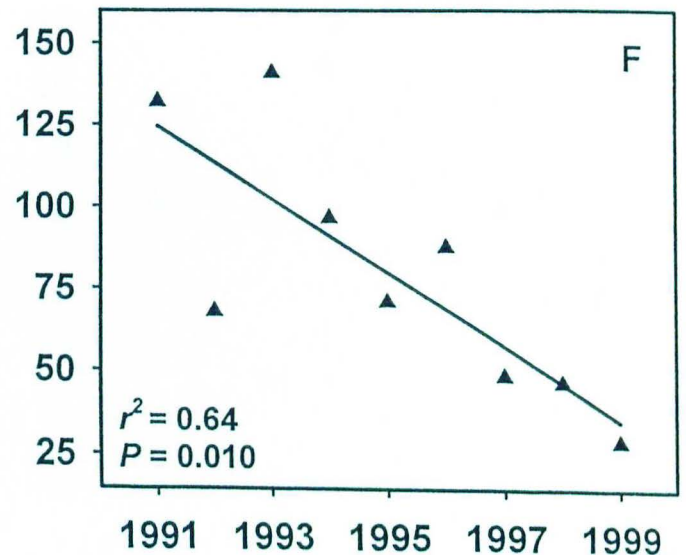
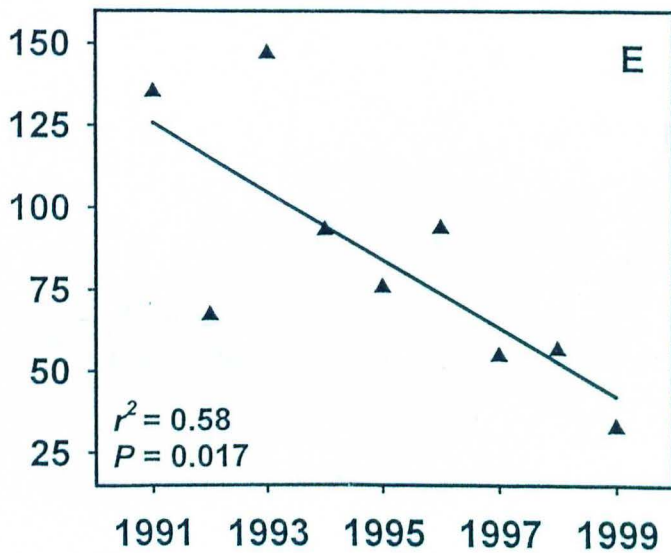
February



1+ Females



1+ Males



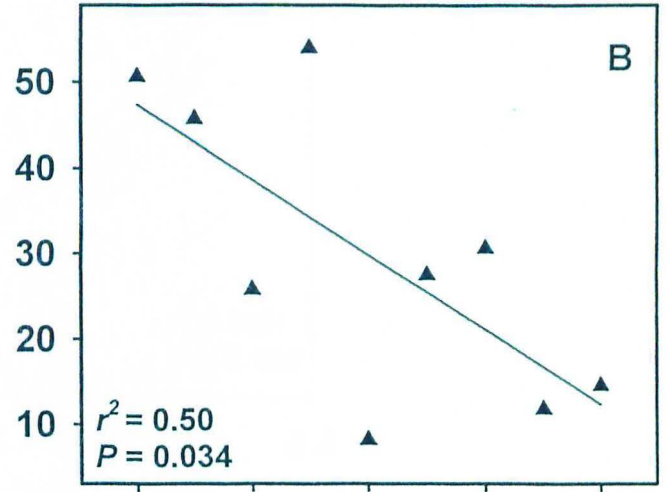
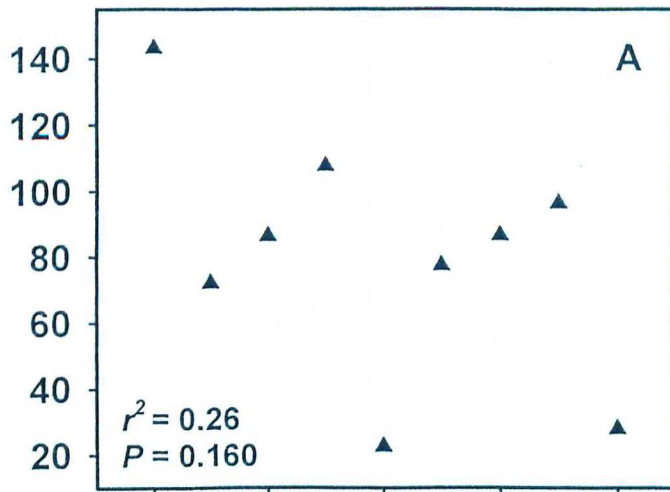
Year



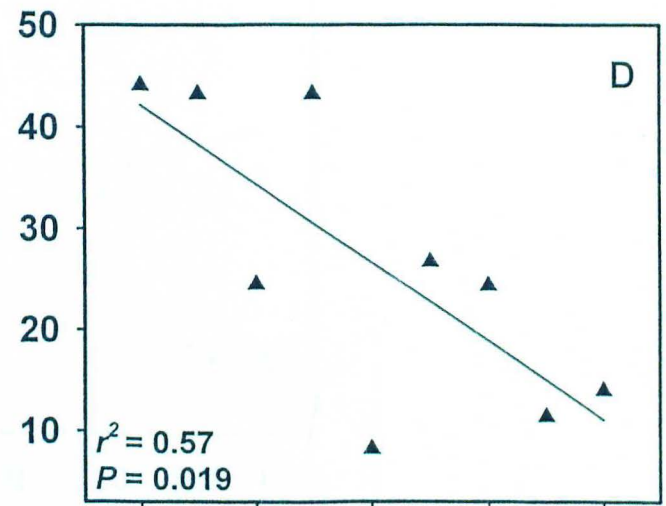
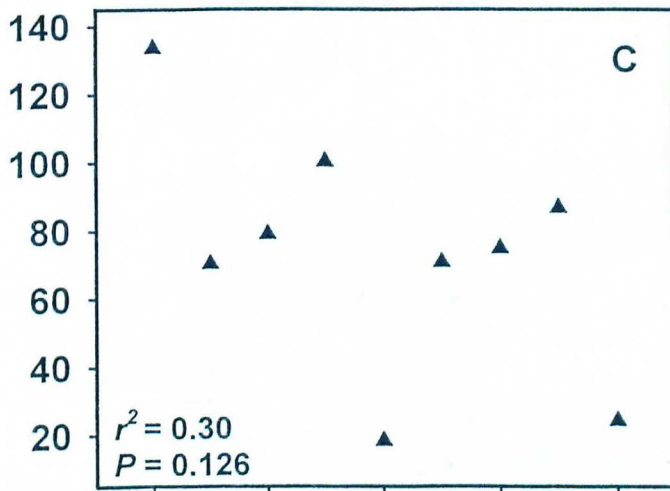
November

1+ Crabs

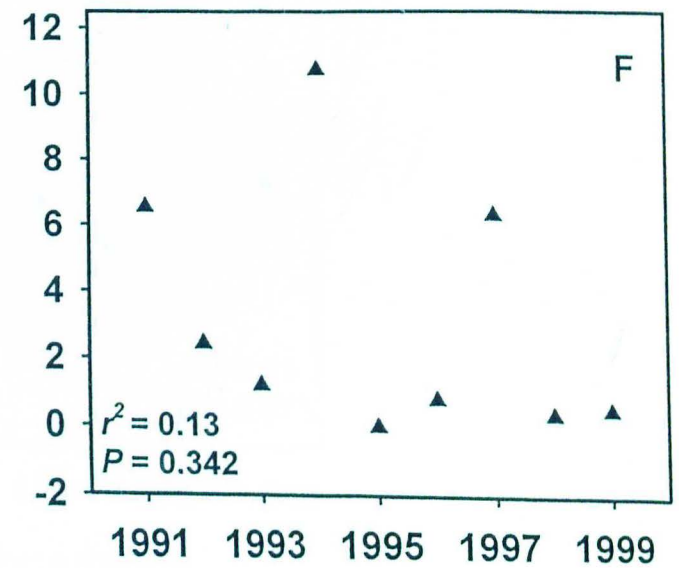
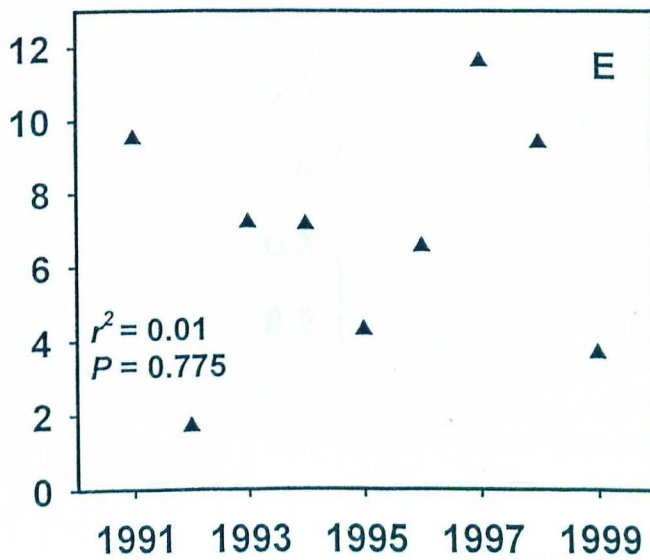
February



1+ Females

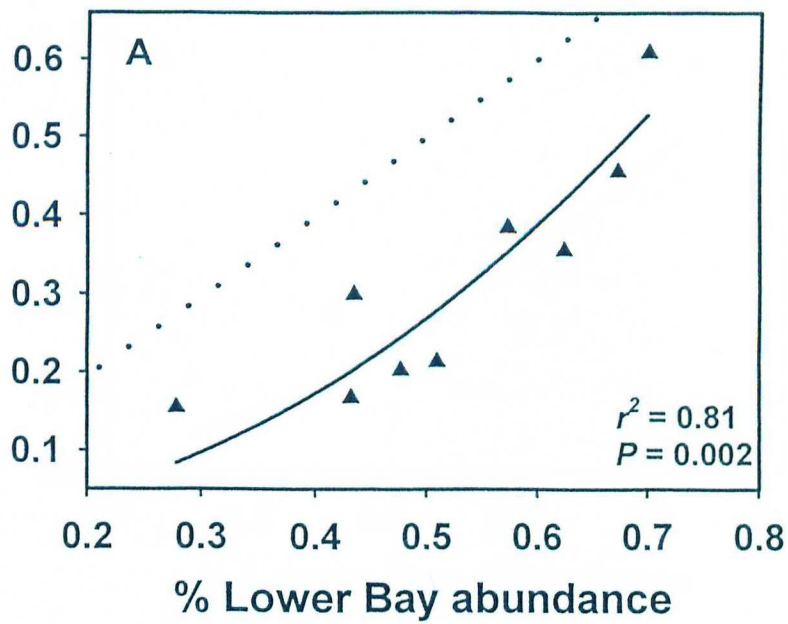


1+ Males

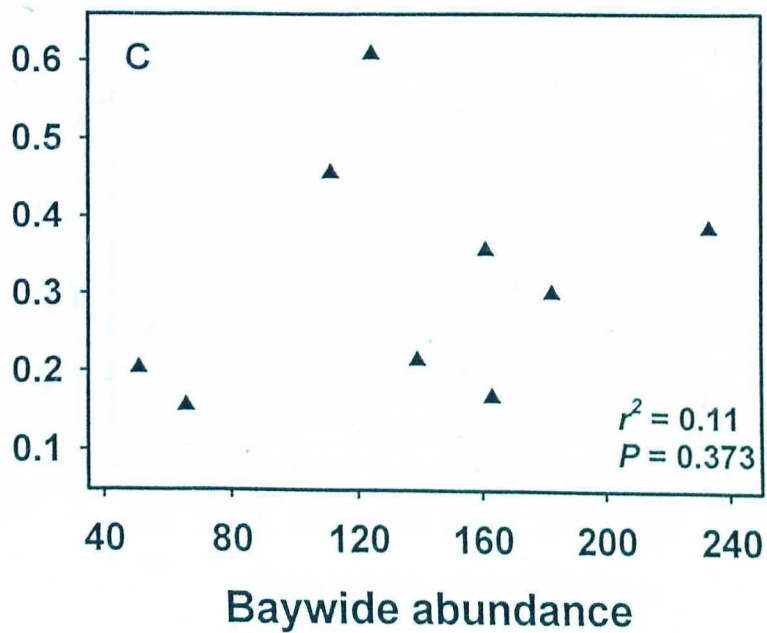
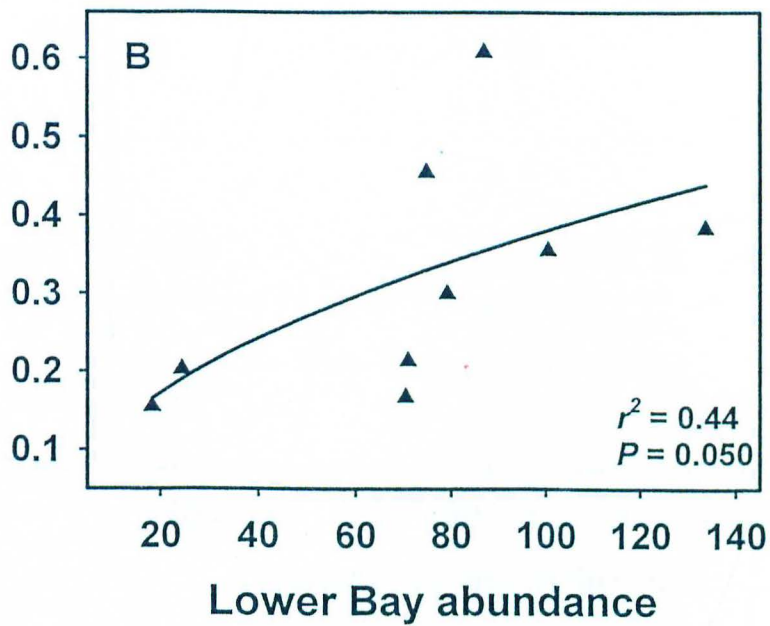


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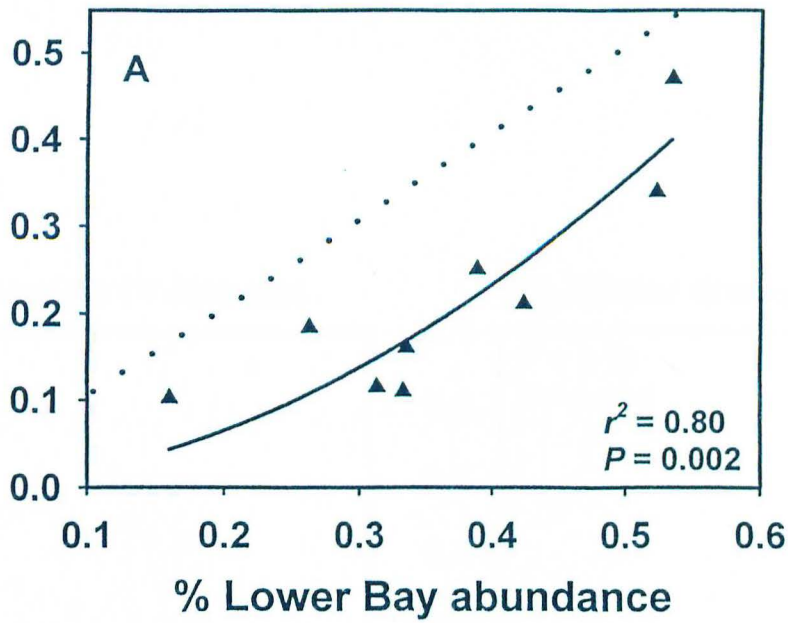
Lower-Bay abundance (millions of crabs)



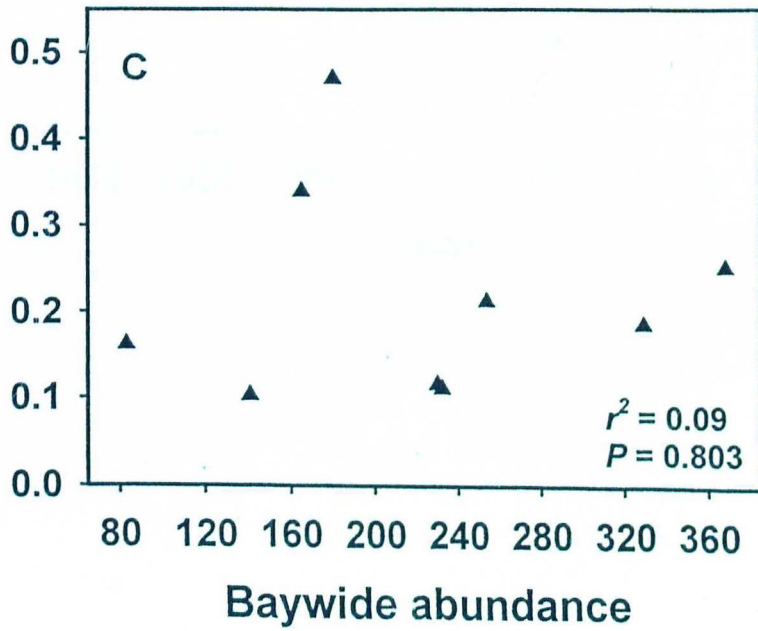
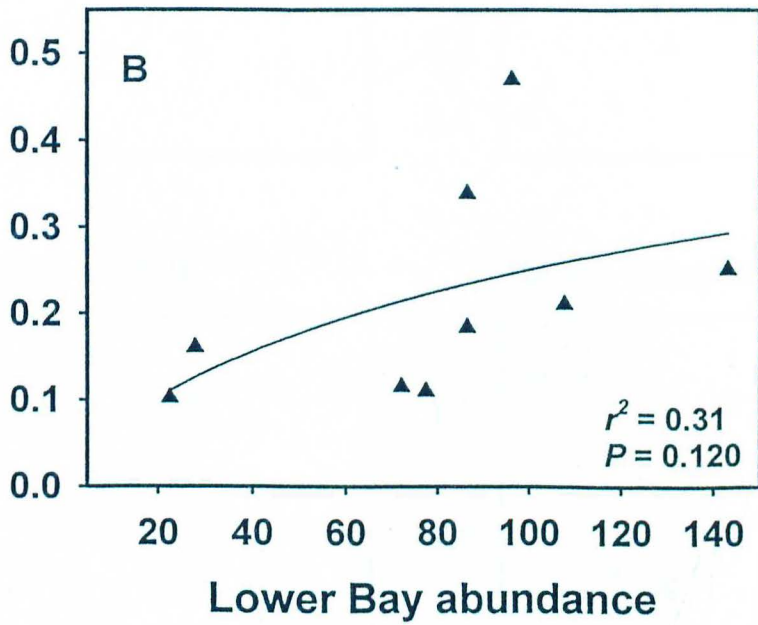
Exploitation rate of 1+ females





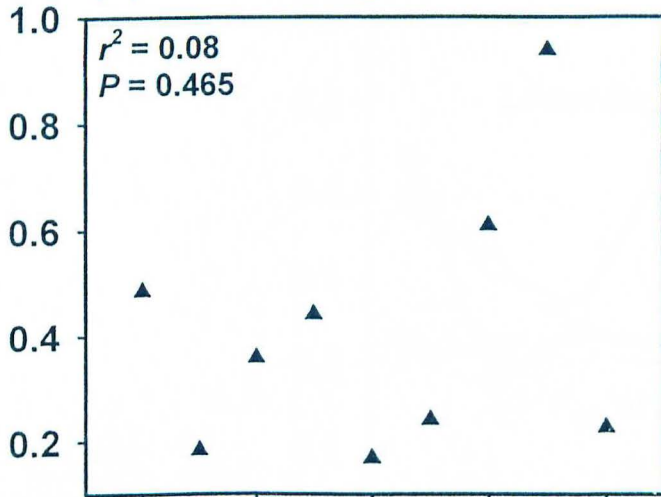


Exploitation rate of 1+ crabs

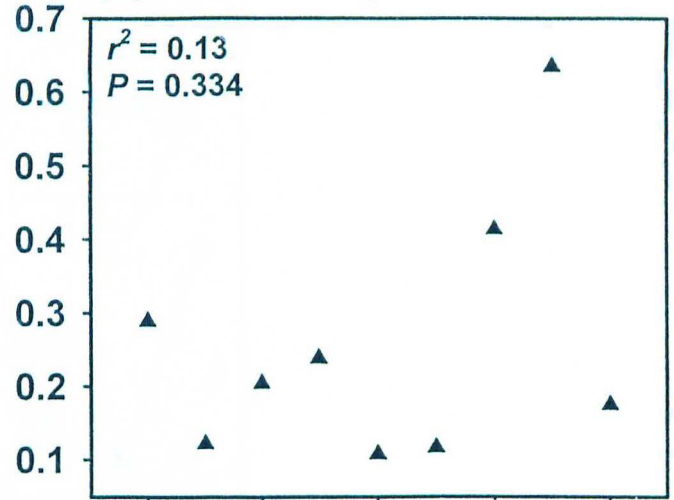


Fishing mortality rate

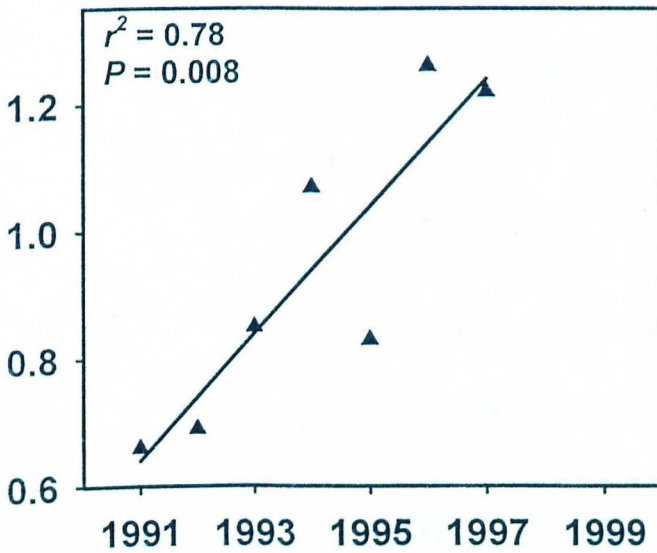
(A) Winter dredge 1+ females



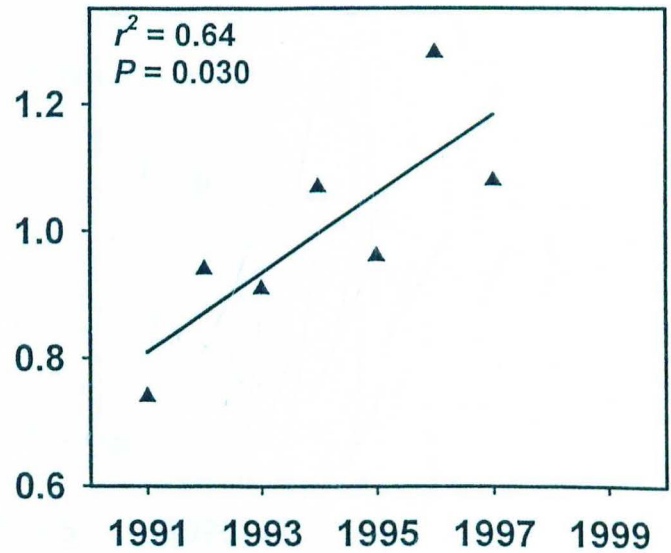
(B) Winter dredge 1+ crabs



(C) All fisheries - VIMS



(D) All fisheries - Calvert Cliffs

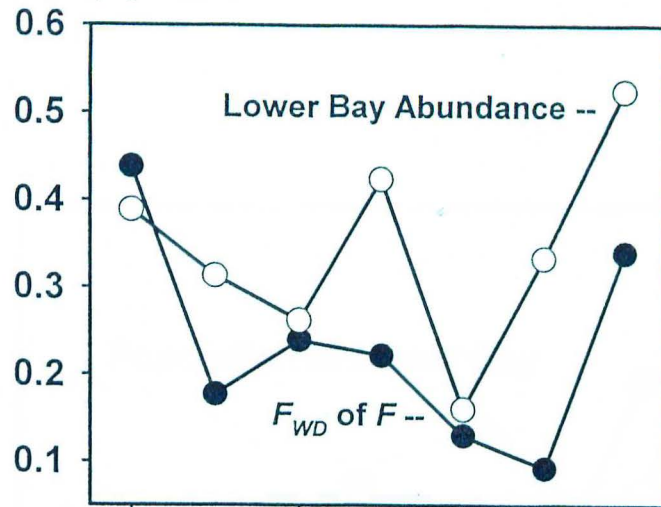


Year



Proportion

(A) VIMS



(B) Calvert Cliffs

