MULTISPECIES INTERACTIONS IN A FISHERY ECOSYSTEM AND IMPLICATIONS FOR FISHERIES MANAGEMENT: THE IMPACTS OF THE ESTUARINE SHRIMP TRAWL FISHERY IN NORTH CAROLINA

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ABSTRACT

GALEN ANNA JOHNSON: Multispecies Interactions in a Fishery Ecosystem and Implications for Fisheries Management: The Impacts of the Estuarine Shrimp Trawl Fishery in North Carolina
(Under the direction of Charles Peterson)

Shrimp trawler discards account for 1.9 million mt of the 6.8 million mt of annual global fisheries discards. This study examined the effects of dead discards from the North Carolina estuarine shrimp trawl fishery on scavenger populations and examined the trophic changes resulting from fishery practices. Bycatch and discards onboard estuarine shrimp trawlers were quantified, identified, and monitored for short-term survival. The major taxa in the bycatch both by weight and number were juvenile finfish and portunid crabs. Crabs showed high survival while 78% of fish died, generating a substantial amount of carrion in the estuaries, most of which sinks. Scavenging for discards occurred mainly by blue crabs and pinfish in the lower meter of the water column. In laboratory experiments blue crabs fed on discards six times more than on a natural prey, the juvenile hard clam, and this was replicated in mesocosm experiments lasting three days, where predation on juvenile hard clams was 33-60% less in treatments where discards were added. Thus, the shrimp, blue crab, and bivalve fisheries in estuarine waters of North Carolina are interconnected. Early and late summer quantitative ecosystem mass-balance models were constructed for two years of varying intensity of disturbance from hypoxia with four fishing treatments within each of the four time periods modeled: no fishing or discarding, fishing extraction alone, discarding alone, and combined fishing extraction and discarding of carrion. The effects of fishing on trophic structure, carbon flow and system network properties as calculated by Ecopath software were minimal compared to differences due to season and disturbance by hypoxia. However, fishing and discarding changed the trophic level at which many consumers fed, decreased transfer efficiency of energy through and out of the system, and altered trophic interactions. Pathways for energy transfer increased when discards were present, increasing measures of system stability. More system production was retained as detritus when discards were included in models. Management must acknowledge the ecosystem impacts of fisheries, and ecosystem-based management will be more successful if eutrophication is minimized and if the suite of interactions between fisheries and fished species are considered in management plans.

DEDICATION

To my grandmother Ida Crane, for her example of courage, strength and generosity.

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Abstract

The most recent estimate of global fisheries discards is 6.8 million mt annually. The largest bycatch contribution by a single type of fishery is from the shrimp (prawn) trawl fisheries, with estimated annual discards of 1.9 million mt. World-wide bycatch and discard issues include biological and ecological effects on bycatch populations as well as on the ecosystem, economic effects for fisheries and management, and socio-cultural issues that arise among fishers and within communities. Of particular ecological concern is the effect of bycatch mortality on the sustainability of populations and on community structure. In North Carolina, the most prevalent bycatch concern is the perceived loss of recreationally valuable species to bycatch mortality in the estuarine shrimp fishery. However, a possible anthropogenically introduced interaction between the shrimp trawl fishery and local blue crab populations (which represent the most valuable fishery in North Carolina) may be of enough significance for managers to seriously consider before implementing an inshore net-ban. Trawler discards of dead fish equaling or exceeding the shrimp catch by estuarine trawlers may provide a valuable prey subsidy to blue crabs. Prey subsidies have the potential to increase predator numbers, as demonstrated in both natural and fisheries-influenced systems. Bycatch and discards present a suite of problems for fisheries managers and scientists, but improved reporting of all catch and mortality, continued attention to gear

improvement, and enhanced understanding of the ecological effects of fishing on community structure and trophic relationships can help focus management on the most critical issues.

Introduction

Fisheries management encompasses biological, economic and social issues and objectives, and managers must develop plans that balance often conflicting needs. The role of fisheries scientists is to provide the most complete information possible to managers on the systems of interest, which might include a stock assessment for a particular species, experimental results on the environmental impacts of a fishing gear (for example, benthic impacts of trawling), and, increasingly, quantitative models of the ecosystem effects of fishing. The aim of this paper is to summarize and analyze the suite of issues related to fisheries bycatch and discards, especially for trawl fisheries, and to discuss important ecological concerns that merit further investigation.

Global, National, and North Carolina Bycatch Estimates

The global waste generated by fisheries bycatch and discarding is now recognized as one of the largest management issues in fisheries (Ohaus 1990; Alverson and Hughes 1996; Crowder and Murawski 1998). Definitions of bycatch vary somewhat, but bycatch is broadly defined as the non-target species, size classes and sexes captured by fisheries due to non-selective gear. Discards are those components of the bycatch not kept for market, consumption, or other uses and that are returned to the sea. Offal, or waste from the processing or cleaning of catch at sea, also represents a source of dead material returned to the sea by fisheries but is separate from discards; however, the ultimate ecological fate may be the same as that of dead discards. Bycatch may be discarded because it is illegal to land or because there is no economic gain associated with sorting or retaining it. Other sources of mortality resulting from fisheries, such as organisms killed by the passage of trawls and dredges and by ghost fishing (capture in abandoned gear) are not included in this summary.

The Food and Agricultural Organization (FAO) of the United Nations has published two major studies of global bycatch in the last two decades, in 1994 (Alverson et al. 1994) and 2005 (Kelleher 2005). Two different methodologies were used to estimate discards, with Alverson et al. (1994) using data from the 1980s on catch and average discard:catch ratios, which were multiplied to obtain discard estimates and Kelleher (2005) using data from the period 1994-2003 on the quantity of discards by fishery, which the author defined as "a combination of fishing *area* or zone *plus* a fishing *gear plus* a target *species*.". In their 1994 estimate of global discards from fisheries, Alverson et al. (1994) found that approximately one-third of all discards globally are derived from shrimp trawl fisheries, especially those in the tropics. Of the estimated 27.0 million mt of annual discards (range: 17.9 to 39.5 million mt), shrimp fisheries accounted for about 9.5 million mt (or 35% of the total discards; Alverson et al.1994). The discards estimate was based on global landings of 77.0 million mt in marine commercial fisheries only, excluding molluscan fisheries except for cephalopods, and focused only on bycatch of finfish and some invertebrates. Approximately 27% of global fisheries landings were discarded (Alverson et al. 1994). Kelleher (2005) computed a much lower amount of discards, estimating 6.8 million tones of discards for 78.4 million tones of catch landed (a discard rate of 8%); these figures came from compilations of bycatch from marine commercial fisheries and included marine mammals, turtles and seabirds as well as fish. Kelleher (2005) also found the greatest amount of discards (1.9 million tones) and average discard rate (62%) in shrimp trawl fisheries, especially in the tropics. In most shrimp trawl fisheries, the weight of bycatch exceeds the weight of landed shrimp (Andrew and Pepperell 1992); however, whether that bycatch is discarded varies by region. Alverson et al. (1994) report that the majority of bycatch is discarded in shrimp and prawn fisheries in North and South America, Europe and northern Australia, contrasting with higher retention of bycatch in many shrimp and prawn fisheries in Africa and Asia. Of the approximately 1.3 million mt of bycatch reported for the West Central Atlantic region, roughly 80% came from shrimp fisheries off the southeastern U.S. and in the Gulf of Mexico (Alverson et al. 1994). Kelleher (2005) found that the Gulf of Mexico shrimp trawl fishery had the largest amount of discards of any fishery in the entire database, with 480,000 tonnes of discards annually. Harrington et al. (2005) estimate that in the United States, 1.06 million tonnes of finfish and fishable invertebrates were discarded in 2002, with 3.7 million tonnes of commercial landings. Shrimp trawl fisheries were responsible for 47% of these discards (Harrington et al. 2005).

The differences in methodology between the Alverson et al. (1994) and Kelleher (2005) studies preclude direct comparison, but certainly the large difference in estimates of global bycatch deserves closer attention. Kelleher (2005) points out that differences in methodology are not solely responsible for the reduction in the estimate of global bycatch, given that a number of important fisheries have reduced bycatch (including the US shrimp trawl fisheries, which now require TEDs and BRDs) and other fisheries have increased retention of bycatch. In the foreward of Kelleher (2005), the original authors of Alverson et al. (1994) note that greater utilization of bycatch, increased selectivity of fishing gears and methods, declines in fishing for some species and management changes may have contributed to the decline in global discards. Zeller and Pauly (2005) also note that while discard rates are falling, so too are the total fisheries catches (landings plus discards). Hall and Mainprize (2005) express some concern over the Kelleher (2005) estimates due to uncertainties in both the definition of fisheries and data on the fisheries level. The growing public concern over bycatch may also have affected reporting by both fishers and managers (L. Crowder, *pers. comm.*). Attempts to improve the methodology in estimating global bycatch such as that developed by Kelleher (2005) are valuable, and many of the criticisms of global bycatch estimates reflect a need for increased monitoring of bycatch rather than problems with specific methodologies.

Few studies have focused on the extent of discard mortality. Discard mortality can result from damage to individuals while dragged in a trawl, damage done by the fishing gear, exposure to predators while concentrated in the trawl net, effects of pressure changes as gear is hauled up, or oxygen deprivation or desiccation while a catch is sorted (Ramsey et al. 1997). Quantifying the mortality of discards is essential for estimating the mortality rate of discarded species, which often include species of fishery value (Crowder and Murawski 1998, Davis 2002). Most studies of discard mortality are conducted to improve gear, rather than to understand the effects of environmental factors and fishing practices themselves on discard mortality (Davis 2002). Wassenberg and Hill (1990) found that about 20% of discarded animals from prawn trawlers in Queensland, Australia, were dead. In an earlier study on commercial fishing boats in the same area, Wassenberg and Hill (1989) found that over 86% of crustaceans survived 30 minutes on deck, but few fish survived 20 minutes. Crabs that died were usually damaged or had recently molted. Kaiser and Spencer (1995), working on a beam trawl off North Wales, found that survival of swimming crabs was high (60-100%, depending on species) unless they had a crushed or cracked carapace or greater than 50% limb loss. They found that the fish that died after being caught in a trawl tended to have scale loss and/or bruising from handling. Van Beek et al. (1990) found that plaice (18-27 cm) and sole (20-28 cm) survival from trawls was about 10% over 84 hours following "typical" handling on deck, and that survival of fish that escaped the mesh of the trawl was about 60%. Parker et al. (2003) found lingcod survival of 100% when the fish were immediately discarded after landing of the nets, but that survival decreased to 50% after 30 minutes on deck. However, all these survival experiments were carried out in tanks and may not reflect survival upon return to sea, where discarded species may be more vulnerable to predators or to recapture by fishing nets. Study methods were incomplete regarding the weather conditions and time of day during which the bycatch was exposed to the air, and these factors can affect survival (Davis 2002).

In the United States, 149 species or species groups have been identified in the discards of the nation's fisheries; 63% were finfish, crustaceans or mollusks and 37% were protected marine mammals, turtles or seabirds (NMFS 1997). Because the data resolution for protected species was better than that for finfish and invertebrates, the percent contribution of these protected species is high. Nationally, the majority of discarded fish species or species groups are considered fully- or over-utilized and their stock biomass is considered at or below that necessary to produce the maximum long-term sustainable yield (NMFS 1997). In the shrimp fisheries of the southeast Atlantic from 1992-1996, an average of 27 kg of organisms per hour were taken in trawl fisheries; the catch was made up of an average (by weight) of 51% finfish, 18% commercial shrimp species, 13% other crustaceans, and 18% non-crustacean invertebrates (NMFS 1998). Shrimp catch rates were highest in the late spring. In shrimp fisheries, finfish:shrimp ratios (by weight) were highest (8:1) in the northern Atlantic fishing grounds (>34ºN) decreasing to 2.5-3:1 in the middle and southern

Atlantic (<34ºN). However, the majority of shrimp trawling takes place in the more southern regions, so the quantity of bycatch there is higher despite the reduced ratios (Harrington et al. 2005).

Estuarine bycatch has not received the same attention as bycatch in open-water fisheries such as the groundfish fisheries in the North Pacific and the Northwest Atlantic or the shrimp fisheries in the Gulf of Mexico. Estuarine fisheries, such as the shrimp fishery in the estuaries of North Carolina, are usually comprised of larger fleets of smaller boats, often operated by only one individual. Observer coverage and reporting by fisheries employees at docks is less practical and cost-effective in these fisheries. Estuarine bycatch in the fisheries of the southeastern United States has been documented by only a few researchers, often in concert with the testing of new equipment. Keiser (1977) examined the incidental catch from commercial shrimp trawlers in the south Atlantic states and found an average bycatch:shrimp ratio (by weight) of 4.0:1 for North Carolina, 2.58:1 in South Carolina during the summer, 1.2:1 in South Carolina during the fall, 2.55:1 in Georgia and 3.8:1 in Florida.

Only one study in recent years has focused on the bycatch composition of shrimp trawler catch in North Carolina, outside of gear-testing studies. Gear-testing studies reviewed did not reflect the normal practices of fishermen, with data collection taking place in locations not commonly fished by commercial fishermen, during times different from usual commercial fishing practices, with short tow durations, and/or without location choice by a fisher trying to maximize his returns. Diamond-Tissue (1999) sampled inshore and nearshore shrimp trawler bycatch in late summer and early fall in 1995. She found that market-size penaeid shrimp made up 30.8% of the species caught by weight, while fishes made up 51.2% of the catch and crabs made up 3.2% of the catch. The greatest contributing fish species, by weight, were Atlantic croaker (*Micropogonias undulatus*), weakfish (*Cynoscion regalis*) and spot (*Leiostomus xanthurus*). Subsamples of the entire catch were taken, and the total bycatch estimated by extrapolating subsample shrimp:subsample ratios based on the weight of shrimp compared to the weight of the entire catch. Fifty-two tows were sampled on 15 trips, covering Pamlico Sound, Core Sound, the Cape Fear River and the nearshore ocean off Carolina Beach.

Global and Local Bycatch and Discard Issues

Bycatch and discards have the potential to affect the ecology of a system, the economy of fisheries and management structures, and the sociology of a community. There is evidence in many fisheries world-wide of low survival of discards, declines in species commonly caught as bycatch, and shifts in species dominance tied to discarding practices (Alverson et al. 1994). Economic losses result from the premature mortality in species that could be caught in the future, costs associated with time taken to sort catches, and the management costs of monitoring bycatch and/or developing methods to decrease bycatch and discards. Social problems include negative public attitudes towards commercial fishing due to publicity of discards and conflicts between fisheries due to one fishery catching as bycatch species targeted in other fisheries. Public concern over bycatch emerged after publicity regarding large charismatic species caught as bycatch, such as dolphins in the tuna purse seines, marine mammals in North Pacific salmon net fisheries, sea turtles in shrimp trawl fisheries in the Gulf of Mexico, and Stellar sea lions in North Pacific trawl fisheries (Alverson and Hughes 1996; Hall 1996). These species tend to be of more concern to the public and are protected under the Endangered Species Act of 1973 or the Marine Mammal

Protection Act (amended in 1994). More research is needed on the biological, ecological, economic and socio-cultural effects of other taxa caught as bycatch.

The paucity of data on bycatch, discards, and the survival of discards is one of the first obstacles to overcome to further the understanding of biological and ecological effects of fisheries and to improve management of fisheries (Alverson et al.1994; Hall 1996). Accurate reports of fishing mortality on managed species is important for most fisheries management models (Alverson and Hughes 1996), such as stock assessment models, but discards often represent unaccounted mortality, similar to ghost fishing and illegal fishing. Without accurate data on the complete fishing-related mortality in a population (mortality due to targeted catch and bycatch), it is difficult for managers to set the appropriate levels for total allowable catch and ensure that overfishing does not occur.

In many studies focused on bycatch and discards, research trawls rather than actual fisheries trawls are used (e.g. Harris and Poiner 1990; Wassenberg and Hill 1990, Kaiser and Spencer 1995). This may lead to low estimates of discards (Dayton et al. 1995) or high bycatch or discard estimates if the research trawls are undertaken in areas that would not be targeted by commercial trawlers due to low catch of target species or high bycatch ratios. Another problem in collecting bycatch and discard data is the high variability; this high variability exists within time periods as short as 24 hours and extends to year-to-year variability (Alverson et al. 1994; Alverson and Hughes 1996).

Impact studies are important for each species in the bycatch, because the removal of large amounts of biomass or large discard mortalities do not necessarily translate into large population effects while the removal or discard mortality of a small amount of biomass may have adverse impacts on a population (Alverson and Hughes 1996). Two studies of southeastern United States trawl fisheries demonstrate the possible population-level effects of bycatch mortality on species. Crouse et al. (1987) developed a stage-based population model of the loggerhead sea turtle (*Caretta caretta*) and demonstrated that increasing survival of later stages of turtles (vs. increasing egg survivorship or fecundity) has the largest effect on population growth. Large juveniles and adults are commonly caught in trawls, accounting for over 40 000 sea turtle deaths annually in the 1980s (NRC 1999). The model findings led the NRC panel to suggest requiring installation of TEDs on trawlers to reduce population declines. Further modification of this model by Crowder et al. (1994) demonstrated that use of TEDs, especially if required year-round in all trawl fisheries, should allow populations of loggerhead turtles to eventually increase. In another population-level study, Diamond-Tissue (1999) demonstrated, using stage-within-age based matrix models, that Atlantic croaker discard mortality from shrimp trawlers has an important, negative impact on population growth rates. Although discard mortality was not the most important factor affecting population growth rates (the most important factor was larval mortality in the ocean), it is the easiest factor for managers to improve (Diamond-Tissue 1999). These population models not only demonstrate that bycatch mortality can induce population effects on affected species, but they also demonstrate that models can be useful in helping managers identify which manageable life stages should be the focus of conservation or sustainability efforts. In another example of bycatch mortality affecting populations in North Carolina, virtual population analysis of the weakfish populations of North Carolina demonstrated that bycatch mortality of weakfish from trawling may be hastening the decline of the spawning stock potential (Vaughan et al. 1991). The weakfish spawning stock potential slowed a slight decline when directed fishery mortality was included in the analysis but not bycatch mortality; when bycatch mortality was added the declines were much steeper.

Fishing can impact community structure both through the selective removal of target species and through differential survival of discards. On Georges Bank, prior to the 1977 implementation of the Magnuson Fishery Conservation and Management Act, small dogfish, sharks and skates were retained by foreign fleets for industrial purposes during targeted fishing of gadids and flounders. When the domestic fleet took over, these small elasmobranchs were discarded, usually with low mortality, and their relative abundance grew to the point that they were the major populations on the Banks (Fogarty and Murawski 1998). However, in the past decade the domestic fleet has begun to increase landings of small elasmobranchs and their relative abundance has begun to decline. Discarding practices can therefore influence relative species abundances, especially when there is differential mortality between targeted species and non-targeted species (NRC 1999).

Economic issues associated with bycatch include lost income due to the discarding of valuable species, lost income due to premature harvest of fish, costs associated with sorting the catch, and management costs. There is loss of potential income when individuals caught as bycatch are landed at a smaller size than is marketable for human consumption and are instead reduced to fish meal, oil or bait. While species harvested too early for human consumption still have economic value, it is typically considerably less than their potential value were they allowed to mature. Discarding of illegal fish, undersize fish, or fish not of interest to a particular fishery due to fisheries regulations or to economic factors can lead to substantial economic losses; for example, in the North Sea groundfish trawl fishery, the biomass of marketable species discarded is estimated to be 25-100% of the quantity landed

(Kelleher 2005). Also, fishers would often appreciate lower bycatch rates because it would save them time when sorting their catch (Murray et al. 1992). Sorting of the bycatch, especially on large boats, can lead to higher processing costs because of lower factory efficiency and additional crew (Alverson et al. 1994). Management costs are affected by the bycatch and discard problem as well. Fisheries management in the U.S. received a budget of $200 million in 1992, which translates into less than five cents per pound of fish landed (Alverson et al. 1994). When some of this money goes to bycatch and discard management, it reduces the amount available for further data collection, habitat improvement, and needed research.

Social concerns mirror economic concerns regarding loss of commercially and recreationally valuable species at a young age to bycatch mortality, but also include conservation concerns for species caught in the bycatch and public perceptions of commercial fisheries in general (Andrew and Pepperell 1992; Alverson and Hughes 1996). Conflicts can arise when fish are harvested as bycatch in one fishery and are then unavailable to another fishery, whose participants feel entitled to the catch (Ohaus 1990). For example, Canadian fishers and fisheries managers believe that harvest of southward-moving juvenile halibut caught as bycatch in Alaskan waters adversely impacts subsequent catches by Canadian fishers targeting the halibut (Ohaus 1990). Conflicts can also arise when consumers in developed countries find fisheries imports from developing countries to be based upon less environmentally sound fishing practices than domestic products; for example, many U.S. consumers chose to boycott Indonesian-produced shrimp in the early 1990's due to high sea turtle bycatch in the fishery, but the Indonesian shrimp fishers who depended on the fishery for income and had little other available technology found the boycott unfair (Alverson et al. 1994).

Another issue associated with bycatch is overcapitalization of fisheries that are high in bycatch. It is estimated that the only a 6% reduction in shrimp catch by the Texas Gulf of Mexico shrimp trawl fishery would result from a 38% reduction in effort (Onal et al. 1991); if bycatch is tied to effort rather than catch then bycatch could be dramatically decreased by reducing the fishing fleet. However, social conflicts are likely to arise over how to reduce effort.

Trophic Impacts of Discards

Britton and Morton (1994) found that all scavenging marine invertebrates are facultative scavengers, scavenging when carrion is available and pursuing a predatory life-style when carrion is unavailable. They note that facultative scavenging may be increasing due to massive human intervention in marine ecosystems. A scavenger need only detect prey and eat it, thus saving the energetic expenses involved in subduing its prey; the energetic value of carrion is therefore equal to or greater than that of live prey. However, a scavenger has the disadvantage of having to wait for the often infrequent availability of carrion and must take advantage of the carrion before competitors and/or before physical processes transport the carrion away. Britton and Morton (1994) note that human activities, such as discarding from shrimp trawlers, can make the occurrence of carrion much more frequent than would be expected in a non-anthropogenically influenced system. Discarding of bycatch from trawlers transfers large quantities of benthic and demersal biomass into carrion, making it available to surface, pelagic and epibenthic scavengers in amounts that would normally not occur (Britton and Morton 1994).

According to Polis et al. (1997), prey inputs to habitats produce numerical responses in consumers. This can lead to top down effects when consumers of prey inputs increase in densities and then reduce local prey resources. When prey inputs occur regularly, consumer success becomes decoupled from the local productivity that usually constrains populations. Therefore, prey dynamics in subsidized habitats decrease in their control of predator population dynamics and consumer-resource models based on in situ productivity become invalid (Polis et al. 1996). Regular allochthonous food subsidies probably dampen the response of consumer populations to any one resource (Anderson and Polis, 2004). Huxel and McCann (1998) demonstrated in a mathematical model that low to moderate levels of allochthonous input to the consumer levels of a tritrophic food web can stabilize food web interactions, depending on the preference of consumers for the alternate food source.

Spatial subsidies, or prey inputs from one habitat to another, can also lead to apparent competition. Apparent competition occurs when two prey species or species groups share a common predator and an increase in one prey species or species group leads to an increase in the predator, causing a decline in the other prey species or species group (Holt 1977, 1984, Schmitt 1987, Holt and Lawton 1994, Wootton 1994). On short time scales, alternative prey may relax predation on focal prey if predator selectivity is increased or if predators are satiated (Holt and Lawton 1994). However, on longer time scales alternative prey may sustain predators at population densities higher than the focal species would support thus leading to higher cumulative impact on focal species (Holt and Lawton 1994).

Examples of discards subsidizing surface scavenger populations and producing numerical responses exist for deeper trawling sites in the North Sea, the Mediterranean, and in Australia. In the North Sea, Garthe et al. (1996) found that the amount of discards (including offal) available to seabirds due to trawler discards was sufficient to support all the scavenging seabirds. About 39% of the more than 760,000 tons of annual discards and offal theoretically available in the North Sea was consumed by birds; this exceeds the amount of live fish and other food calculated to be consumed by these seabirds (Garthe et al.1996). Off Spain, Oro et al. (1995) found that the breeding success of yellow-legged gulls correlated with years of trawling; this led the authors to suggest that trawler discards were of sufficient quantity to subsidize the breeding population and lead to numerical responses in the population. Arcos and Oro (2002) found that about 41% of the breeding season diet of the rare, endangered Balearic shearwater was made up of discards from trawlers. Blaber and Wassenberg (1989) found that the diets of three piscivorous birds in Moreton Bay, Australia, were primarily dependent on fisheries discards from prawn trawlers for food and may have artificially inflated populations as a result.

While evidence exists for subsidization of surface scavenging populations, little is known about the fate of discards that sink to the bottom (Wassenberg and Hill 1990; NMFS 1997). Evidence of crustaceans feeding on trawler discards has been seen in Australia (Wassenberg and Hill 1987), the Irish Sea (Ramsay et al. 1997), and the Clyde Sea (Bergmann et al. 2002), but none of these authors investigated possible responses of population numbers to the subsidy. Link and Almeida (2002) found a weak but significant positive link between sculpin feeding on discarded scallop viscera and sculpin abundance on Georges Bank, indicating that discarding offal may affect scavenger population regulation.

In North Carolina, the bycatch and discards from the estuarine shrimp trawl fishery have recently commanded substantial public attention, largely due to perceived loss of recreationally important species to shrimp trawls before the individuals can mature and reach the ocean. Sports fishermen in the state have repeatedly petitioned the legislature to ban trawling in estuaries and sounds (net bans were proposed in the NC State Legislature in both 1995 and 1997). The situation in North Carolina provides a good example of the complications that can arise in a management situation when gear conflicts, biological and ecological issues, economic and social issues come to a head.

Trawling has been practiced in North Carolina since 1912; trawl nets were originally introduced for fishing for finfish and crabs (they had formerly been used only for fisheries sampling) in the Southport area and gradually spread north (NCDMF 1999). Increased demand for shrimp and improved refrigeration techniques led to a burgeoning shrimp industry after World War II, replacing most trawling for finfish and crabs. While there is an offshore fishery for shrimp in North Carolina, about 75% of the trawling vessels in the state are too small to consistently target shrimp in the ocean and tend to be confined to estuarine waters. About 72% of the state's shrimp landings are caught in estuarine and sound (inshore) waters. Therefore, a ban on inshore trawling would influence the majority of the shrimpers of North Carolina, forcing shrimpers to upgrade their boats to ocean-going quality, change fishing gear for estuarine and sound shrimp fishing, switch fishing effort to another fishery or change jobs completely. Furthermore, 33% of the state fishing income comes from shrimping, so there could be substantial economic repercussions for shrimpers, fish dealers, and perhaps local economies (NCDMF 1999). There are currently no economic models of how decreased inshore shrimp trawling could improve recreational fishing in North Carolina and therefore bring increased income to coastal counties that depend on tourism. Furthermore, from a social standpoint, ending estuarine trawling would put a lot of fishermen out of the only business they know, often a business handed down within a family for generations; many of these fishers are already facing financial stress as cheap foreign shrimp imports now compete with their products.

Shrimping is the second most important commercial fishery in North Carolina in terms of income; the blue crab fishery is the most important fishery (NCDMF: www.ncdmf.net). Most blue crabs are caught in crab pots, but some are caught in a winter trawl fishery. Blue crabs are common in the areas of North Carolina where shrimp trawling occurs, but also live in areas in which trawling is off limits. Blue crabs can be harvested at any size for females and at carapace widths greater than 5 inches for males. Their typical diet consists largely of clams and crabs, with some polychaetes, hydroids, gastropods, insects, fish, crustacea and plants (Mansour 1992); however, blue crabs are facultative scavengers and can eat recently dead material, such as conspecifics and fish (Britton and Morton 1994). Food limitation of blue crabs has been seen in the Chesapeake Bay in late summer and fall, as evidenced by increased cannibalism in areas of relatively low bivalve prey (Mansour 1992).

Dead discards from shrimp trawlers in the sounds of North Carolina occur in areas with substantial blue crab populations (NCDMF 1999). It is therefore possible that the trawler discards of dead fish act as a subsidy, or alternative prey source, to the blue crab populations of trawled areas. Shrimp fishers in North Carolina have hypothesized for years that the discards from their trawling operations were feeding economically valuable species such as shrimp and crabs as well as species of conservation concern such as turtles. If the impact of prey subsidies from dead trawler discards is greater than the detrimental effects of trawling to blue crab populations (direct mortality of blue crabs or their prey), then shrimp trawling may increase blue crab populations and thus landings of blue crabs in North Carolina estuarine and nearshore waters. For shrimp trawl discards to sustain blue crab populations at higher levels than otherwise possible, the limiting factor of blue crab adult populations must be food and not an earlier life history stage (Ramsay et al. 1997). The availability of discards to blue crabs, as well as to other scavengers (such as fish and birds), may also serve to stabilize the system, since broad omnivory is thought to stabilize both consumer populations and communities (Anderson and Polis 2004).

Summary

While the large data-gathering studies of Alverson et al. (1994) and Kelleher (2005) demonstrate the enormity of the global bycatch problem, they also highlight the need for improved bycatch data collection worldwide. The need to reduce bycatch is a global issue, but to minimize conflict and maximize effect, changes are probably best made at a local or regional level with input from scientists, fishers, and managers. However, increasing scientific understanding of ecosystems, including anthropogenically-induced changes to ecosystem through fisheries, will benefit managers by concentrating efforts on the most immediate needs. For example, improved population and ecosystem models will allow the identification of the most endangered stocks and the most feasible life-stages to manage; identification of fisheries interactions with natural ecosystem processes and other anthropogenic disturbance will allow managers to anticipate indirect effects of new policies. The North Carolina shrimp trawl fishery, with its possible interactions with the returns of the blue crab fishery, is a prime example of why in-depth research is needed into ecosystems before fisheries managers can make the most balanced decisions for ecological and economic sustainability (Pew Ocean Commission 2003, USCOP 2004). Fisheries have made an imprint on the ecosystem with many direct and indirect effects, but investigating the ecological interactions resulting from fishing not only aid managers in solving problems but improve our understanding of communities and ecosystems in general.

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CHAPTER TWO:

Bycatch composition and survival in the estuarine shrimp trawl fishery in North Carolina, USA

Abstract

To understand the impacts of fisheries bycatch on marine populations, data on bycatch composition, quantity, and survival are needed. In North Carolina, the shrimp trawl fishery produces the second largest fishery income and its bycatch commonly includes species of commercial and recreational importance. In this study, bycatch and discards onboard estuarine shrimp trawlers equipped with required finfish excluders and TEDs were quantified, classified by species, and monitored for short-term survival and location of carrion in the water column. The major taxa in the bycatch both by weight and number were spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), and portunid crabs (*Callinectes sapidus* and *C. similis*); these three taxa accounted for about 80% of the bycatch by number and 70% of the bycatch by weight. All catch but penaeid shrimps were discarded. The average catch-per-unit-effort for all species combined was 57.7 kg/hr, with 12.0 kg/hr of shrimp caught. Twice as much shrimp was caught early in the five-day trawling week than later in the week, suggesting that more frequent closures may increase the efficiency of the shrimp trawl fishery. Crabs showed high survival while 78% of fish died either in the trawl nets or from subsequent stress on deck, generating a substantial amount of carrion in the estuaries, most of which sinks to the bottom. Although bycatch and discards

represent a significant portion of catch for estuarine shrimp trawlers in North Carolina, the ratio of bycatch:shrimp is relatively low compared to shrimp fisheries worldwide.

Introduction

Incidental catch, or bycatch, has accounted for roughly 8-20% of the world's fishery catch over the past two decades, and shrimp fisheries worldwide produce about one quarter to one third of that bycatch (Alverson et al., 1994; Kelleher, 2005). Bycatch refers to the non-targeted species or targeted species of undesired sex or size caught during fishing activities; discards are bycatch that is not kept for sale, consumption, or other uses. Bycatch can include a prohibited or undesirable portion of the targeted species, such as gravid females or undersized organisms, or non-targeted species including fish, invertebrates, marine mammals, sea turtles, and seabirds. Bycatch can have one of several fates: it can be kept for sale or personal use by the fisher or it can be discarded dead, alive and injured, or alive and healthy back into the system. Fishers may discard organisms due to lack of storage space, damage to the organism, the rate of spoilage of a species, high-grading when quotas or storage needs limit total catch, or possession of the organism may be illegal. In the United States, the Magnuson-Stevens Fishery Conservation and Management Act (Public Law 94-265) mandates that bycatch be minimized and that mortality of unavoidable bycatch be minimized. Bycatch concerns commercial fishers, fisheries managers, scientists and the public because it leads to unnecessary mortality, is wasteful, creates extra work for fishers, can create conflicts between fisheries when bycatch in one fishery would have value in other fisheries and can create or perpetuate changes in the ecosystem such as trophic organization (Alverson et al., 1994; Dayton et al., 1995; Crowder and Murawski, 1998; Pauly et al., 1998; Hall et al., 2000). Conservation of marine megafauna, including sea turtles, sharks, marine mammals and seabirds, depends on the minimization of bycatch throughout the world's oceans (reviewed in Lewison et al., 2004). Minimization of fish and invertebrate bycatch can improve fisheries sustainability and reduce impacts on trophic organization. Although technological innovations in fisheries gear and changes in temporal and spatial fisheries openings have been utilized to reduce bycatch and increase survivorship of discards, bycatch remains significant in most trawl fisheries as well as in most line and net fisheries.

As the paradigm in fisheries management shifts towards ecosystem-based management, it becomes more imperative to elucidate the direct effects of bycatch mortality on fisheries populations and the indirect effects of bycatch on the ecosystem. To understand the effects that bycatch and discarding may have on a system, it is first necessary to monitor what kind of bycatch is caught, determine what is discarded, and monitor survival to best estimate the mortality caused by bycatch. Determining the amount of dead and moribund discards is essential to estimate population mortality of discard species and to estimate the amount of discards available to scavengers in the system. It is further necessary to ascertain the amount of dead or moribund discards that floats and sinks in order to estimate availability to surface, pelagic, and benthic scavengers (Harris and Poiner, 1990; Wassenberg and Hill, 1990).

The penaeid shrimp fishery is the most valuable in the United States (NOAA-Fisheries, http://www.st.nmfs.gov/pls/webpls/mf_lndngs_grp.data_in) and is concentrated in the South Atlantic and Gulf regions. Shrimp are primarily harvested by otter trawl in commercial US fisheries, with one third of the fishing effort in bays, rivers and estuaries (Hall, 1999). Shrimp trawlers bring in large amounts of bycatch with their target catch (an average bycatch:catch ratio of 1.65:1) and usually discard this bycatch (Kelleher, 2005). Bycatch on estuarine shrimp trawlers usually contains juvenile demersal fish and juvenile and adult crabs, and can even include non-targeted size classes of the targeted shrimp species

(Crowder and Murawski, 1998; Diamond-Tissue, 1999). Although some species can survive, juveniles and some adults of many species are badly injured or killed by the trawling and sorting processes (Wassenberg and Hill, 1989; Hill and Wassenberg, 1990; Kaiser and Spencer, 1994**;** Ramsay et al., 1997; Davis, 2002). This has the potential to create conflicts between fisheries when potential catch in one fishery is lowered due to early mortality in trawlers or when quotas are filled in part due to bycatch. Mortality in shrimp trawlers may also cause underestimates of fisheries mortality in management models, potentially overestimating "safe" yields. Dead discards represent an additional food source to scavenging species in the path of trawlers, and the impact of this energy subsidy on commercially valuable species known to scavenge, such as demersal fish, crabs and shrimp, is unknown for estuarine areas of North America. Discards from trawling in the North Sea have the potential to support over 6 million seabirds, although the extent to which they are essential to maintenance of seabird populations remains unknown (Garthe et al., 1996; Camphuysen and Garthe, 2000). Fonds and Groenewold (2000) estimate that discards may generate about 7% of the maximum annual food demand of benthic predators in the southern North Sea, sufficient to maintain populations but not to further population growth. Although the magnitude of discards in these studies exceeds that generated by shrimp trawlers in estuaries, the physical constraints of estuaries concentrate discards in an area used by numerous marine populations.

In this paper I characterize the bycatch onboard estuarine trawlers in the central coast of North Carolina, quantify discards, examine short-term survival of discards, and partition discards into floating and sinking components. I compare the results to other bycatch studies and discuss implications for the management of shrimp and other estuarine fisheries.

Methods

Bycatch CPUE and Species Composition

Bycatch was sampled onboard commercial trawlers in Core Sound, Southern Pamlico Sound and Back Sound, North Carolina (Figure 2.1), in the spring and summer of 1999 and 2000. Fishermen were paid a modest amount to host observers, but were instructed to maintain their normal schedule, locations and tow times in the presence of observers. A local trawl fisherman helped to coordinate trips and insure that sampling trips represented regular fishing trips. Sampling trips were made only when fishermen would have fished anyway without observers. Most boats were 21-40 feet in length, and had two nets; all nets were fitted with the bycatch reduction devices (BRDs) and turtle exclusion devices (TEDs) required by North Carolina and federal law. The Florida Fish Eye (FFE) excluder was the most commonly used BRD; it is an opening at the top of the tailbag where reduced water flow allows fish to escape (Steele et al., 2002). Estuarine trawling is prohibited in North Carolina waters from sundown on Friday evenings to sundown on Sunday evenings; to test the null hypothesis that catch and bycatch do not differ over the fishing week, sampling trips were taken both on the opening night after the weekend closure (Sunday) and mid-week. Fishing trips commenced shortly before sundown and generally ended between 4 am and 9 am. Multiple tows were completed during this time, lasting from 29 to 142 minutes, with an average duration of 90 minutes. Boats traveled between 2 and 2.5 mph during trawling, and the average depth of areas trawled was approximately 8 feet.

On sampling trips, the catch and bycatch of the first and third tows were identified and quantified to test the null hypothesis that catch and bycatch do not differ over the course of a trip. The total catch from both nets was weighed from the first and third tows on each trip and then a subsample (a full five-gallon bucket, or approximately 11.5 kg) was taken from each catch and sorted by species (or to lowest taxonomic division possible). The total catch was mixed with a large plastic shovel before taking the subsample. For each species, the total number and weight in the subsample were recorded. For species that could not be identified in the field, representative samples were frozen or preserved in 10% formalin and returned to the lab for identification. Wet weights were determined using spring scales on board the boats (25 kg spring scale, John Chatillon & Sons, Kew Gardens, New York) or balances in the laboratory (Sartorius Electronic Balance, Sartorius Corporation, New York). Shrimp from the subsample were weighed and returned to the fisherman; the total shrimp catch for each tow was also recorded. Tow duration, towing speed, and location of tow were recorded for each tow.

For each tow, total weight of each species (or lowest taxa to which organisms were identified) of the bycatch was calculated by scaling up the weight from the subsample:

Total weight_i = (weight *i* in subsample/subsample weight) x total weight catch for tow

where *i* is the species. Total numbers of each species in each tow were calculated in a similar fashion:

Total number_i = (number *i* in subsample/subsample weight) x total weight catch for tow

Total weight for the entire catch and total weight for all shrimp, blue crabs, and all fish were converted to catch per unit effort (CPUE) in kg/hr using total weight and tow duration. CPUE was log-transformed to meet the assumption of equality of variances (tested with Bartlett's Test) for analysis of variance (ANOVA), then a three-factor ANOVA was run using tow duration (short, <90 minutes, or long, >90 minutes), time of week (early in week [Sunday] or late in week [Tuesday through Thursday]), and tow time (early [first tow] or late [third tow] in the night) as fixed factors. When ANOVA indicated significant effects of factors and/or their interactions, means were compared with Tukey's test for post-hoc comparisons.

For the pooled data from the entire sampling period, species rankings were determined by summing the numbers and weights from every tow and then ranking the species separately by number and weight, excluding shrimp.

Bycatch:shrimp and fish:shrimp ratios were determined by averaging the ratios of each tow. Pearson correlation coefficients were calculated to determine whether bycatch CPUE and shrimp CPUE or fish CPUE and shrimp CPUE were correlated.

Fate of the Discarded Bycatch

To determine the fraction of discarded bycatch that survives being caught in the trawl and sorted on deck, common species from the bycatch of shrimp trawlers were collected from the nets and their survival monitored after 15 and 30 minutes out of the water. Sorting of the catch is generally completed about 30 minutes after nets are brought out of the water; survival was monitored at 15 and 30 minutes to determine whether survival changed with increased time out of water. Only common species were tested due to the need to rapidly collect organisms for testing when the catch was brought on deck. Ten animals of each common species in the bycatch (defined as having greater than 30 individuals in the subsample) were individually placed in buckets of aerated seawater after 15 minutes and after 30 minutes exposure to air on deck and classified as dead, alive but injured or immobile, or alive and presumed healthy. After individuals were tested, they were measured and discarded, and different individuals were used for the 15-minute and the 30-minute trials.

The proportion of organisms alive from each sampling trip was compared with a two factor ANOVA with taxa (crabs, spot, croaker and pinfish) and time out of water (15 or 30 minutes) as fixed factors. Due to the low survival of spot, homogeneity of variances was not achieved even with data transformations; however, Underwood (1997) states that ANOVA are robust to heterogeneous variances when sample size is large ($n>6$) so analysis was performed anyway. When significant ($p<0.05$) or marginally significant ($p<0.08$) effects were indicated by ANOVA, Tukey's test was used for post-hoc comparisons.

To determine whether dead, discarded bycatch floats or sinks, we recorded whether dead individuals in our survival trials floated or sank within 10 seconds of being placed in a tank of aerated water.

Results

Bycatch CPUE and Species Composition

Fifty trawls were analyzed for species composition. The average catch per unit effort (CPUE) for all catch and bycatch combined in all trawls was 57.7 (SE 10.3) kg hr^{-1}. Average CPUE was 12.0 (SE 1.2) kg hr^{-1} for shrimp, 15.3 (SE 1.8) kg hr^{-1} for fish, and 19.0 (SE 8.4) kg hr^{-1} for blue crabs with the difference made up by other invertebrates, algae, and wood pieces. Overall, shrimp comprised about 21% of the catch by weight, fish 27% of the catch, blue crabs 33% of the catch, and other organisms, such as jellyfish, horseshoe crabs, and other species of shrimp and crabs 20% of the catch. By numbers, an average of 1094 (SE 113) fish and 265 (SE 26) crabs were caught per hour of trawling. The most common bycatch taxa by weight and by number are given in Table 2.1; spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), portunid crabs (*Callinectes sapidus* and *C.*

similis), and pinfish (*Lagodon rhomboides*) dominated in number and weight and were each present in 90% of tows or more.

CPUE of all organisms in the catch, or Total CPUE, was not significantly affected by tow (first or third tow of the trip), day of the week, tow duration or their interactions in analyses of variance (Table 2.2). The interaction between all three factors was marginally significant ($p=0.079$), so post-hoc comparisons were performed with Tukey's test. The only marginally significant relationship ($p=0.066$) indicated by Tukey's test was that early in the week and early in the trip, short tows had more than three times greater total CPUE than long tows (Figure 2.2).

Analysis of variance for shrimp CPUE showed no significant interactions between factors (Table 2.2). ANOVA indicated that significantly more (56%) shrimp caught early in the week than late in the week (Tukey's test $p<0.01$; Figure 2.3). There was a marginally significant ($p=0.056$) effect of time of trip on shrimp catch; an average of 47% more shrimp were caught early in the trip (night) than late in the trip (Tukey's test $p<0.05$; Figure 2.3).

There were marginally significant two-way interactions in the three-factor ANOVA of fish CPUE for tow duration and time of week and for tow duration and time of night (Table 2.2). For tows of long duration, tows early and late in the week had statistically similar CPUEs, but for tows of short duration there was 90% more catch early in the week than late in the week (Figure 2.4); post-hoc comparisons with Tukey's test showed no significant differences. For tows of long duration, tows early in the evening had 16% higher CPUE than tows late in the evening, but for short tows, tow early in the evening caught only 62% of the fish caught later in the evening per unit effort (Figure 2.4); again, no significant differences were indicated by post-hoc comparisons using Tukey's test.

Analysis of variance of blue crab CPUE showed a significant interaction for tow duration and time of week ($p = 0.017$), but no higher order interaction or effect of time of night (Table 2.2). Early in the week, tows of short duration had 86% greater CPUE than long tows, but later in the week this relationship reversed, with shorter tows catching about 40% the blue crabs of longer tows (Figure 2.5); post-hoc comparisons using Tukey's test indicated that short tows were significantly smaller later in the week than short tows early in the week ($p=0.083$).

Bycatch:shrimp ratios varied greatly among tows, but the average bycatch:shrimp ratio by weight for all trawls was 3.9:1 (range across tows 0.1:1 to 11.8:1, median 3.5:1). Fish:shrimp ratios varied dramatically as well, ranging from 0 to 6.9:1 across tows with a mean of 1.65:1 and a median of 1.1:1. The Pearson correlation coefficient for bycatch CPUE and shrimp CPUE was 0.464 ($p=0.001$), but was influenced strongly by one outlier; when removed the correlation was 0.101 ($p<0.489$). Fish CPUE and shrimp CPUE had no significant correlation (Pearson correlation coefficient 0.057, $p=0.695$).

Fate of the Discarded Bycatch

ANOVA indicated a significant effect of species and of time out of water (short, 15 minutes, and long, 30 minutes), but no significant interaction (Table 2.3). Crabs showed 52% greater survival than croaker, 62% greater survival than pinfish, and 77% greater survival than spot (Tukey's test, $p<0.001$, Figure 2.6). Croaker showed 25% greater survival than spot (Tukey's test, $p<0.001$, Figure 2.6). Survival was 12% greater after 15 minutes on deck than 30 minutes on deck (Tukey's test, $p<0.01$, Figure 2.6). Overall, 11% of fish survived uninjured, 11% survived but were injured or unresponsive, and 78% of fish died before being returned to the water.

Overall, 26% of individual fish floated and 74% sank (Table 2.4). The breakdown by species was similar, although flounders always sank.

Discussion

Bycatch and discards of this estuarine shrimp trawl fishery were highly variable. The bycatch and discards in this study were primarily made up of juvenile estuarine fish and juvenile and adult blue crabs. In Diamond-Tissue's (1999) study, which included bycatch composition data from two trawl trips (four tows) in Core Sound, NC, shrimp made up approximately 25% of the catch by weight, only slightly higher than the 21% found in this study. Diamond-Tissue (1999) found more mojarra and mantis shrimp (3% and 2% by number) in the bycatch in Core Sound than this study did (negligible by number and weight for both species), but far fewer blue crabs (about 12% of the amount by weight caught in this study). Coale et al. (1994) examined the catch composition of a commercial shrimp trawler for 25 nights in nearby waters (near Back Sound, NC); their study found similar species composition of the bycatch, which was also dominated by sciaenid fish and portunid crabs with only slight differences in relative contributions to the biomass.

Overall, the ratio of bycatch:catch (3.9:1) was high relative to other commercial fisheries worldwide and high compared to the most recent weighted average ratio of worldwide shrimp fisheries (1.65:1) reported by Kelleher (2005), although low compared to the 1994 review by Alverson et al. which reported an average bycatch:catch ratio of 5.2:1. Fish:shrimp ratios in this study are 20% that of a similar study conducted nearby before

BRDs and TEDs were required (Coale et al., 1994), indicating that such bycatch reduction devices are reducing bycatch more rapidly than shrimp catch. Federal and state regulations requiring the use of bycatch reduction devices (BRDs, also called "fish excluders") and turtle exclusion devices (TEDs) may have decreased the bycatch:catch ratio in North Carolina's estuaries relative to those studies included in Alverson et al. (1994). Bycatch is frequently reported in fish:shrimp or bycatch:shrimp ratios because often the only available information for scaling up from individual observations to the entire fishery is the amount of shrimp catch. However, Diamond (2003) reports that a CPUE estimator is most appropriate for scaling up and that fish:shrimp and bycatch:shrimp tend to overestimate bycatch, which is supported by the low correlation in this study between shrimp catch and bycatch. The numbers reported here for bycatch:shrimp are thus intended for comparison to other studies and not intended for use to estimate the total bycatch in the fishery.

Shrimp CPUE was higher just after the weekend closure, while there was no significant difference in fish or crab CPUE with time of the week. There was also a trend towards higher shrimp CPUE earlier in the trawling trip than later in the trip, suggesting further that shrimp CPUE is higher after even a short break from trawling. Shrimp tend to move through the sounds as they exit the nursery grounds higher up the estuary and move towards the ocean, and the transient nature of the resource and this evidence that it is partially depleted during trawling suggests that it is not being harvested as efficiently as possible. The other significant or marginally significant effects of tested factors on CPUE primarily concerned tow duration or interactions of other factors with tow duration. This suggests that tow duration may be important for managing bycatch, but patterns were inconsistent with short durations sometimes producing less bycatch and sometimes producing more bycatch. Tow duration can change due to a variety of factors, including fishing conditions, weight of catch, decisions by the fisher to move to a better fishing ground, or physical constraints of the fishing ground (fishers may raise nets to negotiate a tight turn, for example). This study suggests that managers or fishers interested in decreasing bycatch may wish to design further experiments to elucidate the possible benefits of manipulating tow duration to decrease bycatch and consequently sorting time, which would increase survival of finfish bycatch as well. Further, the low correlation between shrimp CPUE and bycatch CPUE suggests that bycatch might be reduced without concomitant loss of shrimp catch.

The spot, Atlantic croaker, and pinfish that made up the majority of the fish bycatch showed low survival (0-40%), and were thus often returned dead to the water following trawling. Crab survival in this study was seven times greater than fish survival, and crab survival did not decrease with increasing time on deck. Therefore, mortality for crabs probably occurs primarily in the nets during trawling or the hauling back of nets; most dead crabs were juveniles or recently molted crabs (pers. obs.). Coale et al. (1994) also looked at survival of organisms caught as bycatch in estuarine shrimp trawlers in North Carolina, but their methodology differed in that organisms were immediately placed in a large onboard tank following emptying of the net which reduced the exposure of the bycatch to air. Survival of portunid crabs was high in their study (94%), and survival for finfish (pinfish, 76%; croaker, 63%; spot, 34%) was lower than that for crabs, with spot showing the lowest survival among the four taxa as in this study (Coale et al., 1994). Wassenberg and Hill (1989) and Kaiser and Spencer (1995) also studied survival of organisms caught as bycatch in trawlers, although in deeper waters and, in the second study, on research vessels rather than commercial trawlers. Wassenberg and Hill (1989), working in Moreton Bay, Australia, found relatively high survival of portunid crabs (86%) and high mortality of most fish species (80%) when testing survival following exposure to air on deck. Kaiser and Spencer (1995), working in North Wales, United Kingdom, found higher mortality than this study among swimming crabs caught as bycatch (50-57%), but similar mortalities for small finfish (60-97%); however, their study followed mortality for much longer, up to 144 hours, after trawling was completed and their methodology was unclear about the time the bycatch was exposed to air before being placed in tanks. These studies, combined with the present study, show a widespread pattern in higher finfish mortality than crustacean mortality in a variety of trawling areas and that finfish bycatch mortality is generally high (over half the finfish bycatch died in every study).

Survival tests in this study looked at short-term survival (up to 30 minutes) of the common species captured by trawlers, and may overestimate survival if injured or apparently healthy discards show lasting effects of their time in the net or on board the boat (Davis, 2002). The shock of being returned to the water, the swarming of scavenging birds around the boat and the effect of shock on the ability of a survivor to evade predators or to avoid recapture all increase the risk of mortality following capture in a trawl even if an organism survives the immediate process of capture. Bergmann et al. (2001) found that even crustaceans that survived trawling and sorting on deck of trawlers demonstrated negative physiological effects from the experience, which could lead to decreased fitness following return to the water. Thus, trawling likely imposes greater mortality on juvenile fish and invertebrate populations than calculated here. Furthermore, the effects of trawling on benthic organisms that are damaged but not caught in the nets (often referred to as “bykill” or “collateral mortality”) have not been considered in this study, and represent additional mortality (Van Dolah et al., 1987; Van Dolah et al., 1991; Bergman and Hup, 1992; Kaiser and Spencer, 1994; Bergman and Van Santbrink, 2000).

To fully understand the impact of discarding on the system, a rough calculation of the amount of discards entering the system is helpful. If each trawler tows for about 8 hours per trip, for fish discards alone (15.3 kg/hr) each boat produces122 kg of bycatch per trip. This may be a slight overestimate if some bycatch is caught more than once. Mortality for fish is 78%, so on average 95 kg of dead fish are discarded per boat per trip. Of these discards, approximately 24% floats and 76% sinks, so each boat produces about 23 kg of floating discards, available to surface scavengers such as gulls and terns, and 72 kg of sinking discards, available briefly to scavengers at the surface and in the water column but then primarily to benthic scavengers. In just one week (five days) of trawling, a single boat can produce 475 kg of dead discards of fish alone. Fish discards alone from these estuarine trawlers represent a large potential food source for opportunistic and obligate scavengers. In North Carolina, many valuable fishery species such as blue crabs, shrimp, and sciaenid fish are opportunistic scavengers, as are many marine mammals and sea turtles. Transfer of benthic production to surface and pelagic scavengers potentially alters food web and community dynamics by increasing scavenger populations in the subsidized areas (Garthe et al.,1996; Polis et al.,1997; Hall et al., 2000).

This research suggests new directions in the management of the shrimp fishery. Shrimp CPUE was higher earlier in the week than late in the week, and earlier in the trip than late. This suggests that breaks in trawling, both weekend closures and breaks during the heat of the day during the summer, allow a “replenishment” of the shrimp. Thus, the efficiency of the fishery may be improved by increasing the number of breaks in the week, either by having two one-day closures during the week rather than one two-day closure, or by reducing the number of total days during the week for which trawling is allowed. Management changes restricting commercial fishing tend to be contentious, but minimizing trawling time has the added benefit of lowering fuel costs, reducing labor and reducing benthic disturbance. The Gulf of Mexico shrimp fishery is overcapitalized (Onal et al., 1991; Ward and Sutinen, 1994), with increases in effort leading to little increase in catch. Onal et al. (1991) suggest that in the Texas shrimp fishery, a 38% reduction in effort would result in only a 6% reduction in shrimp catch with the added benefit of reducing bycatch and benthic disturbance. A similar evaluation of whether decreasing effort would be economically and environmentally beneficial would be a valuable management exercise in North Carolina.

This study has multiple applications to the management of other valuable North Carolina fisheries. This study demonstrates that substantial mortality for finfish species occurs in the estuarine shrimp trawling fishery in North Carolina. Large losses of fish species to bycatch mortality alters mortality estimates in fisheries management models, and must be considered to most accurately predict species responses to management plans, especially in the necessary shift towards ecosystem-based fisheries management (Botsford et al., 1997). For example, Diamond-Tissue (1999) found that while shrimp trawling was not the main source of mortality for Atlantic croaker, decreasing bycatch mortality could increase population size. In the Gulf of Mexico, the Gulf of Mexico Fishery Management Council concluded that red snapper was severely overfished and their management plan for recovery included bycatch reduction onboard shrimp trawlers. Especially as fishing mortality grows closer to or exceeds sustainable limits, bycatch mortality becomes more important for fisheries management (Hall et al., 2000). Bycatch mortality for commercially and recreationally valuable species should be considered in stock assessments and management plans when data is available. Of the most common species in the bycatch, spot, croaker, blue crabs, pigfish and flounder are all commercially and recreationally fished in North Carolina, and pinfish are recreationally fished. Of these, only blue crabs are listed as a "species of concern" for fisheries management by the North Carolina Division of Marine Fisheries, meaning that some indicators suggest the fishery is overfished but stock assessments are unavailable or incomplete.

The blue crab fishery in North Carolina is the most valuable commercial fishery, followed by the shrimp fishery. This study suggests that management of the shrimp fishery may affect the blue crab fishery as well, both directly (through bycatch mortality) and indirectly (through provision of discards that could feed blue crabs). Although mortality was low for blue crabs discarded in the shrimp trawl fishery, the magnitude of catch of blue crabs means that even low mortality could affect a large number of blue crabs. Including trawler mortality in blue crab stock assessments is necessary to determine the significance of this mortality to the population dynamics of blue crabs.

The magnitude of bycatch and discards resulting from even small trawling operations in estuaries has important implications for food web dynamics and for fisheries management. The availability of large amounts of dead fish and invertebrates to scavengers has the potential to alter food web dynamics in a system, or support larger scavenger populations than would otherwise be possible. In estuaries, this food subsidy may have greater potential to impact food web dynamics because the food subsidy is contained in a smaller area with tighter connectivity between populations. While discard availability to scavengers in the open ocean could still provide a significant food source, the spatial extent of the discarding is much larger and the same populations are unlikely to be constantly provided with a food subsidy. Blue crabs are known opportunistic scavengers and food availability may drive their distribution at broad scales (Seitz et al., 2003). The possibility that blue crabs in trawled estuaries could be subsidized by trawler discards suggests that management of shrimp trawl fisheries must be viewed in the context of its effects on other valuable fisheries, both negative and, possibly, positive.

Improved data collection for direct fishery mortality and for bycatch mortality is necessary for understanding and therefore better managing fisheries worldwide, and this study demonstrates that the collection of such data with specific hypotheses in mind allows statistical demonstration of catch and bycatch patterns which can better serve managers. This study suggests that fisheries managers in North Carolina could improve the efficiency of the shrimp fishery by increasing the frequency of closures and should examine the possibility that the North Carolina shrimp fishery is overcapitalized. The evidence of large quantities of finfish mortality and possible interactions with the blue crab fishery in the North Carolina shrimp fishery provides further evidence for the importance of managing fisheries in a multispecies context rather than as unconnected units.

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Table 2.1. Most Common Taxa in the Bycatch. Rankings of taxa in bycatch by number, with percent of total number and total weight of bycatch, percent of trawls in which taxa was present, and average length where applicable.

Species	Rank, By number	Percent of total number	Percent of total weight	Percent of trawls in which present	Average length (mm)
Spot, *Leiostomus xanthurus*	1	45%	21%	98%	84.3
Atlantic Croaker, *Micropogonias undulates*	2	23%	8%	96%	114.6
Crabs, *Callinectes sapidus* and *C. similis*	3	11%	40%	98%	83.5
Pinfish, *Lagodon rhomboides*	4	9%	4%	90%	73.3
Silversides, *Menidia menidia*	5	5%	<1%	84%	66.1
Pigfish, *Orthopristis chysoptera*	6	1%	2%	68%	117.2
Summer flounder, *Paralichthys dentatus*	7	1%	1%	76%	110.6
Blackwing Searobin, *Prionotus rubio*	8	1%	<1%	68%	85.8
Key brotula, *Ogilbia cayorum*	9	1%	<1%	18%	99.9
Fringed flounder, *Etropus crossotus*	10	<1%	<1%	52%	75.0
Other Invertebrates (jellyfish, mantis shrimp, etc.)		NA	18%	98%	NA

Table 2.2: ANOVA Results for CPUE Data. ANOVA tables for Log(Total CPUE), Log(Shrimp CPUE), Log (Fish CPUE) and Log (Crab CPUE) by fixed factors tow duration (Dur), time of night of tow (TN), and time of week (Day) and their interactions. Post-hoc Tukey's simultaneous test results shown for p<0.10. *df* – degrees of freedom; MS – mean square; F – test statistic; *p* – probability value.

		df	MS	F	*p*
Log (Total CPUE)	Dur	1	0.0035	0.03	0.855
	TN	1	0.2056	2.01	0.164
	DAY	1	0.2648	2.59	0.115
	Dur*TN	1	0.2533	2.48	0.123
	Dur*DAY	1	0.1743	1.70	0.199
	TN*DAY	1	0.0006	0.01	0.940
	Dur*TN*DAY	1	0.3317	3.24	0.079
	Error	42	0.1023		

Tukey's Test: short Dur, early TN, early DAY > long Dur, early TN, early DAY (p=0.066)

		df	MS	F	*p*
Log (Shrimp CPUE)	Dur	1	0.0874	1.87	0.178
	TN	1	0.1801	3.86	0.056
	DAY	1	0.3299	7.07	0.011
	Dur*TN	1	0.0009	0.02	0.891
	Dur*DAY	1	0.0080	0.17	0.681
	TN*DAY	1	0.0618	1.33	0.256
	Dur*TN*DAY	1	0.1409	3.02	0.089
	Error	42	0.0466		

Tukey's Test: early DAY > late DAY (p<0.01); early TN > late TN (p<0.05)

		df	MS	F	*p*
Log (Fish CPUE)	Dur	1	0.0237	0.11	0.739
	TN	1	0.0114	0.05	0.817
	DAY	1	0.4118	1.95	0.170
	Dur*TN	1	0.7510	3.55	0.066
	Dur*DAY	1	0.6978	3.30	0.076
	TN*DAY	1	0.5043	2.39	0.130
	Dur*TN*DAY	1	0.3890	1.84	0.182
	Error	42	0.2113		

Tukey's Test: No significant relationships

		df	MS	F	*p*
Log (Crab CPUE)	Dur	1	0.2693	0.83	0.368
	TN	1	0.0155	0.05	0.828
	DAY	1	0.1851	0.57	0.454
	Dur*TN	1	0.3124	0.96	0.332
	Dur*DAY	1	2.0263	6.25	0.017
	TN*DAY	1	0.0073	0.02	0.882
	Dur*TN*DAY	1	0.7056	2.17	0.148
	Error	41	0.3245		

Tukey's Test: early DAY short Dur > late DAY short Dur (p=0.083)

Table 2.3. ANOVA Results for Survival of Discards. ANOVA table for proportion of organisms alive by taxa (blue crab, Atlantic croaker, pinfish, spot) and time out of water (short, 15 minutes; long, 30 minutes). *df* – degrees of freedom; MS – mean square; F – test statistic; *p* – probability value.

	df	MS	F	*p*
Species	3	3.3578	76.15	0.000
Time out of water	1	0.3772	8.55	0.004
Species*time out of water	3	0.0792	1.80	0.152
Error	116	0.0441		

Tukey's Test: Crabs > Croaker, Pinfish, Spot (p<0.001)
Croaker > Spot (p<0.001)
Short > Long (p=0.004)

Table 2.4. Results of Floating/Sinking Experiments. Number and percent of dead organisms floating and sinking upon discarding, by species.

Species	Number Floating	Number Sinking	Percent Floating	Percent Sinking
Croaker	23	86	21	79
Flounder	0	38	0	100
Pigfish	5	12	29	71
Pinfish	41	71	37	63
Spot	53	145	27	73
Total	122	352	26	74

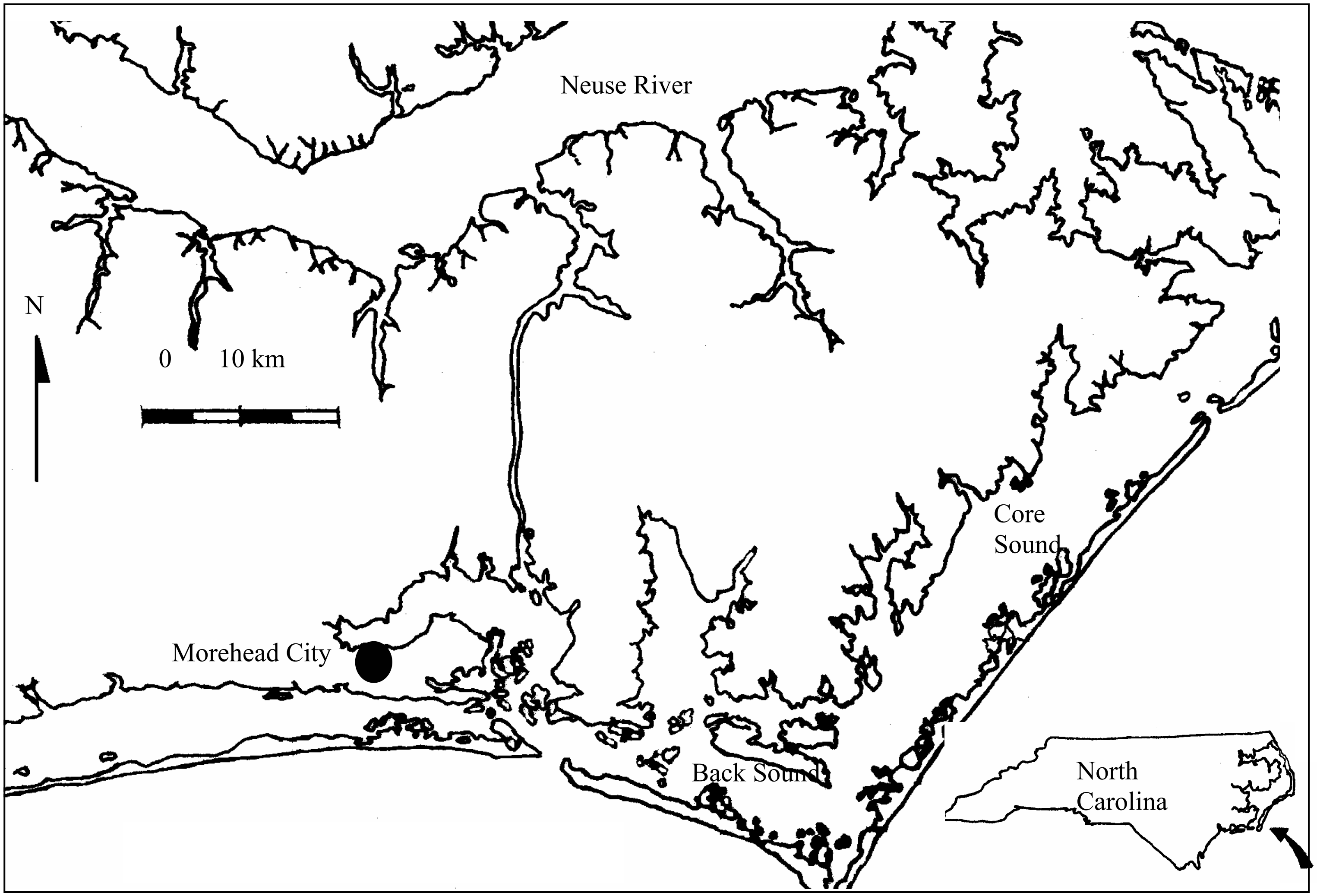

Figure 2.1. Map of North Carolina's Central Coast. Field sites included Core Sound and Back Sound, North Carolina.

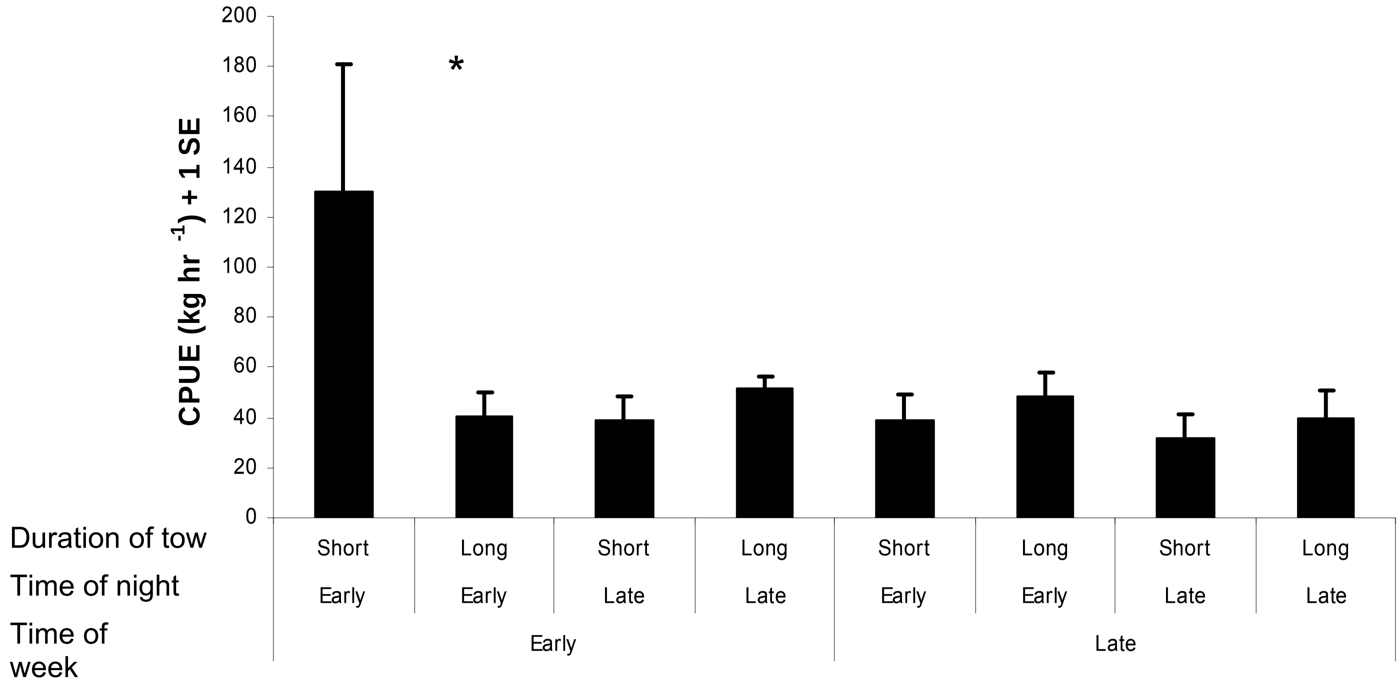

Figure 2.2. Mean total catch CPUE (kg/hr) by time of week, time of night, and tow duration. ANOVA indicated a marginally significant three-way interaction of factors, with the only Tukey's test with $p<0.10$ between the first two bars.

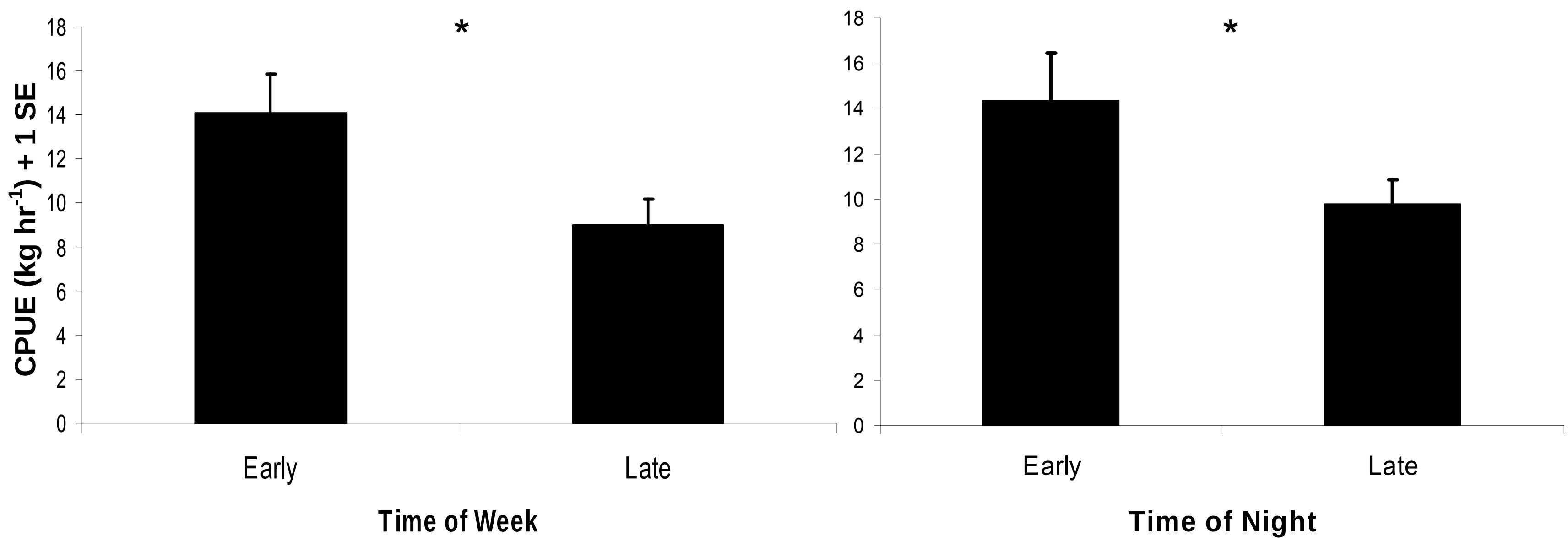

Figure 2.3. Mean shrimp CPUE (kg/hr) + 1 SE by time of week and time of night. Replicates were pooled across other treatments. ANOVA indicated a significant effect of time of week, and a marginally significant effect of time of night. Tukey's tests indicated significantly greater catch earlier in the week ($p<0.01$) and early in the night ($p<0.05$).

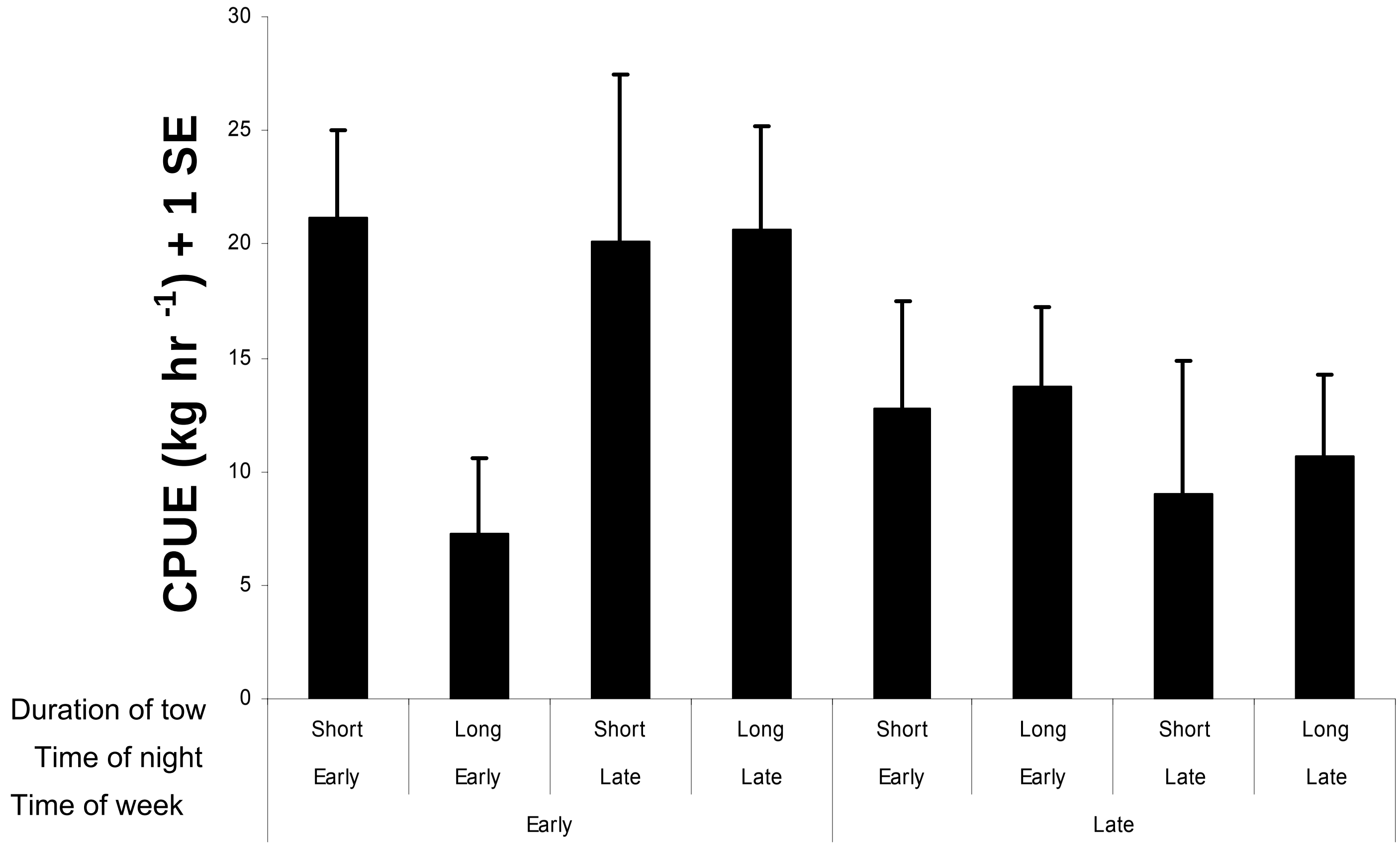

Figure 2.4. Mean fish CPUE (kg/hr) by time of week, time of night, and tow duration. ANOVA indicated marginally significant interactions between tow duration and time of night, and tow duration and time of week; no significant relationships were indicated by post-hoc Tukey's tests.

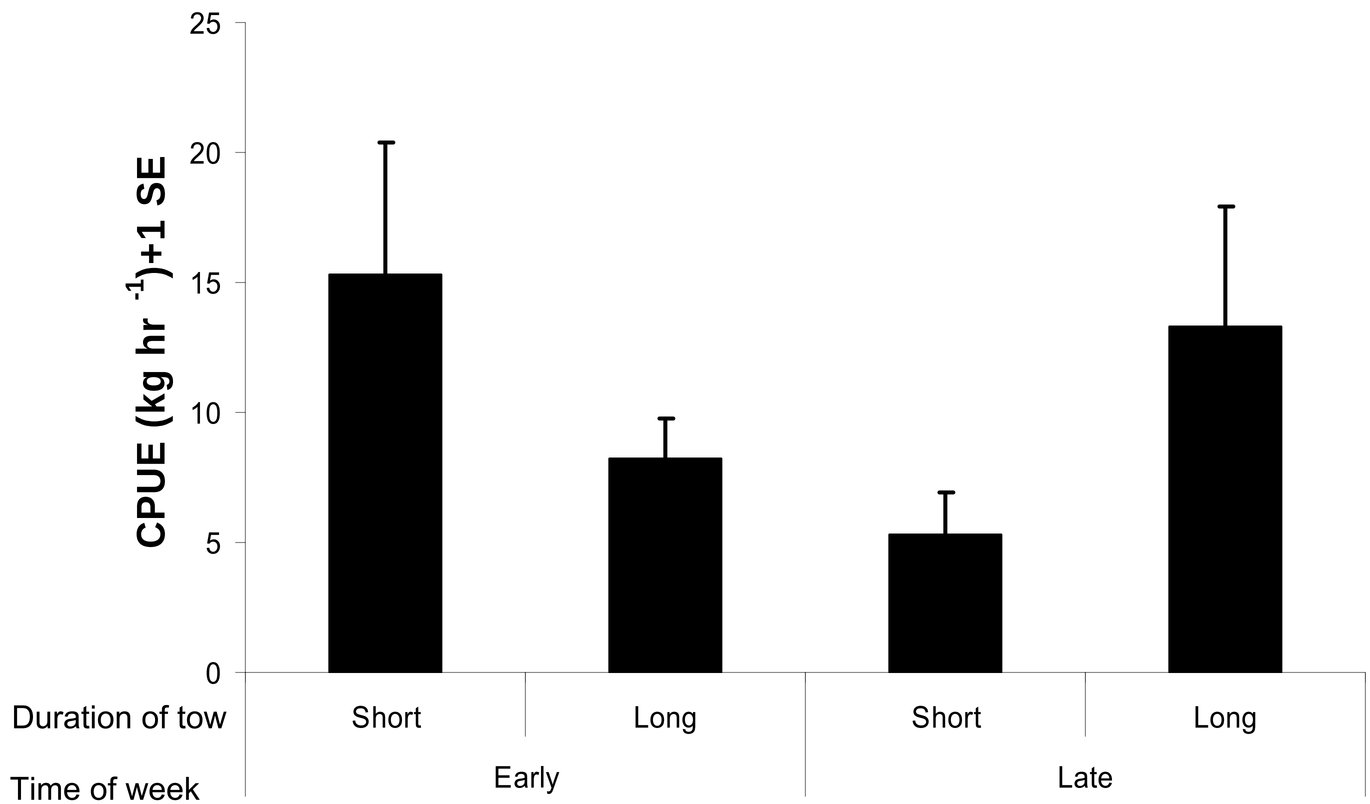

Figure 2.5. Mean crab CPUE (kg/hr) by time of week and tow duration. Replicates were pooled across time of night. ANOVA indicated a significant interaction of between tow duration and day, with the only Tukey's test of $p<0.10$ between the short tows, with early > late ($p=0.08$).

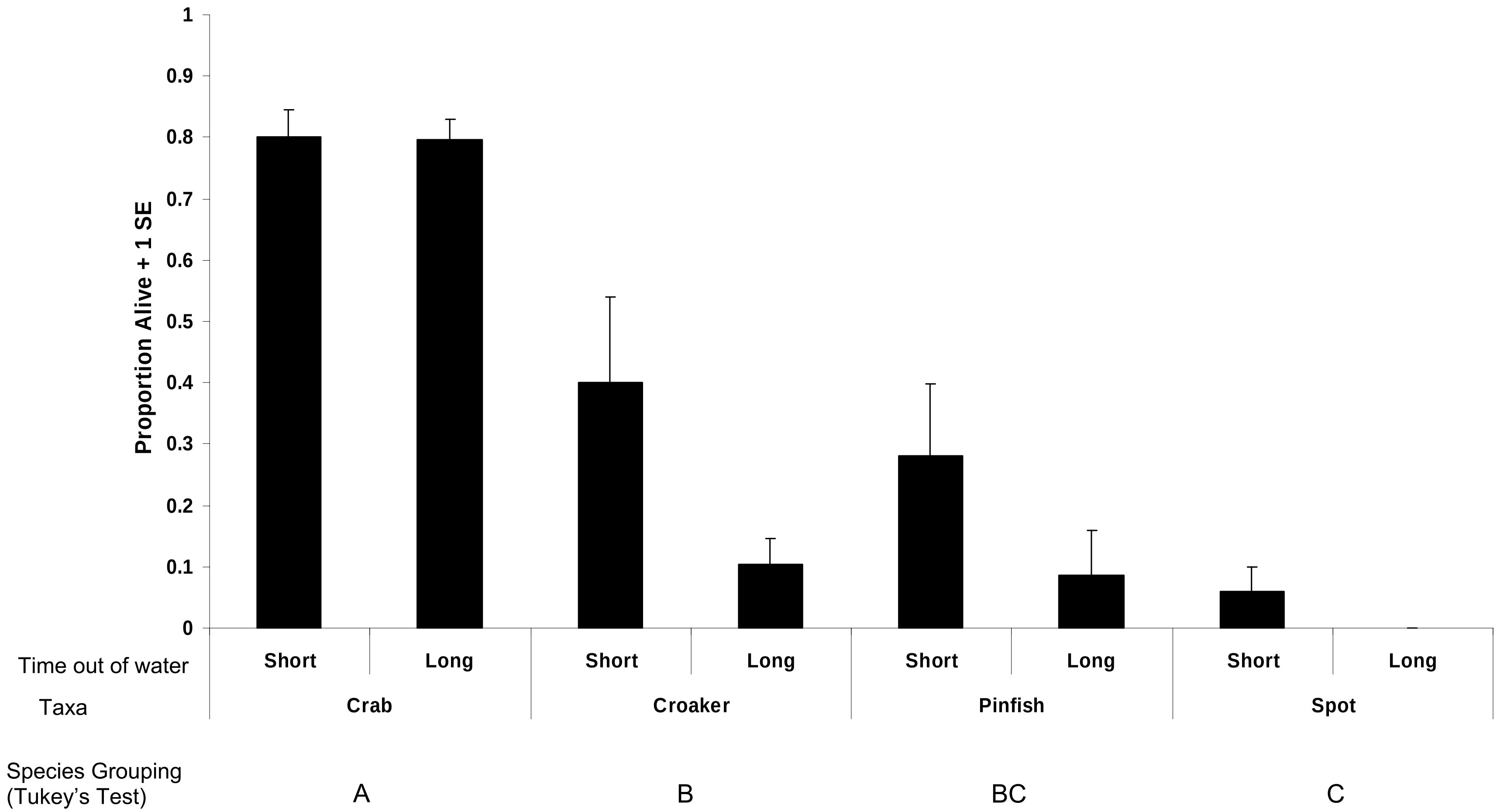

Figure 2.6. Survival of Commonly Discarded Organisms. Proportion of organisms alive after 15 minutes (short) and 30 minutes (long) on deck after trawling. For pooled data, survival after 15 minutes was greater than survival after 30 minutes on deck (Tukey's test, p=0.004).

CHAPTER THREE

Do shrimp trawler discards benefit other fisheries species?

Scavenging upon discards and its potential food web impacts

Abstract

The waste generated through bycatch by fisheries is a major concern of scientists and managers, but little attention has been given to the ecological impacts of fisheries discards on trophic relationships. Large quantities of discards, especially from shrimp trawlers, which produce the highest bycatch:catch ratio of commercial fisheries, may have great impact in estuaries or rivers where the distribution of discards is more concentrated than in large shelf areas. I examined the occurrence of scavenging on discards in the central coast estuaries of North Carolina and the preference of scavengers for discards over their natural prey in the field, laboratory, and mesocosm experiments. Scavenging for discards occurred mainly by birds during the short time discards were on the surface and by benthic scavengers in the lower meter of the water column, where the main scavengers responding to discards in lift nets and pots were blue crabs and pinfish. Blue crabs captured by commercial trawls showed greater amounts of fish and shrimp in their guts than seen in studies of natural feeding in the literature, and crabs with fish and shrimp in their guts had twice as much food in their guts than those that fed only on natural prey. In short laboratory feeding preference experiments blue crabs showed a statistically significant, six times greater feeding on discards then one of their natural prey, the juvenile hard clam, and this was replicated in mesocosm experiments

lasting three days, where predation on juvenile hard clams was 33-60% less in treatments where discards were added. Feeding by blue crabs and other scavengers on shrimp trawler discards can temporarily reduce predation on natural prey such as clams, which may eventually allow greater biomass of scavengers. Both the relaxation of predation on hard clams and the possible increase in blue crab numbers could benefit their respective fisheries. This impact of shrimp trawler discards on blue crab feeding should be taken into account by managers seeking to reduce bycatch in the shrimp fishery, as it could decrease blue crab populations where food is limited or increase feeding on alternate prey such as the commercially valuable hard clam.

Introduction

Food subsidies have the potential to alter local food web dynamics, decoupling the dynamics of consumers from those of local producers and altering competitive interactions (Polis et al. 1996, Polis et al. 1997). Consumers with access to food subsidies may be released from resource limitation, allowing coexistence of greater numbers of individuals or species, and competitive interactions for food resources among consumers may also be altered by food subsidies (Polis et al. 1996, Polis et al. 1997). Natural examples of food subsidies and their effects include the flow of marine production to coastal communities increasing numbers of spiders, lizards and coyotes and, often, also increasing their predation on alternate prey (Polis and Hurd 1996, Rose and Polis 1998). Macrophyte deposition in intertidal communities allows the coexistence of limpet species at higher densities when kelp is present than allowed by local food sources (Bustamante et al. 1995) and increases numbers of predators including endangered shorebirds when wrack input to beaches is high (Dugan et al. 2003). The movement of anadromous salmon to streams provides an important food subsidy to consumers including mammalian, avian, and piscine predators and opportunistic scavengers (reviewed in Willson and Halupka 1995), and the bald eagle, which increase in number as salmon abundance increases (Restani et al. 2000). Anthropogenic food subsidies to animal populations include garbage, which can increase populations from microbes to insects to coyotes and gulls, and agriculture from the industrial scale to the small home garden, which can subsidize insects, birds, and other mammals. Garbage availability has been linked to increased numbers of grizzly bears in Yellowstone National Park (Knight and Eberhardt 1985), and increased body weight in mongooses (Otali and Gilchrist 2004) and baboons (Altmann et al. 1993), which has the potential to increase reproductive fitness and survival. Because of the abundance of agricultural lands in the midwestern United States through which they migrate, many geese are no longer subject to density-dependent food limitation during their migration to the eastern Canadian arctic resulting in increased numbers at summer grounds (reviewed in Jefferies 2000). As humans continue to exert greater influence over natural communities, including the increased delivery of food subsidies, understanding the community response to these changes is necessary for proper ecosystem-based management of valued resources.

Extracting fish from the sea represents a major perturbation of a natural system by humans, through removal of organisms, through disturbance of the seafloor and associated habitat structures, and through the delivery of food subsidies back into marine systems with the discarding of unwanted bycatch and offal. The magnitude of discarding of fish and invertebrates worldwide has been most recently estimated at 7.3 million tones annually (Kelleher 2005), which is substantially lower than the previous FAO estimate of 27 million tonnes by Alverson et al. in 1994. The reduction is likely the result of increased utilization of bycatch (non-targeted) species and technological advances that allow avoidance of some bycatch through increased gear selectivity and spatial or temporal avoidance of high bycatch areas (Kelleher 2005, Zeller and Pauly 2005). Consistent among bycatch assessments of world-wide discards is the high bycatch among shrimp fisheries globally. Shrimp fisheries have the highest bycatch:catch ratio (Alverson et al. 1994), primarily due to the small size of the target catch and the tendency for shrimp to live in areas also populated by other juvenile crustaceans and juvenile fish.

The influence of discards on trophic relationships in marine food webs is poorly understood, but discards from shrimp fisheries represent a large foodfall to marine scavengers. Scavengers on carrion generated by fisheries may be obligate or facultative, but facultative scavengers tend to be more abundant (Britton and Morton 1994). Most studies on scavenger utilization of discards have focused on large shelf and sea areas and on feeding by seabirds, which demonstrated changes in foraging behavior, competitive interactions, and mating success due to discards (e.g. Blaber and Wassenberg 1989, Garthe et al. 1996, Oro and Ruiz 1997, Martinez-Abraim et al 2002, Votier et al. 2004). Studies that have addressed the response of non-avian scavengers on discards have primarily looked at organisms that respond to discards by camera observation, gut contents studies, and correlations between discard presence and scavenger abundance (e.g. Wassenberg and Hill 1987, Ramsay et al. 1997, Groenewald and Fonds 2000, Veale et al. 2000, Bergmann et al. 2002). No studies experimentally evaluated the possible effects of discards on community trophic relationships. The large scale of most previous studies may neglect important effects of fisheries on local communities; for example, in estuaries where fishing is more concentrated, benthic scavengers may be more dramatically affected than in open environments. The phenomenon of scavenging on fisheries waste, and specifically on trawler discards, has been widely neglected in the United States, with the exception of a study by Link and Almeida (2002), which demonstrated a small but positive significant link between scallop fishery discards on Georges Bank and sculpin abundance.

The fate of discards varies by fishery as well as location, seasonal timing, and environmental conditions. Discards may survive or die, with dead discards available to scavengers immediately; even if discards survive to the time of release, injury or stress may reduce their ability to survive or to effectively avoid predation. If discards are eaten, they have the potential to alter local food webs because they represent a possibly substantial and, prior to fishing activities, usually unavailable food source. In North Carolina, shrimp trawling is permitted in areas of estuaries and sounds behind barrier islands and roughly 600 fishermen state-wide trawl in these waters for at least part of their income. Shrimp trawlers capture an average of 3.9 kg of juvenile fish, blue crabs, and other invertebrates for every 1 kg of shrimp caught (Chapter Two), discarding all bycatch back into the estuary. The major macrofauna that scavenge in this area include species of commercial and recreational fisheries importance, such as blue crabs, and therefore the potential of discards from the shrimp fishery to feed and perhaps influence the population or community dynamics of fisheries species is important to proper management of the system. Management decisions that could reduce discards to the system include reductions in numbers of trips by trawlers, or gear requirements that reduce bycatch, as well as the occasionally proposed elimination of estuarine trawling in North Carolina. Understanding the degree to which other fisheries are linked to the shrimp fishery is critical to making informed management decisions.

The goal of this chapter is to identify the scavengers on discards in the inshore shrimp fishery in North Carolina and to evaluate the preference of major scavengers for discards compared to their typical prey and the impacts of discards on trophic relationships.

Methods

Field experiments were carried out in two areas in North Carolina used by inshore trawlers, the Neuse River Estuary and Core Sound (Figure 3.1). The high salinity sound site, Core Sound, NC, has a primarily sandy benthic environment with 35% coverage by patches of sea-grass (Ferguson et al. 1993) in which trawling is unlawful. The low-salinity estuarine environment is the lower portion of the Neuse River Estuary, North Carolina, which extends southeast from Minnesott Beach to the mouth of the Neuse River at Pamlico Sound (Baird et al. 2004) and is characterized by muddy to mud-sand bottom with little benthic macroalgae or seagrasses. Both areas support sizeable shrimp trawl fisheries and crab-pot fisheries, and contain primary and secondary nursery areas, which are protected by regulation from bottom-fishing for all or part of the year as indication of their value to juvenile fish and crustaceans.

Scavenging by Depth

To determine where in the water column scavenging on discards occurs, I designed lines to hang vertically in the water column with hooks every 0.5 m to hold dead fish (using the three most common discard species, spot, *Leiostomus xanthurus,* pinfish, *Lagodon rhomboides,* and Atlantic croaker, *Micropogonius undulatus*). Polypropylene rope was tied to a brick at one end and to a buoy at the other end. One fish (8-12 cm), collected from a commercial trawler and stored on ice until use (less than 24 hours), was attached to each hook with species used in approximately equal amounts but randomly chosen for each hook. I deployed these lines, three to a site at three sites each in Core Sound and the Neuse River Estuary for thirty minutes each month from May to August, 1999. Experiments were carried out in early morning, when trawlers were still discarding after the night's fishing but when nets were no longer set out to avoid entanglement. Lines were deployed in water that was roughly 3 m deep; the knot at the buoy was adjusted as necessary so that the rope hung approximately vertically in the water column. When the lines were collected, I scored each fish as whole, 25% eaten, 50% eaten, 75% eaten, or missing. The proportion of fish remaining was analyzed with a two-factor ANOVA with location (Core, Neuse) and height off the bottom (6 levels, 0.0-2.5 m by 0.5 m increments) as factors. Data were not normally distributed, but balanced ANOVA is robust to violation of this assumption with large sample sizes (Underwood 1997). Post-hoc comparisons were carried out with Tukey's test.

Nets and pots.

To determine which benthic organisms respond to discards in the bottom meter of the water column, lift nets and small-mesh crab pots (peeler pots) were deployed and the organisms responding to baited and unbaited nets and pots recorded. Lift nets were 1 m^2 steel frames covered with 1/4" Delta knotless netting (Memphis Net & Twine Co., Inc., Memphis, TN), with enough excess net to form a cone when pulled upwards by the polypropylene lines attached to the four corners and coming together 1 m above the frame and attached by further line to a buoy. Plastic cable ties attached bait to the mesh in the baited treatments and were left empty in the unbaited (control) treatments. Small mesh crab pots, used commercially for catching peeler crabs in North Carolina (blue crabs about to molt), were constructed on 60 cm x 60 cm steel rebar frames with irregular hexagonal stainless steel mesh (4 cm x 6 cm), 45 cm high, with two circular openings of 6 cm diameter and a bait well in the middle. Once a month in August 1999 and monthly from May to August 2000, linear arrays of 3 baited and 3 unbaited peeler pots and 3 baited and 3 unbaited lift nets weredeployed in three locations in both Core Sound and Neuse River, North Carolina (Figure 3.1), alternating baited and unbaited treatments within arrays and with minimum 500 m separation between pot and net arrays. Peeler pots were deployed for 3 hours, and lift nets for 30 minutes after pilot studies showed that scavengers responded to but did not deplete bait during that amount of time. Peeler pots and lift nets were deployed in early morning in areas trawled during the previous night, to avoid entanglement in fishing gear. When retrieved, the organisms in each lift net and crab pot were identified and measured. The differences between baited and unbaited responses for total crabs and total fish were pooled across dates and compared with a non-parametric 1-sample sign test for each location. The number of fish and crabs in pots and nets were separately analyzed with a two-factor ANOVA with location (Core, Neuse) and treatment (baited or unbaited) as factors. Data were not normally distributed, but balanced ANOVA is robust to violation of this assumption with large sample sizes (Underwood 1997). Post-hoc comparisons were carried out with Tukey's test.

Scavenging of Discards by Birds

To quantify the attraction of birds to trawlers that are discarding and therefore make changes in their behavior to take advantage of trawler discards, I made counts of the number (by species) of birds following the trawlers during various fishing activities. I was limited by the number of daylight trawls that we were able to observe because most birds hovered beyond the limited reach of trawler lights during the night. For each tow that I observed in the daylight, I conducted three 2-minute counts of the numbers (by species) of birds following the trawler (defined as the number of birds within approximately 25 m of the boat, in a 45 degree arc from the back center line of the boat). These three 2-minute counts were conducted when the boat was trawling but had not discarded for at least 30 minutes ("trawling"), when the fishermen were hauling back catch but not yet culling and discarding ("hauling back"), and when the fishermen were actively discarding ("culling"). The numbers by species for the three 2-minute counts in each category were averaged for each trawl, and then the average count for each category for all trawls were analyzed using a one-way

ANOVA by treatment (trawling, hauling back, and culling) after square root transformation to meet the requirements of ANOVA for homogeneity of variances (Bartlett's test = 3.05, $p>0.05$). Data were normally distributed (Ryan-Joiner test = 0.971, $P>0.100$). Post-hoc comparisons were performed with Tukey's test.

Stomach Contents of Blue Crabs

Stomach contents of blue crabs from the first trawls of the trip and later trawls from the trip were collected on commercial trawlers in Core Sound to quantify blue crab feeding patterns during periods with and without discard availability in the water. The size and sex of each blue crab, as well as the date and tow number, were noted. Stomachs dissected from crabs onboard the trawlers immediately after collection and placed on ice for transport to the Institute of Marine Sciences in Morehead City, where they were placed in 10% formalin and rose bengal stain within 10 hours of collection. Stomachs were later examined for gut contents under a dissecting microscope and the percent of each food item by volume noted for each stomach. For stomachs containing food items, the presence of shrimp carapace, shell, bones, and tissue (typical prey items of blue crabs and those that may increase or decrease with feeding on discards) were analyzed with a chi-square test with tow (first v. third) as a factor to determine whether feeding patterns differed with differing availability of discards at the benthos. The number of empty stomachs versus stomachs with food remains was analyzed in the same way. The ash-free dry weight of non-empty stomachs was compared between stomachs with and without signs of feeding on shrimp and fish using a 2-sample t-test to determine whether the availability of food due to trawling affected blue crab feeding success.

Feeding preference experiments

Laboratory feeding experiments were conducted in the spring and summer of 2000 at the Institute of Marine Sciences in Morehead City, NC, to test the hypothesis that blue crabs prefer to feed on discards over one of their typical prey, the hard clam, *Mercenaria mercenaria.* Sand to a depth of 6.5 cm was placed in six aquaria (24 cm wide x 38 cm long x 27 cm deep) that were filled with gravel filtered seawater pumped directly from Bogue Sound, which then ran constantly during the experiments. Each trial (n=40) lasted three hours. Male and female intermolt blue crabs of various sizes (mean 11.7 cm, SD 1.09 cm, range 9.3 to 14.4 cm, n=40) were used in the experiments, with the sex and carapace width noted for each trial. Six (low density) or 12 (high density) *M. mercenaria* were placed on the sand and allowed to burrow for at least one hour. Clam lengths were noted for the individuals in each experiment. Prior to beginning the experiment, 24 clams from the same batch used for the experiment were measured, weighed alive, their tissue removed, and weighed again. Clams used in the experiment were 1.1 cm to 2.2 cm long (mean = 1.53 cm, SD = 0.35, n of subsample = 24). The length of the clams was then regressed against the tissue weight ($R^2 = 0.95$, $p<0.001$), and used to estimate the total clam tissue weight available in each aquaria. An equivalent weight of recently killed fish (the three most common discard species were used, pinfish, spot and Atlantic croaker) was then added to the tank. A blue crab was introduced and allowed to feed for three hours with minimal disturbance (the room was not used during feeding times), and then the crab was removed and the remaining fish tissue weighed. The remaining clam tissue was estimated by counting crushed clams as eaten and whole clams as uneaten, using the pre-determined regression equation to estimate the weight of soft tissue remaining. Thus, the method may overestimate the amount of clam tissue eaten if some was left floating in the tank after handling by the crab.

After confirming the normality of the data with an Anderson-Darling test (test statistic = 0.332, $p>0.05$), a two-sample t-test was run on the difference between fish tissue and clam tissue consumed depending on the density of clams available. Then a one sample t-test was run on the pooled data for the difference between fish tissue and clam tissue consumed to determine whether there was a preference for one prey.

Mesocosm Experiments

To test on a larger scale whether blue crabs prefer discarded fish over benthic prey and whether such a preference could decrease predation on those benthic prey, feeding experiments with differing availability of discards were carried out in an experimental pond behind the Institute of Marine Sciences, Morehead City, NC. The pond had a sandy mud bottom and received unfiltered seawater from adjacent Bogue Sound. The pond was divided into quarters, each quarter approximately 12 m by 8 m, separated from each other and enclosed by ¼-inch plastic Vexar mesh. The pond was completely drained for a month before beginning experiments to ensure elimination of benthic organisms, and monitored for invasions over the course of the experiments through observation and sieved (on 1 mm mesh) core samples. Reflective foil tape was hung around and across the pond to deter gulls from feeding on organisms and discards, and twice daily checks of the pond (8 a.m. and 4 p.m.) showed low densities of gulls around the ponds and none approaching close enough to feed.

Juvenile hard clams, *Mercenaria mercenaria,* 1.1 to 2.1 cm length (average 1.532 cm, SD=.351, n=48), were attached to metal landscaping staples using 15-lb test clear monofilament fishing line using cyanoacrylate glue secured further with small (< 0.25 inch square) pieces of electrical tape. Clams were buried in life position to approximately 1 cm depth, 180 per enclosure. The pond was then filled to 1.2 m with seawater from adjacent Bogue Sound. Blue crabs (male and female intermolt), at two densities (2 and 4 per treatment, similar to field densities in Core Sound [Johnson, unpub. data] and double field densities), were left for three days in enclosures. Zero, one or three additions of 1.0 kg discards (spot, pinfish and Atlantic croaker of the size caught in trawlers, caught the previous evening and stored on ice) were added in the morning on the first day of the experiment (one discard addition treatment) or each morning of the experiment (three discard addition treatment).

After 72 hours, the pond was drained (which took two-three hours), blue crabs were removed, and the remaining clams were excavated and counted. Clams were scored as alive, dead (shell intact), dead (shell broken), or missing. In each run, one section of the pond was kept free of blue crabs as a control for clam survival in the absence of blue crab predation. Clams missing or dead with crushed shells were considered to have been eaten by the blue crabs since only 1% of clams was missing in control enclosures. Experiments were replicated in time over the summers of 2000 and 2001. The proportion of clams missing or crushed in each treatment was compared using a two-factor ANOVA with density of crabs (2, 4) and discard frequency (0, 1, 3) as factors after testing for normality with the Anderson Darling test and homogeneity of variances with Levene's test. The per capita predation on clams was also calculated and analyzed in the same way. Tukey's test was used for post-hoc comparisons.

Results

Scavenging by Depth

ANOVA demonstrated a significant interaction in the amount of scavenging between site and height off the bottom (Table 3.1). Scavenging was greater in Core Sound (average of 20-60% of fish eaten) than the Neuse River (average of 0-20% of fish eaten), and greater near the bottom (1.0 m and below) than in the top two meters of the water column (Figure 3.2).

Nets and Pots

There was a significant interaction between location (Core, Neuse) and treatment (baited, unbaited) for all ANOVA except for total finfish responding to lift nets (Table 3.2). More finfish, crabs, and blue crabs responded to crab pots in Core Sound, with more responding to baited than unbaited pots. More total crabs and blue crabs responded to lift nets in Core Sound than in the Neuse River, with more responding to baited than unbaited nets. Blue crabs, *Callinectes sapidus*, were the most common crab caught in the nets and preferred baited over unbaited pots and nets, while pinfish, *Lagodon rhomboides*, were the primary finfish caught in nets and pots and preferred baited over unbaited crab pots.

Scavenging of Discards by Birds

Birds, specifically gulls and terns, were significantly more likely to be present around a boat that was hauling back nets or boats where a fisher was actively sorting and discarding from the catch than a boat that is simply fishing ($F=10.46$, $p = 0.001$; Figure 3.4). Numbers of birds around boats when discards were present were about ten times greater than when the boats nets were in the water and no discarding was taking place.

Stomach Contents of Blue Crabs

There was no difference between early and late trawls in the occurrence of empty stomachs of blue crabs, with 44% of stomachs empty in early trawls and 42% of stomachs empty in late trawls. No significant differences were found for the identity or biomass of stomach contents between early and late trawls (Table 3.3). Feeding on fish and shrimp was indicated in all trawls, and those stomachs with fish and shrimp had significantly more biomass than those without, with almost twice as much biomass in stomachs with fish and shrimp (Table 3.3). Crabs were an average size of 12.97 cm carapace width (SD = 1.727 cm).

Feeding preference experiments

No difference in tissue consumption was seen with density of clams (2-sample t-test for difference between low and high density of the difference between clam and fish tissue consumed: T=0.67, P=0.510, df=38). Samples were pooled and a t-test run to determine whether the difference between clam and fish tissue was different from zero. Six times as much fish was consumed than clams in the feeding preference experiments (1-sample t-test for difference from 0 for clam tissue consumed minus fish tissue consumed: T= 10.10, p=0.000, n=40; Figure 3.5).

Mesocosm Experiments

ANOVA revealed no significant interaction between discard additions and crab density, and showed a significant effect of fish additions on total crab predation on clams (Table 3.4). Twice as many clams were eaten in treatments without discard additions (Figure

3.6a). Per capita predation of crabs on clams was not significantly different with different numbers of crabs or fish additions, but there was a trend towards lower numbers of clams eaten per crab in treatments with discard additions at lower densities of crabs and in all treatments when crab density was high (Table 3.3; Figure 3.6b).

Discussion

Scavenging of discarded fish primarily takes place near and at the bottom of the water column by blue crabs and demersal fish. Experiments to identify the region of the water column in which scavenging takes place demonstrated that significantly more discards are eaten near the bottom. While mid-water scavengers, such as large fishes, sharks, and marine mammals reside in the areas in which experiments were carried out, they are rare compared to the large numbers and biomass of fish and crustaceans that use the estuaries as nursery areas, especially in the summer. Fishermen offer anecdotal evidence of dolphins and sea turtles taking advantage of discards from trawlers on occasion.

Experiments to determine the identity of demersal scavengers demonstrated that blue crabs and pinfish are the most common scavengers of discards in the area that responded to baited nets and pots. Scavenging fish were likely underestimated by both nets and pots; fish, due to mobility, were likely able to more easily escape the lift nets when they were retrieved and only certain sizes of fish would be able to both enter and be trapped by the peeler pots. The large response to discards in nets and pots demonstrated by blue crabs corresponds to the natural history of these animals, known to be opportunistic scavengers with a diverse diet (Laughlin 1982, Hines et al. 1990, Stoner and Buchanan 1990), and their known behavior in response to a large variety of baits in crab pots. Blue crabs often feed upon benthic organisms such as clams that require effort both to locate and, in many cases, to break apart to access tissue. By taking advantage of dead organisms at the sediment-water interface, crabs save energy and wear on chelae in digging and cracking shells or carapaces. Furthermore, dead discards are probably much easier to locate by odor plume, due to their size relative to clams and tissue damage due to handling during the fishing process.

Blue crab diets typically include bivalves, crabs, fish, shrimp, gastropods, plants and detritus (Laughlin 1982, Hines et al. 1990, Stoner and Buchanan 1990). Gut contents of blue crabs from shrimp trawlers were dominated by fish and shrimp tissue to a much larger degree than would be expected from the literature (Table 3.5) and amounts did not increase over the evening of trawling as would be expected if blue crabs were feeding only on discarded fish. However, blue crabs are common in the bycatch of shrimp trawlers and, depending on the weight of the catch in the cod end of the trawl net and on time on deck as the catch is sorted, blue crabs can take advantage of immobile or dead shrimp and fish both in the trawl net and on deck. Blue crabs were observed feeding on shrimp and fish in the sorting tray on the trawlers (G. Johnson, *pers. obs.*). Blue crabs may also be eating organisms such as shrimp and fish in the net as well as in the water after discarding. Therefore, the lack of a statistically significant increase in fish tissue over a night of trawling probably indicates multiple pathways by which blue crabs take advantage of nutritional subsidies from trawling rather than a lack of effect of discards on diet. The importance of this feeding in the nets is indicated by the greater biomass present in the stomachs of crabs with fish and shrimp in their stomachs than in stomachs without fish or shrimp but with food items (polychaetes, unidentified tissue, algae and detritus).

In laboratory feeding experiments, blue crabs showed a significant preference for fish tissue (imitating discards) over their typical prey, juvenile bivalves. This preference was expressed independent of whether the bivalves were at low or high density. Because less effort is needed to locate and access discards, blue crabs may prefer discards to bivalves and perhaps other buried prey items. This suggestion was further supported by decreased predation on clams in the presence of discards in the mesocosm experiments, where both clams and discards required search time, but access to discards on the surface of the sand was presumably simpler than access to buried bivalves.

The decreased total predation on juvenile clams in mesocosm treatments in which discards were available to blue crabs supports the hypothesis that discards alter trophic interactions in the estuarine community. In the experiments, blue crab predation on benthic infauna relaxed when a food subsidy that did not require searching, digging, and breaking open was available. Per capita predation on clams was lower in the high density than low density crab treatment, as expected among agonistic species (Clark et al. 2000), and decreased with one and three discard additions in the low density treatment and with three discard additions in the high density treatment. Therefore, utilization of discarded fish may have varying impacts on blue crab predation on other prey depending on the density of crabs in the area. The availability of discarded fish could partially release clams and other infauna from predation, as indicated by the mesocosm experiments, or, over the long term in areas of trawling, blue crab numbers could increase and over time fully utilize both food resources. Both possibilities have important fishery implications for North Carolina. Clams and other benthic bivalves, such as oysters and scallops, are targets of commercial fisheries. Reduction in predation by blue crabs at the juvenile stages hard clams could leave more bivalves for fishers, as hard clams escape predation by blue crabs once they reach a size of about 40 mm (Arnold 1984, Peterson 1990, Micheli 1995). Increases in blue crab numbers or biomass would be similarly beneficial for commercial fishers that target them, but may in times of low discarding actually lead to increased predation on their usual prey, potentially affecting bivalve catches in later years. Thus, changes in the discarding regime of shrimp trawlers, either through increased avoidance or reduction of discards or through changes in the intensity of trawling could have unintended impacts on bivalve and/or crab fisheries.

While the experiments here dealt with possible effects of blue crab scavenging on discards, demersal fish utilization of discards could also have community effects. Pinfish, which respond to the discards, are generalist consumers in the estuarine environment and directly and indirectly influence algal and invertebrate populations (Bishop et al. 2004, Bishop and Wear 2005, Bruno and O'Connor 2005). Pinfish are harmed directly by trawling through mortality in the nets and from exposure to air (Chapter Two), but the field experiments suggest that pinfish may also benefit from trawling through consumption of discards. To fully understand the community impacts of trawling in the estuaries of North Carolina, demographic and community experimental work is needed to identify the impacts of trawling on population dynamics, behavior, and consumptive impact of pinfish.

The response of scavengers to discards has ecologically important implications for the estuarine trophic webs in fished areas, and economically important implications for estuarine fisheries. First, discards provide large numbers of highly mobile, protein-rich foods at minimal capture effort for scavengers on a regular basis over the shrimp fishing season. Thus, scavengers have access to foods of high quality that would otherwise be unavailable to them. Some estuarine nursery areas are increasingly affected by eutrophication in the summer months, which can limit the amount of production reaching higher trophic levels (Baird et al. 2004). Huxel and McCann (1998) demonstrated that low to moderate levels of allochthonous input to the consumer levels of a tritrophic food web can stabilize food web interactions, dependent on the preference of consumers for the alternate food source. Discards, which have been made seasonally available now for decades in fished areas, may dampen food shortages due to the die-off of immobile benthic organisms due to eutrophication in the estuaries.

Second, the management of estuarine fisheries needs to take into account ties among fisheries when the actions of one fishery affect the stocks of other fisheries. Typically, concerns for managers regarding multiple fisheries in an area are bycatch in one fishery containing target species of another fishery (Hall and Mainprize 2005) or degradation of habitat by fisheries gear (Dayton et al. 1995, Kaiser et al. 2006). However, my research suggests that halting discarding in the shrimp fishery could increase or decrease the stock of blue crabs (depending on the magnitude of mortality in the bycatch vs. the effect of the increase in food availability on survivorship or emigration) and clams, which could have higher survivorship in the presence of discards if blue crab diets shift but numbers do not increase.

Understanding the direct and indirect impacts of fishing activities is of growing importance to fisheries managers as human population growth continues and pressures to feed the population become stronger. The move towards ecosystem-based management demands an increased understanding not just of individual fishing stocks, but the interactions between stocks and between stocks and the environment (Botsford et al. 1997). This work demonstrates that the discarding of fish in an estuarine fishery affects not only the discarded organisms, but can change feeding patterns of ecologically and economically valuable species. Management of all affected stocks, whether for fishery or conservation value, must recognize the changes that decades of trawling may have brought to the natural system and consider trophic relationships in decisions regarding trawling. This work highlights the importance of considering not just the direct impacts of fisheries on the environment, but their indirect impacts on trophic relationships in the environment and how those changes may cascade through the environment in ecologically and economically important ways.

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Table 3.1. ANOVA Results for Scavenging at Depth Experiments. Summary of analysis of variance for differences in the scavenging of fish (reported as percentage of fish remaining after 30 minute trials) as a function of location (2 levels, Core Sound and Neuse River) and depth (6 levels, 0-2.5 m by 0.5 m increments).

	df	MS	*F*	*P*
Location	1	11.1727	32.85	0.000
Depth	5	4.2824	11.08	0.000
Location * Depth	5	1.2941	3.65	0.003
Error	420	0.1294		

Bartlett's Test Statistic = 15.76, P>0.05

Table 3.2. ANOVA Results for Lift Nets and Crab Pots. Summaries of analyses of variance for the numbers of fish, crabs, and blue crabs responding to lift nets and crab pots as a function of location (Core Sound and Neuse River) and treatment (baited and unbaited).

		Crab pots				Lift nets			
Taxa	Source	*df*	MS	*F*	*P*	*df*	MS	*F*	*P*
Finfish									
	Location	1	69.881	14.06	0.000*	1	8.209	2.07	0.152
	Treatment	1	48.436	9.74	0.002*	1	0.160	0.04	0.841
	Loc*Trt	1	35.042	7.05	0.009*	1	2.304	0.58	0.447
	Error	157	4.971			155	3.967		
	Levene's Test Statistic = 12.43, P<0.05					=0.89, P>0.05			
	Tukey's Test:	Core > Neuse							
		Baited > Unbaited							
Pinfish									
	Location	1	61.106	12.58	0.001*				
	Treatment	1	44.383	9.14	0.003*				
	Loc*Trt	1	33.607	6.92	0.009*				
	Error	157	4.856						
	Levene's Test Statistic = 10.25, P<0.05								
	Tukey's Test:	Core > Neuse							
		Baited > Unbaited							
Crabs									
	Location	1	293.74	69.36	0.000*	1	10.546	31.83	0.000*
	Treatment	1	234.67	55.41	0.000*	1	7.3367	22.14	0.000*
	Loc*Trt	1	194.30	45.88	0.000*	1	7.3367	22.14	0.000*
	Error	157	4.24			155	0.3313		
	Levene's Test Statistic = 12.88, P<0.05					=31.51, P<0.05			
	Tukey's Test:	Core > Neuse				Core > Neuse			
		Baited > Unbaited				Baited > Unbaited			
Blue Crabs									
	Location	1	258.86	64.15	0.000*	1	8.7453	27.55	0.000*
	Treatment	1	211.68	52.46	0.000*	1	6.5587	20.66	0.000*
	Loc*Trt	1	173.43	42.98	0.000*	1	6.5587	20.66	0.000*
	Error	157	4.04			155	0.3175		
	Levene's Test Statistic = 16.32, P<0.05					=30.38, P<0.05			
	Tukey's Test:	Core > Neuse				Core > Neuse			
		Baited > Unbaited				Baited > Unbaited			

Table 3.3. Chi-square Results for Crab Stomach Content Analysis. Summary of chi-square (1 df) tests for presence/absence of food items in crab stomachs for early and late tows and 2 sample t-test for AFDW biomass in stomachs showing signs of feeding on from the trawl versus those without.

	% Present			
Food Item	Early	Late	*Chi-sq*	*P*
Tissue	81	68	1.056	0.304
Shell	47	64	1.361	0.243
Shrimp carapace	47	46	0.007	0.934
Fish bones	10	21	1.245	0.265
Empty stomach	19	25	0.375	0.540

AFDW	Mean (w/fish or shrimp)	Mean (w/o)	df	T	*P*
	0.1442 g	0.0765 g	34	-2.9	0.006

Table 3.4. ANOVA Results for Mesocosm Experiments of Crab Predation on Clams With and Without Discards. Summaries of analyses of variance for the predation on clams (reported as proportion clams remaining after three day trials or per crab proportion of clams remaining after three day trials) as a function of crab density (crab; 2 levels, 2 and 4) and discard additions (fish,;3 levels, 0, 1 and 3) .

	Proportion total predation				Proportion total predation per crab			
Source	*df*	MS	*F*	*P*	*df*	MS	*F*	*P*
Fish	2	0.23260	4.30	0.027	2	0.03746	3.40	0.052
Crab	1	0.03881	0.71	0.410	1	0.03245	2.95	0.101
Fish * Crab	2	0.13053	2.38	0.117	2	0.02425	2.20	0.135
Error	21	0.05490			21	0.01100		

Bartlett's Test Statistic = 6.47, P>0.05 =9.70, P>0.05

Tukey's Test: Fish: Fish (0) < Fish (3) — Fish: Fish (0) < Fish (3)

Table 3.5. Summary of feeding by blue crabs from the literature. BC=Blue crab, Biv=bivalves, Polych.=polychaetes, An. Tiss.=unidentified animal tissue.

Source	Size (mm)	BC	Fish	Biv.	Shrimp	Polych.	An.Tiss.	Detritus	Other
Hines et al. 1990									
June, Mud	125 mm	3	10	29	0	2	20	2	34
June, Sand	124	3	17	37	0	6	9	1	27
Sept, Mud	133	10	17	52	0	0	20	0	1
Sept, Sand	133	12	4	56	0	0	21	2	5
Laughlin 1979									
	>60 mm	11	14	39	5	0	3	2	26
Stoner and Buchanan 1990*									
	81-100 mm	42.5**	15	10	22.5	0	0	5	5
	100-125	30**	0	30	20	0	0	5	15
	126-150	40**	7.5	40	0	0	0	7.5	5

*Percentages estimated from graphical format.
**Includes all crabs (not broken down by species).

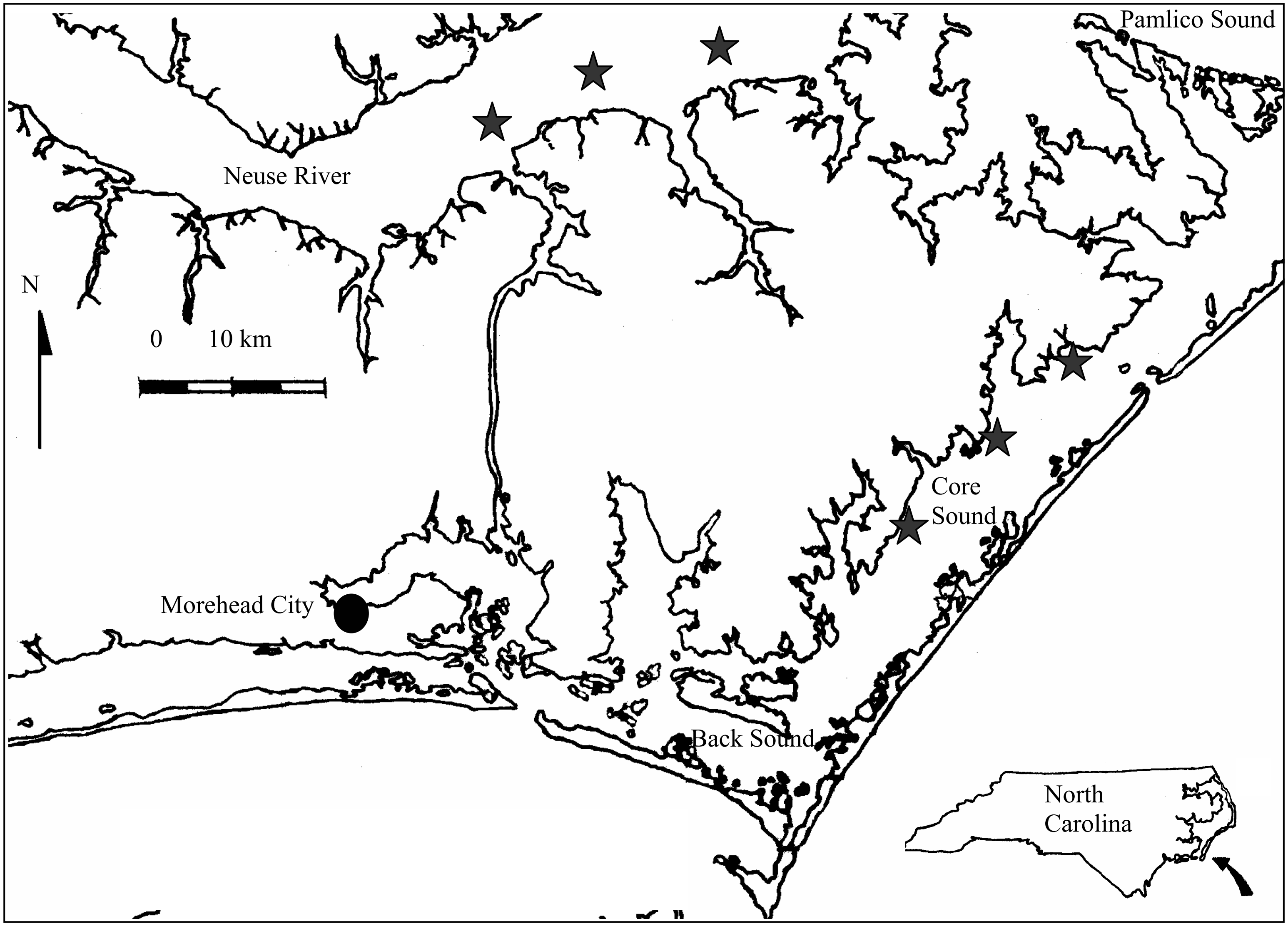


Figure 3.1: Core Sound and the Neuse River, North Carolina. Stars mark sites of field experiments.

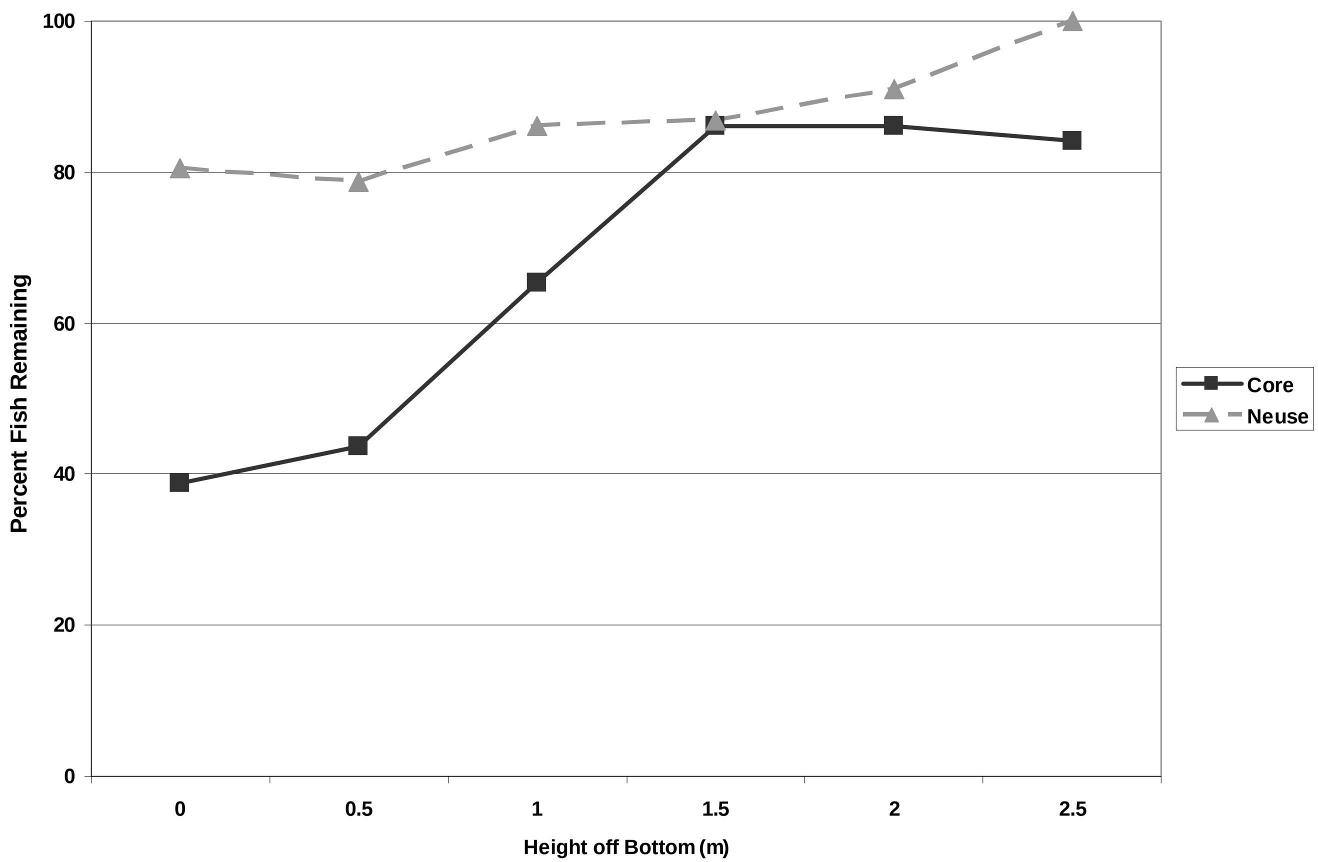
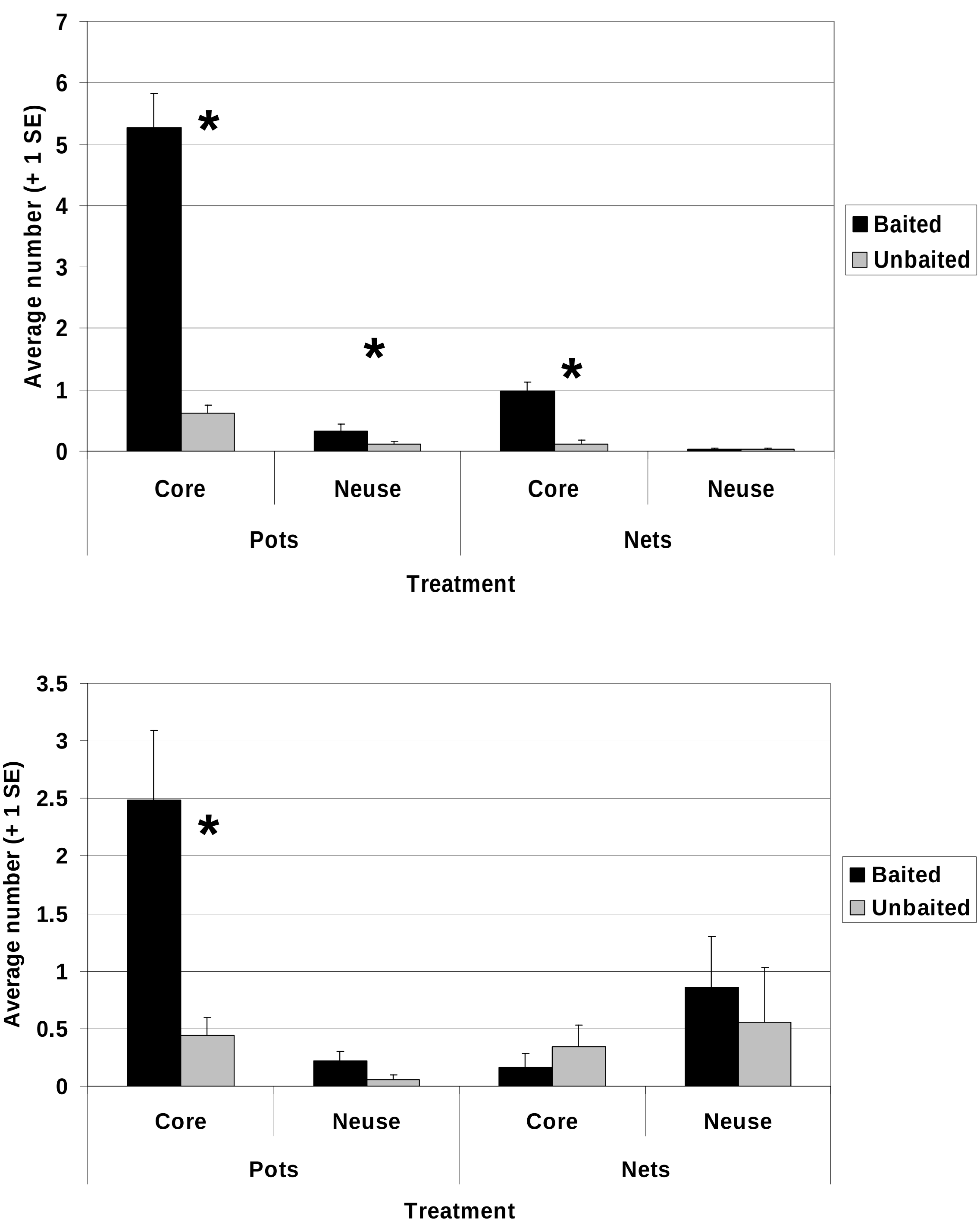


Figure 3.2. Percentage of fish remaining by height off the bottom for Core Sound and the Neuse River Estuary. With Tukey's test ($p<0.05$), statistically similar groups are (C=Core, N=Neuse):

C(0) C(0.5) C(1) C(1.5) C (2) C(2.5) N(0) N(0.5) N(1) N(1.5) N(2) N (2.5) a.



b.

Figure 3.3. Scavenger Response in Lift Nets and Crab Pots. Average number (+ 1 SE) of crabs (a) and fish (b) responding to baited and unbaited lift nets and crab pots in Core Sound and Neuse River, NC.

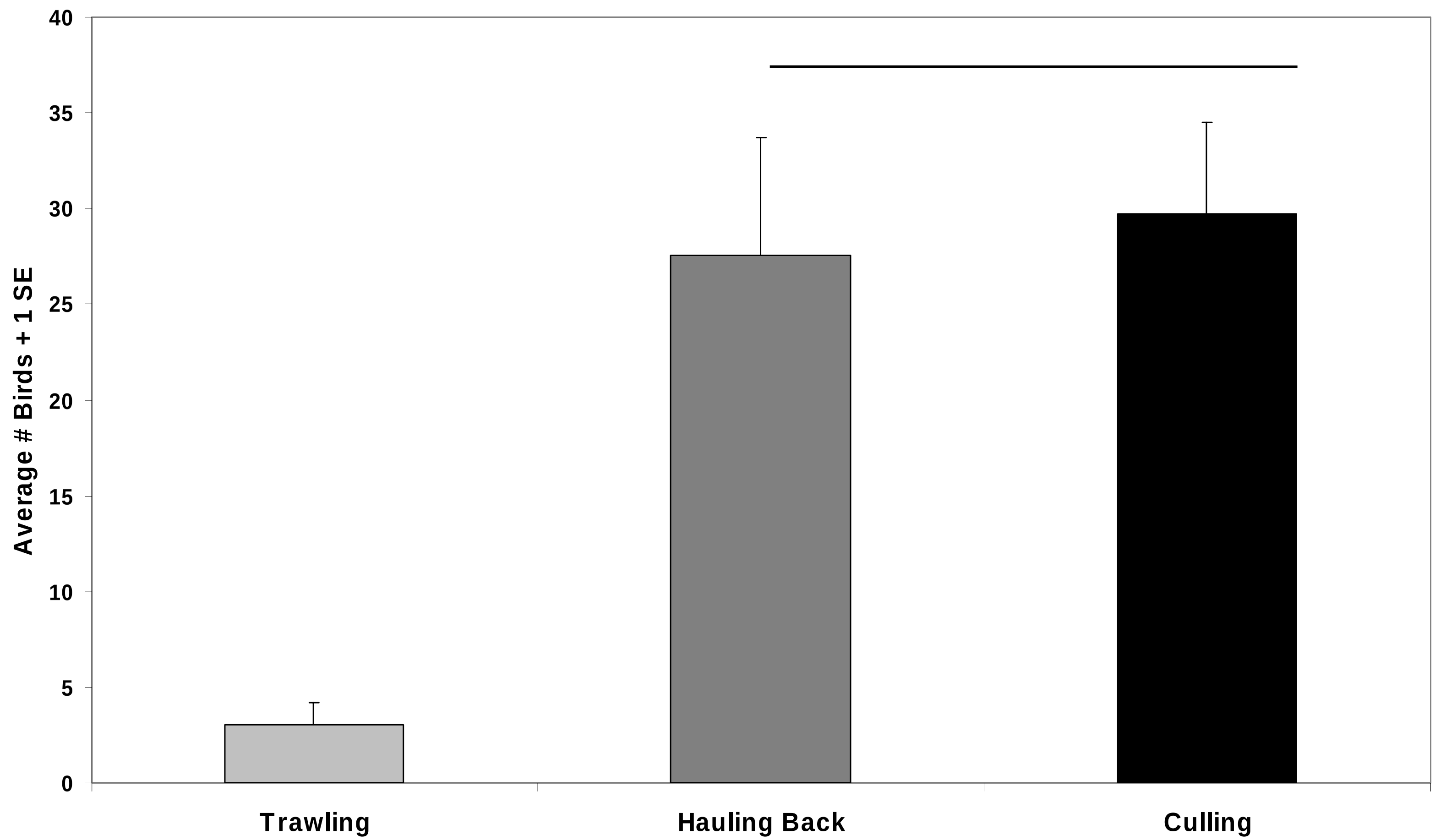


Figure 3.4. Bird Abundances at Trawlers. Number of birds (+ 1 SE) present in 90 degree arc behind boat during trawling, hauling back of nets, and culling of the catch. Line indicates categories that are not significantly different (ANOVA, $p<0.000$).

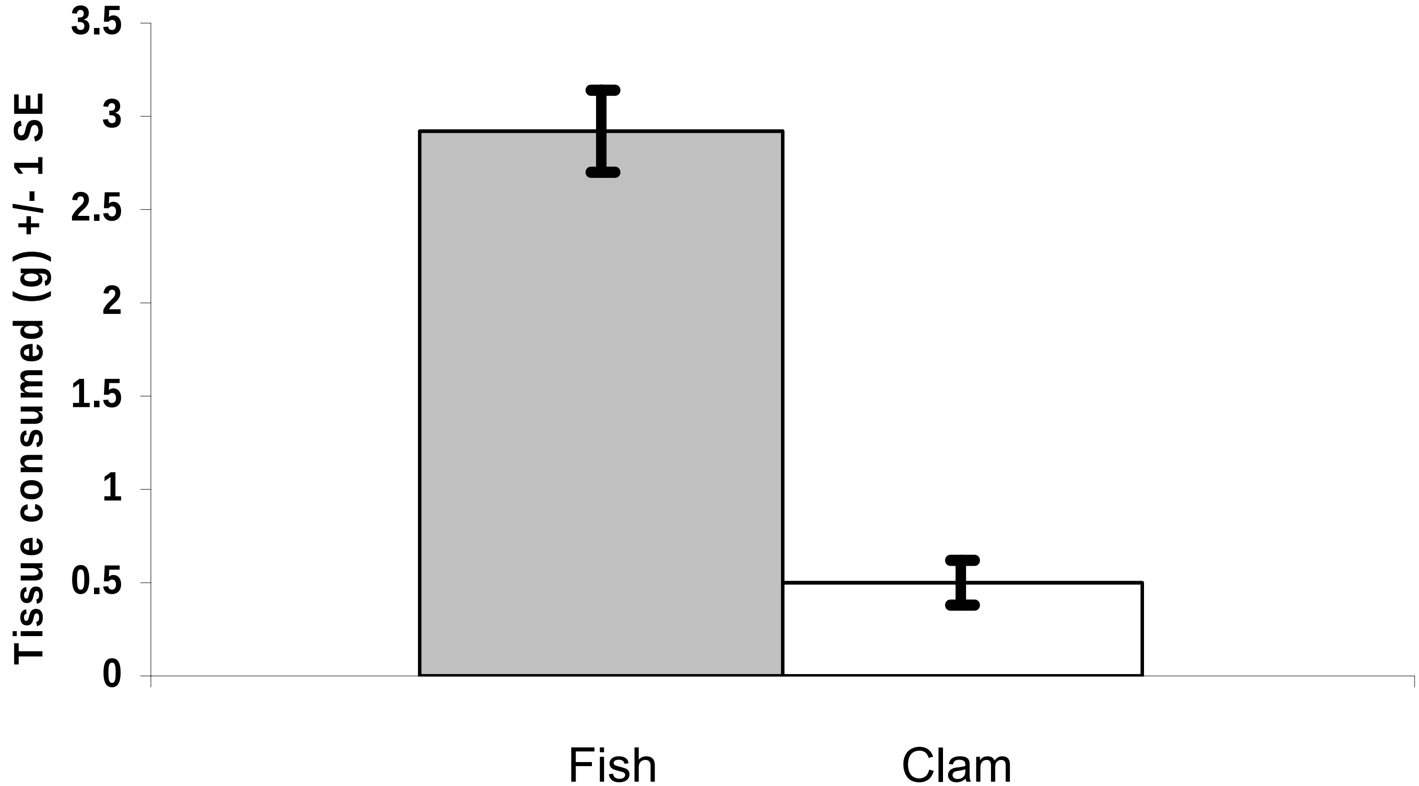


Figure 3.5. Blue crab Feeding Preference Experiments. Blue crabs were offered similar amounts of “discard” tissue (laying on substrate) and clam tissue (buried in substrate) in aquaria; paired t-tests showed a significant preference for discarded (fish) tissue over clam tissue.

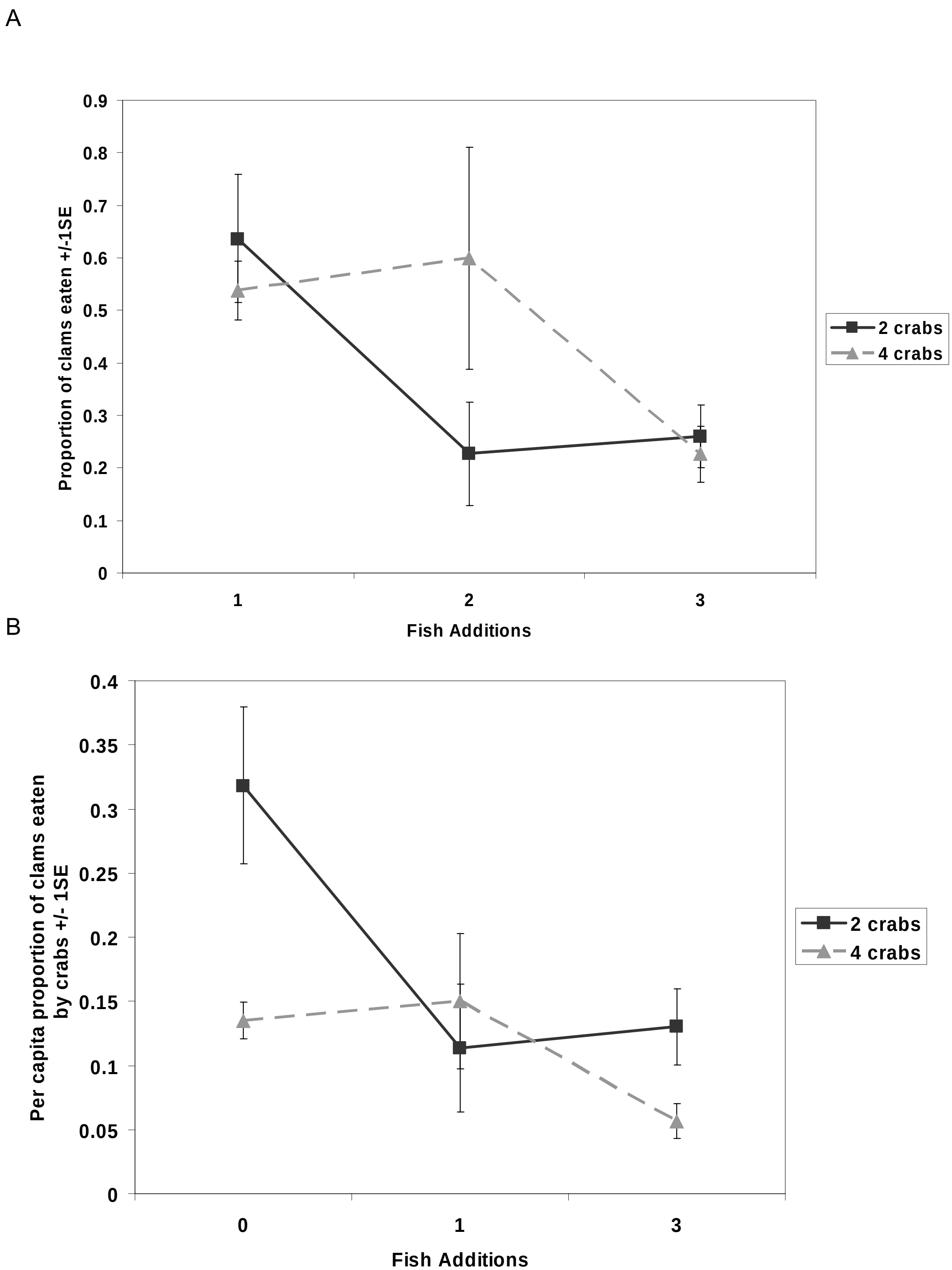


Figure 3.6. Mesocosm Experiment Results. Results of mesocosm experiment for (a) total proportion of clams preyed upon, and (b) per capita predation by crabs on clams.

CHAPTER FOUR:

Contrasting the effects of anthropogenic disturbance on estuarine trophic structure and system functioning: Fishing vs. eutrophication in the Neuse River Estuary, North Carolina

ABSTRACT.

Direct anthropogenic effects on estuarine systems can occur at various trophic levels, from eutrophication at the primary producer level to fishing and hunting at various consumer levels. Understanding the individual effects of these disturbances on trophic structure and ecosystem properties can be difficult due to their co-occurrence. Here, early and late summer quantitative ecosystem mass-balance models are constructed for two years of varying intensity of disturbance from hypoxia with four fishing treatments within each of the four time periods modeled: no fishing or discarding of carrion (dead discards), fishing extraction alone, discarding of carrion alone, and combined fishing extraction and discarding of carrion. The effects of fishing on trophic structure, carbon flow and system network properties as calculated by Ecopath software are then compared against the background of seasonal changes and the different degrees of hypoxia disturbance. Fishing disturbances are minimal compared to differences due to season and to disturbance by hypoxia for total system properties, but some marked effects of fishing emerge. Fishing and discarding of carrion change the trophic level at which many common consumers feed and decrease the efficiency of energy transfer up through and out of the system, and alter indirect positive trophic

interactions. Slightly more system production is retained as detritus when discards are included in models, and the connectance and system omnivory indices, which tend to increase with increasing system stability, increase when discarding is included in the models. Although fishing disturbance had a far smaller effect on system properties than eutrophication in these models, it does impact energy flow and system properties related to stability. System management could be improved by considering the change in energetic pathways induced by fishing as well as the system changes produced by eutrophication.

INTRODUCTION

Overfishing has altered the structure and function of coastal ecosystems and acted synergistically with other disturbances to further change the character of these productive ecosystems (Jackson et al. 2001). While fishing is generally thought of only as an activity that removes biomass from the system, it also adds food subsidies to some trophic levels through baiting, ghost fishing (capture of organisms in abandoned fishing gear), destruction of organisms on the sea floor by heavy equipment and discarding of unwanted organisms and offal. Therefore, fishing has the potential to interact with some species by simultaneously removing their predators or competitors and increasing their food supply. Studies of energy subsidies in the sea are typically focused at the primary producer level, where eutrophication is the major concern, but the energy subsidies introduced by fishing are most likely felt at mid- to upper-trophic levels, analogous to terrestrial examples of energy subsidies such as garbage dumps (Knight and Eberhardt 1985, Altmann et al. 1993, Otali and Gilchrist 2004). Determining the impacts of fisheries, both direct (mortality) and indirect (e.g. changing predation pressure or food availability), is important for refining and improving management, especially in light of moves towards ecosystem-based management (Pew Ocean Commission 2003, USCOP 2004). Numerous examples of fisheries affecting the ecosystem through changes in predator and prey availability exist; in Georges Bank, elasmobranches appear to have replaced haddock as the major predator group after the removal of haddock through years of fishing, probably preventing some recovery of the overfished bottom fish (Fogarty and Murawski, 1988). Baird and Ulanowicz (1989), in their seminal network analysis of Chesapeake Bay, showed that overfishing of oyster stocks had likely reduced the ability of the ecosystem to resist eutrophication, further explored by Ulanowicz and Tuttle (1992).

The discarding of dead bycatch from fisheries represents a possible food subsidy for scavengers, whether obligate or facultative (Britton and Morton 1994). In some fisheries, for example shrimp trawl fisheries, discard levels are substantial (2 or more times the biomass actually landed [Kelleher 2005]) and survival of finfish bycatch is low (Johnson 2006). The direct and indirect effects of such a subsidy to consumers in the system is almost always neglected in both conceptual and quantitative fisheries models of ecosystems, but monitoring in the North and Mediterranean seas has demonstrated changes in seabird populations as a result of discard availability (Oro et al. 1995, Garthe et al. 1996, Arcos and Oro 2002) and mesocosm experiments have demonstrated that the presence of discards can affect predation rates by blue crabs on their usual bivalve prey (Chapter Three). Quantification of such indirect effects of fisheries requires the recognition of trophic and behavioral changes that may results from the presence of fisheries through models or monitoring; evaluation of recognized pathways of possible changes through experiments or modeling can guide scientists and managers to focus on interactions that might affect species or ecosystem functions of interest.

Mass-balance modeling and analysis of trophic networks provide a useful tool for examining the changes in energy flow induced by fishing activities. In addition to the study by Baird and Ulanowicz (1989), over one hundred other studies have been performed utilizing programs such as Ecopath (Pauly et al. 1998) and NETWRK (Ulanowicz and Kay 1991) to examine energy or material flow in ecosystems. For example, Pauly et al. (1998) used Ecopath to calculate the effective trophic level of exploited fisheries species and found that the average trophic level of exploited species had declined over the past 45 years.

In this paper, I develop an ecosystem model for the lower Neuse River Estuary, North Carolina, to determine the individual and combined effects of fishing removal and carrion additions, via dead discards, to the system. For two years and for two seasons within each year, four models are constructed: a baseline model (without fisheries removal or carrion addition), a model with fishing removal only, a model with carrion addition only, and a model with both fisheries removal and carrion addition. Trophic flow and pathways and system properties are compared and contrasted between fishing treatment, seasons, and years.

METHODS

Mass-balance modeling and analysis of trophic networks was carried out using the Ecopath software maintained by Walters, Christensen and Pauly (Christensen and Pauly 1992; see www.Ecopath.org). For Ecopath, the food web for an ecosystem is divided into compartments, either by species or by groups of functionally similar species relative to diet and predators. Ecopath requires inputs of primary production, detritus biomass, and biomass, production:biomass ratio, food consumption per unit biomass, ecotrophic efficiency (proportion of the production that is either consumed by predators or exported), diet composition, and annual fishery catch for each compartment. These inputs are then entered into a system of simultaneous linear equations, which are then solved by the program for unknowns or imbalances. For example, if production and respiration rates are known but the amount of food unassimilated is unknown, unassimilated food can be determined by solving the equation: unassimilated food = food consumed – production – respiration. When imbalances occur in the equations, due to conflicts in the data due to methodology of collection, scale, time, or quality, small adjustments to inputs can be made to data manually by the user. The simultaneous linear equations are based on the assumption of no change in standing biomass of any compartment, and each compartment (i) is represented by a biomass equation based on the assumption that:

Production by (i) – all predation on (i) – nonpredation losses of (i) – export of (i) = 0 (1)

There are limitations to the Ecopath model, but when cautiously interpreted the use of mass-balance modeling and trophic network analyses can provide important information on trophic transfer of energy and system properties that can be compared across time periods or systems. The Ecopath software and similar programs have been used to examine the seasonal differences in system properties in Chesapeake Bay (Baird and Ulanowicz 1989), the effects of over-exploitation of top trophic levels through fishing (Pauly et al. 1998), the effects of hypoxia on energy transfer in the Neuse River Estuary (Baird et al. 2004), and to examine the trophic flows and system properties of over 100 other fishery systems (see www.Ecopath.org). Limitations of Ecopath include (a) that the model is steady-state and therefore multiple networks must be constructed to compare different time periods or management scenarios (Whipple et al. 2000), (b) that indirect effects unrelated to feeding are not reflected (Menge 1995), and (c) that the models are only as good as the data that is input. These limitations and others are elaborated upon in the discussion section.

I constructed a model for the mesohaline portion of the Neuse River Estuary, from Minnesott Beach to the mouth of the river at Pamlico Sound, an area of muddy-sand bottom characterized by little submerged aquatic vegetation (Figure 4.1). The area supports shrimp trawl, crab-pot, and invertebrate and finfish recreational fisheries and contains primary and secondary nursery areas, which are protected by regulation from bottom fishing for all (primary nursery areas) or part (secondary nursery areas) of the year as indication of their perceived value to successful production of juvenile fish and crustaceans. The area is subject to excess anthropogenic nutrient loading, leading to hypoxic and anoxic conditions of varying intensity in most summers (Lenihan and Peterson 1998, Paerl et al. 1998, Buzzelli et al. 2001, Eby and Crowder 2002). The total surface area of the mesohaline portion of the estuary included in the model is 267 km^2, with an average water depth of 3.8 m (Baird et al. 2004). Most of the shrimp trawling in the Neuse River takes place within the model boundaries. Both early and late summer models were constructed because they include the most active seasons of both shrimping and blue crab production, bracket the most productive period of fishery production, and because the most extensive data on important primary producers and consumers were available for these time periods. The model was based on 24 compartments (Table 4.1), defined by either a single species or a guild of species characterized by similar diets, consumers, and habitats. The standing stock of each compartment was expressed in grams of carbon (g C) per square meter, and carbon flows were expressed in g C per square meter per day. Each model expresses the average conditions in the study area for early or late summer.

Compartments for the model were formed by pooling species based upon similarities in diets and predators among organisms, and the species of most interest to the project. For example, blue crabs comprise one compartment because they are the focus of central questions of this modeling exercise. Input information for each compartment was collected from local experts, field sampling, and the scientific and gray literature, giving preference to information that matched the model temporally and spatially, then information that matched spatially (Table 4.1, Appendix 1). When information specific to the Neuse River Estuary was unavailable, the most complete information from the most similar location was used. The availability of discarded carrion and the changes in the diets of scavengers in the presence of discards were based on field sampling in the Neuse River Estuary and Core Sound (Chapters Two and Three; Johnson, *unpub. data*).

First a base model, without including fishery catches or discarding, was constructed for each time period. The base model should not be considered “pristine”, as it reflects a system impacted by years of human intervention in the region. Then three additional models were developed for each season to determine the effects of different aspects of the fishery impacts and whether their effects are additive or synergistic: (1) fishing alone (only removal of commercially fished organisms from the system), (2) discarding alone (no fishing removal, but with transfer of demersal fish to the carrion compartments to mimic discarding), and (3) fishing and discarding together.

Although many data were collected within the model boundaries during the modeled seasons, some were not, especially for apex consumers and for diet composition of major predator groups. Therefore, the models on the first run were always unbalanced. Changes from original estimates were made based on the following guidelines: (1) diets for organisms were changed only to reflect changes in the proportion of each prey that made up the diet, rather than adding or eliminating a prey item, (2) biomass of a compartment was changed only when the new value fell within the range of 1 SE of the original estimated value, and (3) values of least certainty were changed first. In most cases, only small changes in biomass or in the proportion of prey items in diet had to be changed to balance the model.

Numerous trophic structure indices were evaluated for each of the 16 models. The effective trophic level, or non-integer trophic level as introduced by Odum and Heald (1975), is calculated by Ecopath for each compartment in each model. The omnivory index, which is the variance of the trophic level for a consumer, was calculated for each consumer compartment in each model. When the omnivory index is zero, the consumer feeds on one trophic level, but a larger value of the omnivory index indicates that the consumer feeds at many trophic levels. The ecotrophic efficiency (EE), calculated for each compartment in each model, is the proportion of the compartment that is consumed or exported from the system. Niche overlap was calculated for each pair of compartments, and is an index ranging from 0 to 1 which measures the extent to which pairs of species share resources (for predators) or predators (for prey) (Christensen et al. 2000). Low niche overlap indices for predators or prey indicate low overlap in prey or predators, respectively, while values approaching or equaling one indicate high overlap.

Changes in direct and indirect trophic interactions were quantified using the “Mixed Trophic Impact” (MTI) module of ECOPATH, which measures the effect that a small, constant change in the biomass of one component will have on other components. This can be negative (for example, when the greatest impact of one compartment on another is through direct predation or competition), zero (neutral), or positive (for example, when the greatest impact of one compartment on another is through direct removal of a competitor or predator of the impacted compartment). The MTI of one group on another is a composite of all trophic interactions in the model between the two groups, whether direct or indirect.

ECOPATH also computes various system indices (Christensen et al. 2000), and I focused on the system omnivory index and connectance index to examine the effects of discarding on the system. The system omnivory index (SOI) measures how feeding interactions are divided among trophic levels (Christensen et al. 2000). It is the average of all the omnivory indices of all consumers in the system, weighted by the biomass of the consumers. I used this index to compare the amount of omnivory among consumer diets with and without the presence of discards to evaluate the extent to which discard availability increases diet breadth. The connectance index (CI) is the ratio of the number of actual feeding links in the system to the number of possible feeding links (Christensen et al. 2000). I used CI to quantify the extent to which discard availability changes scavenger feeding patterns across the ecosystem.

The amount of carbon cycled through the system was calculated by Ecopath, as was the average path length of a unit of carbon that passes through the system. The amount of flow was calculated for each trophic level of each of the 16 models, as well as the total system throughput (the sum of all flows in the system). The contribution of total system throughput provided by the detritus and by primary production was calculated for comparison between models. Ascendency, developed to measure ecosystem size and development, is computed by multiplying the total system throughput (size of the ecosystem) by the average mutual information in the system (a measure of the organization of the system) (Ulanowicz 1986, Christensen 1995); ascendancy and the maximum value of ascendancy, the development capacity, were calculated for all the models.

RESULTS

Changes to the original estimates of biomass and diet composition had to be made for all models to create balanced models, as is typical in mass-balance models (Christensen et al. 2000). The major changes made were in the relative proportions of prey items in the diets of the major predators in the system, demersal fish and blue crabs. For late summer 1997 and early summer 1998, demersal fish and blue crab prey had to be adjusted to decrease consumption of soft-bodied benthic invertebrates and increase consumption of mollusks and detrital compartments. None of the changes made departed from the estimated range of values from the literature regarding the diets of these predators.

The effective trophic level of each compartment was calculated for each fishing scenario and for each time period (Table 4.2). The effective trophic level of oysters, mollusks, and the bluefish and large flounder compartment did not vary across time or fishing scenario. Zooplankton and meiobenthos had higher effective trophic levels in the early summer of 1997, regardless of fishing scenario, and for all other models their effective trophic level did not change. Jellyfish and shrimp had higher effective trophic levels in the early summer of 1997 compared to other time periods, and showed no differences between fishing scenarios. Pelagic fish and soft-bodied benthos had higher trophic levels during early summer 1997 and late summer 1998, regardless of fishing scenario. The effective trophic level of sea turtles and gulls declined when discards were present, alone or with fishing, and varied from season to season. The effective trophic level of sea turtles declined over each summer and the effective trophic level of gulls was highest during early summer 1997. Demersal fish trophic level was higher in early summer 1997 and late summer 1998, and sometimes showed slight declines when carrion was available with and without fishing although the pattern was inconsistent. Blue crab trophic level also declined when discards were included alone or with fishing in the model, and was highest in early summer 1997 and late summer 1998.

Ecotrophic efficiency (EE), the proportion of production by a compartment that is eaten or exported from the system, of some of the major fishery groups varied seasonally and with fishing scenario (Table 4.3). The EE of pelagic fish declined in both models that included discarded carrion, except in the late summer of 1997. Demersal fish EE declined in early summer 1997 and late summer 1998 with addition of fishing, discarded carrion, and their combination, but increased with the combination of discarded carrion and fishing in late summer 1997 and early summer 1998. The EE of blue crabs was decreased by the availability of discarded carrion, and slightly decreased with the combination of discarded carrion and fishing.

Biomass per trophic level and flow in gC/m2 per day through trophic level changed by season but little or none by fishing scenario (Table 4.4). The early summer of 1997 and the late summer of 1998 had the greatest sum of energy passing through the system, also called total system throughput (Table 4.4). Despite differences between years and seasons, approximately the same amount of production moved to the fourth trophic level in each season. The most biomass reached the third trophic level in early summer 1997, with little difference across other seasons. Carbon originating from detritus dominated the total system throughput in early summer 1997 and late summer 1998, while primary production from phytoplankton was more important in the other seasons.

For most groups, prey overlap varied more between seasons than between fishing scenarios. Of notable exception is that bycatch availability decreased prey overlap between gulls and large predators in early summer 1997. Sea turtles, gulls, bluefish and large flounder, demersal fish, and blue crabs had large prey overlap during all time periods and fishing treatments.

The omnivory index (OI) of most consumers varied by season due to differences in prey availability (Table 4.5). Gulls, large predators, and demersal fish (except in early summer of 1997) had larger OIs when discarded carrion was available, either alone or with fishing. Pelagic fish became more specialized (OI decreased) with the combination of fishing and discard availability. In the early summer of 1997, blue crab OI increased with the availability of discards, both alone and with fishing, and in the other seasons discard availability alone increased blue crab OI but the combination of fishing and discards increased blue crab feeding specificity.

There were more positive trophic interactions (mixed trophic interactions [MTI] greater than 1) in early summer of 1997 and late summer of 1998 (Table 4.6). Gulls exerted a positive influence over demersal fish and some benthic invertebrates during some seasons with some fishing scenarios, but never had positive MTI when fishing and discarded carrion were both considered. Pelagic fish tended to have a positive influence on benthic invertebrate groups but with no particular pattern although positive MTI was more common for pelagic fish in late than in early summer. Demersal fishes and blue crabs have positive influence in the more productive seasons (early summer 1997 and late summer 1998), with demersal fish positively affecting more groups.

Most system attributes showed little change with fishing scenario and varied instead by season, such as cycling index, amount of biomass cycled, average path length, total system throughput, ascendency, and development capacity (Table 4.4). However, the connectance index and the system omnivory index showed large changes with season but smaller changes with fishing scenario. The connectance index and the system omnivory index both increased with the availability of bycatch, alone and with fishing.

DISCUSSION

In general, fishing removal and discard availability exerted changes on feeding relationships but not on system properties. System properties tended to demonstrate destabilizing trends over the summer of 1997, during which anoxia was extensive, and increasing trends over the summer of 1998, which experienced a milder disturbance in terms of the areal extent of anoxia (Baird et al. 2004). The most marked changes in system properties due to fishing and the discarding of carrion were in the system omnivory index, which indicated greater omnivory in the system when discarded carrion was included, and incremental increases in ascendancy and capacity. Discard additions also increased by a small amount the biomass of the bottom level of the food web, the primary production/detritus level, indicating that more energy remains in the system.

Demersal fish and blue crabs, which are important in both biomass and fishing value in the Neuse River Estuary, showed decreases in trophic level with fishing and bycatch availability. One limitation of Ecopath is that the detritus compartments (which includes carrion made available through the bycatch components) are always considered to have a trophic level of 1, regardless of its composition (see Christian and Luczkovich 1999 and Heymans and Baird 2000). Therefore, decreases in the trophic level can occur when consumers eat carrion from higher level consumers, which may be of higher nutritional value than the original diet components.

The decline in ecotrophic efficiency (EE) of pelagic fish in the scenarios that included discarded carrion indicates that pelagic fish may be released from predation by larger consumers when carrion is available, which could have the result of increasing pelagic fishery production. The EE of demersal fish declined with fishing and discarded carrion in early summer 1997 and late summer 1998, time periods of higher production in the system in total, and increased in late summer 1997 and early summer 1998 in the combined discarded carrion and fishing treatment. The increases are most likely due to the capture of the demersal fish by the shrimp trawl fishery (which increases EE). The decreases in the less productive seasons, late summer 1997 and early summer 1998, are partially due to increased demersal fish biomass during those times, so that capture has less of a positive effect on EE, and decreased predation on demersal fish when alternative prey is available. Therefore, fishing and bycatch availability have varying effects on demersal fish when combined with other environmental conditions. The EE of blue crabs was decreased by the availability of bycatch, and slightly decreased with bycatch and fishing. Because fishing included the removal of blue crabs, this shows that predation on blue crabs by other consumers declined enough by diverting consumption to discards that the indirect benefits of fishing on blue crabs outweighs the negative impacts. Because blue crabs are the most economically valuable commercial fishery species in North Carolina, fisheries managers considering changes to the shrimp fishery, such as requiring decreases in bycatch or minimizing estuarine trawling, should recognize that blue crab populations may be affected negatively by such changes.

Biomass by trophic level and flow through trophic level changed by season but not by fishing scenario. Because the numbers of large predators in the system did not change from season to season due to data limitations (estimates by experts were not specific to year or season, and were therefore constant between models), the amount of production reaching the fourth trophic level did not change between years or fishing scenarios. During the time periods with greater total system throughput, more production from the third trophic level may eventually leave the system for harvest or impact elsewhere. Significantly more biomass was present in the third trophic level in early summer 1997 than in other seasons, indicating that the system before disturbance by hypoxia (Baird et al. 2004) was much more productive for fishery species (most of which occur at or around the third trophic level).

Prey overlap was high between many of the higher-level consumer components of the Neuse River Estuary. In part, this is due to my aggregation of species at lower levels of the food web, but it also reflects the importance of the high productivity of an estuary and its value as a nursery area for large amounts of demersal fish and blue crab biomass. Sea turtles, bluefish and large flounder, gulls, demersal fish, and blue crabs had greater than 50% prey overlap in all the models. The presence of discarded carrion in the system did not change this overlap, but it increases the amount of food available to these consumers and thus has the potential to decrease competition between these groups. Further research into the competition between these groups for resources under varying levels of system production are merited, considering the economic value of the demersal fish, blue crab, and bluefish and large flounder compartments and the social and conservation value of sea turtles.

The omnivory index, which indicates the degree of feeding specialization of a compartment, showed marked changes with the different fishing scenarios for many important consumer groups. Gulls, large predators, and demersal fish all decreased their specialization when bycatch was available, indicative of their feeding on the new categories of demersal and pelagic carrion. Blue crab specialization appears to be more dependent on both the availability of discarded carrion and the natural prey of blue crabs. In highly productive seasons (those not impacted by high anoxia), blue crab diets were broader when discarded carrion was available; in less productive seasons, when blue crab prey was less numerous, balancing the models required a greater contribution of detritus, bacteria, and discarded carrion (when available). Such changes in diet during periods of hypoxia have been seen for sciaenid fish in the Neuse River Estuary (Powers et al. 2005), and changes in blue crab diets to reflect the availability of food in the system are common (Laughlin 1982, Hines et al. 1990). Pelagic fish became more specialized (OI decreased) with the combination of fishing and discarded carrion.

There were more instances of positive effects of predators on their prey through indirect means (MTI > 0 for consumers impacting one of their own prey) in the more productive seasons (early summer 1997 and late summer 1998). There are two possible explanations for this phenomenon. During more productive times, consumers may focus on a compartment that negatively affects the prey benefited in the MTI matrix. Alternatively, consumers may have a more broad diet during more productive times, therefore consuming a smaller proportion of the prey benefited in the MTI matrix. This is contrary to optimal foraging theory, which would predict consumers to focus on a preferred prey when it is more abundant, but such results were observed in blue crab diets during periods of differing prey availability in a mesohaline portion of the Chesapeake (Hines et al. 1990). Perhaps during the more productive seasons, when large numbers of prey close in energetic value occupy a patch, consumers may opt to minimize travel time between patches and instead reach satiation on a patch of diverse prey. These alternate theories could be tested experimentally.

No other multi-year, multi-season studies have examined the effects of productivity on positive mixed trophic impacts. The positive mixed trophic impact of gulls on demersal fish and benthic invertebrates increased at times, but never when fishing and discarded carrion were considered together; this is somewhat counter-intuitive because gulls should be limiting their predation on demersal fish and benthic invertebrates when carrion are available. Competition for carrion between gulls and demersal consumers (fish and crabs) may outweigh the benefit of reduced predation of gulls on the demersal consumers. The role of gulls as consumers in the Neuse River Estuary and their interaction with species of fisheries interest deserves further study, especially through diet studies and experiments with and without gulls as consumers. Micheli (1997) demonstrated that the presence of gulls changed blue crab foraging behavior in North Carolina marsh systems and therefore influenced patterns of blue crab prey abundance; Ellis et al. (2005) found that gulls remove 15-64% of some crabs in intertidal and subtidal areas in the Gulf of Maine. Those studies, and the various trophic interactions suggested by the Ecopath model, suggest that gull influences on demersal fish and blue crabs may be larger than previously understood and that further studies of gull diets and influences on their prey abundance are merited.

Most of the system attributes showed little or no change with fishing scenario, but the system demonstrated large changes by season and disturbance by hypoxia, as demonstrated by Baird et al. (2004). Because the disturbance introduced by fishing removal and discard availability occurs high in the food web and the majority of the system biomass is in the phytoplankton, detritus, and benthic invertebrate categories, large changes in system attributes would be surprising. The system attributes that showed marked responses to the availability of discards, the connectance index (CI) and the system omnivory index (SOI), are measurements that reflect more changes in upper trophic levels more than changes in producer and detritus characteristics. The CI showed seasonal differences, but within season the CI increased with the availability of discards to scavengers both alone and with fishing. Therefore, the number of feeding links utilized compared to the number of possible feeding links in the system increased with the availability of discards. If this difference was solely a result of new feeding links resulting from the addition of carrion feeding pathways, there would not have been differences between fishing scenarios within seasons; this increase was not identical between seasons so the changes in the CI were not related only to the addition of carrion feeding pathways. The SOI also showed differences between season and within season by discard availability, reflecting differences in the distribution of feeding relationships among trophic levels in the system. The increase in SOI with the availability of discards shows a greater move towards web-like structure as opposed to linear trophic relationships with the availability of discards. Because the utilization of more pathways for energy transfer reflects system maturity (Odum 1969, Christensen 1995) and provides alternate pathways when one or more compartments experience disturbance, the increases in CI and SOI demonstrate that the availability of carrion may confer additional stability to the system during disturbances.

One of the limitations of mass-balance modeling and network analyses is that the results are dependent on the quality of the input data. The Neuse River is a well-studied and monitored estuary, and although some data used in these models were a mismatch by time period (e.g. the carrion) or location (e.g. sediment bacterial biomass), the data on the majority of the living biomass in the model (benthos, phytoplankton) was collected in the location and time of interest. The modeling exercise exposes gaps in the data, and also indicates through analyses such as MTI and the basic balancing exercise which groups are most likely to have the biggest impact on other groups and therefore may be most valuable to add to studies of the system. The first critical gap in the input data is the biomass of detritus and the extent to which it might be utilized by consumers; detritus groups were important in all seasons and fishing scenarios in carbon cycling and flow in the system. The second data need is for improved sampling of demersal and pelagic fish in the system. Sampling had low replication in the Neuse River Estuary and was inconsistent between seasons, and was conducting using demersal trawls which likely undersample pelagic fish communities and larger fish, which may be able to avoid capture. Gulls appear to have a number of direct and indirect effects on important groups in the system and no data was available on their abundance and diets specific to the Neuse River Estuary. Monitoring of birds in the system and examination of their diets may be valuable to fisheries managers. Finally, this study focused on the removal of species of commercial interest, blue crabs and shrimp. However, recreational fishing is common in the system as well and data on the removal of recreational species are unavailable. Since recreational fisheries are likely to target not just common species such as those in the demersal and pelagic fish categories and blue crabs and shrimp but more rare species such as bluefish and flounder, this removal may be of some importance to transfer of energy to the highest trophic levels. A recent study by Coleman et al. (2004) found that in the South Atlantic region recreational fisheries accounted for 38% of the mortality of species of concern (species listed by the National Marine Fisheries Service as overfished); if recreational fisheries are responsible for that much mortality in the Neuse, then such a contribution should be documented and included in future ecosystem models.

Another limitation to interpretation of the data is the extent to which species in the ecosystem are pooled into compartments. Many of the calculated indices, including effective trophic level, cycling indices, and the connectance index, are sensitive to the degree of aggregation in the model. This particular model had most species grouped in rather broad categories, not uncommon in similar studies of species-rich systems with the exception of the model of St. Marks National Wildlife Refuge (Baird et al. 1998). Because estimates of pelagic fish biomass and identity are limited by the sampling with demersal trawls, grouping pelagic fish into one compartment probably had limited effect on the model compared to decreasing aggregation and increasing conjecture regarding abundances of individual species. Demersal fish were grouped because their impacts on the benthos are similar and the trawls which capture them as bycatch are unselective; the diet of the demersal fish was calculated based on weighting the known diets of the species making up the compartment by abundance of the species in the sampling. Information gained by increasing the number of compartments of demersal fish would have been counter-balanced by further increasing the disparity between the compartmentalization of groups on lower vs. higher trophic levels. Furthermore, the effects of fishing and bycatch on the system itself are unlikely to differ much with further detail in the trophic groups. Ecopath does not incorporate diet switching based on prey abundance or density dependent foraging, so the results are dependent on the diet input entered by the user. Although the diet information for scavengers in the scenarios including discarded carrion reflects the results of field studies, it is not known whether the amount of feeding on carrion differs with the availability of alternate prey. Studies in the Neuse River Estuary have also shown that cannibalism among blue crabs is common late in the summer and when hypoxia is common (Bell et al. 2003, Eggleston et al. 2005), and this was not incorporated into the models since the effect of carrion availability on this phenomenon is unknown.

The contrast between seasons and the contrast between years of differing intensity of hypoxia were greater than the contrast between fishing scenarios, especially for system-level indices. Thus it appears that ecosystem-based management of the Neuse River Estuary must focus on the larger problem of eutrophication to have the most impact on the productivity at all levels of the system. One possible caveat in interpreting the impacts of eutrophication compared to fishing is that all data were collected from a system already impacted by fishing; only energy flow pathways, removal of fishing species, and addition of carrion in the model were changed to assess the effects of fishing. Sampling of the system with and without fishing and discarding was impossible. Therefore, changes to the ecosystem likely to have arisen due to years of fishing disturbance (changes in benthic primary and secondary productivity and species composition, changes in populations of fished species) are already incorporated in the model and a pristine state cannot be modeled from actual data. Even against this backdrop, fishing, through both direct removal and through indirect changes to the system, does create detectable changes to the trophic structure of the system especially by changing the magnitude and number of pathways of carbon flow (most particularly through discard availability) and by changing the amount of detritus available in the system. The detritus added by discarding of dead bycatch is of higher nutritional quality than much benthic detritus, so it may be of particular benefit to scavengers. Adding a means of computing trophic level based on the source of detritus may be a valuable next step in modeling software, as implied by numerous previous studies in addition to this one (Christian and Luczkovich 1999, Heymans and Baird 2000, Allesina et al. 2005).

The Neuse River Estuary, though heavily impacted by humans through eutrophication and fishing disturbance, continues to be a productive fishing grounds and nursery area for juvenile fishery species. This study demonstrates that shrimp trawling, through provision of carrion in the form of discarded dead fish, increases the diet breadth of fisheries species such as blue crabs and demersal fish, keeps more energy in the system at the detritus level for longer periods of time, and provides more feeding pathways through which energy can flow in the system. The indirect effects of fishing, through provision of a new food source, therefore increase system properties that are often thought of as stabilizing. By elucidating indirect linkages between species and groups of species, this model provides managers a means of predicting where changes in fishing regulations might be felt up and down the trophic web and how fishing might affect the system in years of differing productivity. Effective ecosystem-based management requires an understanding of how anthropogenic disturbances impact a system and whether combined disturbances might interact additively or synergistically. Mass-balance trophic models and analyses of their system properties are a beneficial tool for investigating such issues when combined with field studies and adaptive management, and this set of models is the first to show that the effects of fishing, both direct and indirect, differ depending on the degree of hypoxic disturbance on the system.

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Table 4.1. Summary of Ecopath Input. Neuse River Ecopath model compartments ("det" means compartment was considered a detrital compartment), sources of information for biomass, and whether the information was directly measured in the Neuse River Estuary ("local").

#	Compartment	Sources	Local
1	Large predators	F. Schwartz, D. Gannon	yes
2.	Sea Turtles	Epperly et al. 1995	
3.	Gulls and Turns	Parnell et al. 1993	
4.	Large predatory fish	NCDENR Pamlico Sound Surveys	yes
5.	Jellyfish	J. Purcell	
6.	Pelagic Fish	NCDENR Pamlico Sound Surveys	yes
7.	Demersal Fish	NCDENR Pamlico Sound Surveys, G. A. Johnson	yes
8.	Blue Crabs	NCDENR Pamlico Sound Surveys, G. A. Johnson	yes
9.	Brown/Pink Shrimp	NCDENR Pamlico Sound Surveys, G. A. Johnson	yes
10.	White Shrimp	NCDENR Pamlico Sound Surveys	yes
11.	Oysters	H. Lenihan	yes
12.	Mollusks	MODMON surveys	yes
13.	Soft-bodied benthos	MODMON surveys	yes
14.	Meiobenthos	Baird and Ulanowicz 1989	
15.	Zooplankton	Mallin and Paerl 1994	yes
16.	Phytoplankton	MODMON surveys	yes
17.	Benthic Microalgae	J. Fear, T. Richardson	yes
18.	Free-living bacteria	Christian et al. 1984	yes
19.	Sediment bacteria	Baird and Ulanowicz 1989	
20.	Suspended POC (det)	C. Buzzelli	yes
21.	Sediment POC (det)	C. Buzzelli	yes
22.	DOC (det)	Baird and Ulanowicz 1989	
23.	Pelagic carrion (det)	G. A. Johnson	yes
24.	Demersal carrion (det)	G. A. Johnson	yes

Year	1997								1998							
Month	June				Sept.				June				Sept.			
Treatment	N	F	B	FB	N	F	B	FB	N	F	B	FB	N	F	B	FB
Large Predators	3.93	3.92	3.76	3.76	3.76	3.76	3.67	3.57	3.82	3.82	3.61	3.64	4.02	4.02	3.81	3.79
Sea Turtles	3.42	3.36	3.26	3.26	3.34	3.34	3.12	3.17	3.43	3.43	3.26	3.14	3.26	3.26	3.12	3.1
Gulls	3.61	3.57	3.19	3.18	3.38	3.38	3.09	3.13	3.42	3.4	3.09	3.08	3.49	3.49	3.15	3.15
Bluefish and large flounder	3.14	3.13	3.07	3.07	3.04	3.04	3.04	3.04	3.05	3.05	3.05	3.05	3.05	3.05	3.05	3.05
Jellyfish	3.81	3.81	3.81	3.81	3.05	3.05	3.05	3.05	3	3	3	3	3	3	3	3
Pelagic Fish	2.87	2.87	2.87	2.87	2.75	2.75	2.75	2.74	2.8	2.8	2.8	2.8	2.94	2.94	2.93	2.92
Demersal Fish	3.38	3.37	3.35	3.35	2.8	2.8	2.8	2.76	3	3	2.98	3	3.2	3.2	3.2	3.14
Blue Crabs	3.18	2.89	2.89	2.88	2.87	2.87	2.69	2.69	2.81	2.81	2.76	2.78	3.01	3.01	2.96	2.83
Brown/Pink Shrimp	3.02	3.02	3.02	3.02	2.35	2.35	2.35	2.35	2.41	2.41	2.41	2.41	2.43	2.43	2.43	2.43
White Shrimp	2.66	2.66	2.66	2.66	2.35	2.35	2.35	2.35	2.41	2.41	2.41	2.41	2.43	2.43	2.43	2.43
Oysters	2	2	2	2	2	2	2	2	2.01	2.01	2.01	2.01	2	2	2	2
Other Molluscs	2.18	2.18	2.18	2.18	2	2	2	2	2.01	2.01	2.01	2.01	2	2	2	2
Soft-bodied Benthos	2.27	2.27	2.27	2.27	2.14	2.14	2.14	2.14	2.15	2.15	2.15	2.15	2.26	2.26	2.26	2.26
Meiobenthos	2.23	2.23	2.23	2.23	2	2	2	2	2	2	2	2	2	2	2	2
Zooplankton	2.81	2.81	2.81	2.81	2.05	2.05	2.05	2.05	2	2	2	2	2	2	2	2

Table 4.2. Effective trophic level of consumers in the Neuse River Estuary, NC, by season and fishing scenario. Treatments: N = base model, no fishing extraction or discards present; F = fishing extraction only; B = discards only; FB = fishing extraction and discards.

Year	1997								1998							
Month	June				Sept.				June				Sept.			
Treatment	N	F	B	FB	N	F	B	FB	N	F	B	FB	N	F	B	FB
Large Predators	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sea Turtles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gulls	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bluefish and large flounder	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jellyfish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelagic Fish	0.965	0.965	0.808	0.807	0.367	0.367	0.367	0.365	0.156	0.161	0.138	0.131	0.708	0.708	0.678	0.63
Demersal Fish	0.997	0.924	0.927	0.855	0.94	0.94	0.869	0.965	0.749	0.749	0.672	0.877	0.698	0.698	0.691	0.668
Blue Crabs	0.188	0.642	0.168	0.628	0.886	0.886	0.879	0.861	0.159	1	0.129	0.977	0.752	0.752	0.705	0.719
Brown/Pink Shrimp	0.746	0.881	0.739	0.875	0.928	0.945	0.927	0.924	0.605	0.924	0.528	0.876	0.853	0.905	0.84	0.899
White Shrimp	0.123	0.123	0.123	0.123	0.992	0.992	0.991	0.971	0	0	0	0	0.87	0.87	0.868	0.869
Oysters	0.594	0.798	0.59	0.797	0.436	0.436	0.436	0.406	0.662	0.663	0.611	0.658	0.421	0.421	0.417	0.404
Other Molluscs	0.003	0.003	0.002	0.003	0.299	0.299	0.305	0.286	0.066	0.066	0.065	0.066	0.051	0.051	0.05	0.049
Soft-bodied Benthos	0.301	0.324	0.303	0.327	0.99	0.99	0.991	0.983	0.98	0.98	0.974	0.976	0.945	0.945	0.943	0.919
Meiobenthos	0.06	0.062	0.06	0.062	0.083	0.083	0.083	0.081	0.441	0.441	0.438	0.441	0.279	0.279	0.279	0.278
Zooplankton	0.001	0.001	0.001	0.001	0.106	0.106	0.106	0.106	0.009	0.009	0.008	0.009	0.001	0.001	0.001	0.001
Phytoplankton	0.997	0.997	0.997	0.997	0.77	0.77	0.77	0.77	0.081	0.081	0.081	0.081	0.109	0.109	0.109	0.109
Benthic Microalgae	0.952	0.953	0.953	0.953	0.946	0.946	0.944	0.947	0.799	0.799	0.799	0.799	0.673	0.673	0.672	0.673
Free-living Bacteria	0.994	0.994	0.994	0.994	0.762	0.762	0.732	0.762	0.9	0.9	0.9	0.9	0.104	0.104	0.104	0.104
Sediment Bacteria	0.641	0.641	0.641	0.641	0.156	0.156	0.156	0.156	0.418	0.418	0.418	0.418	0.19	0.19	0.19	0.19
DOC	0.931	0.931	0.931	0.931	0.27	0.27	0.27	0.27	0.528	0.528	0.528	0.528	0.193	0.193	0.193	0.193
Suspended POC	0.986	0.987	0.986	0.986	0.054	0.054	0.054	0.054	0.126	0.126	0.126	0.126	0.035	0.035	0.035	0.035
Pelagic Carrion	0	0	0.935	0.041	0	0	0.809	0.352	0	0	0.734	0.056	0	0	0.343	0.938
Demersal Carrion	0	0	0.806	0.139	0	0	0.052	0.008	0	0	0.294	0.143	0	0	0.034	0.177

Table 4.3. Ecotrophic efficiencies of compartments for each season and fishing scenario. Treatments: N = base model, no fishing extraction or discards present; F = fishing extraction only; B = discards only; FB = fishing extraction and discards.

System Measure	Units	1997 June N	F	B	FB	Sept. N	F	B	FB	1998 June N	F	B	FB	Sept. N	F	B	FB
Total System Throughput	gC/m2/day	13.06	13	13	13	7	7	7	7	8	8	8	8	12	12	12	12
Detritus: Throughput	gC/m2/day	11.08	11.08	11.08	11.08	3.021	3.021	3.02	3.033	3.809	3.808	3.809	3.815	7.994	7.994	7.994	7.995
Primary Prod. Throughput	gC/m2/day	1.77	1.77	1.77	1.77	4.372	4.372	4.372	4.372	4.305	4.305	4.304	4.304	3.702	3.702	3.702	3.702
Finn Cycling Index		0.1	0.1	0.1	0.1	1.51	1.51	1.5	1.5	0.01	0.01	0.01	0.01	0.04	0.04	0.04	0.04
Connectance Index		0.238	0.238	0.26	0.26	0.238	0.238	0.258	0.258	0.238	0.238	0.26	0.258	0.227	0.227	0.247	0.252
System Omnivory Index		0.156	0.167	0.192	0.192	0.147	0.147	0.154	0.162	0.121	0.121	0.141	0.137	0.156	0.156	0.177	0.173
Ascendency	flowbits	7	7	7	7.1	8.9	8.9	8.9	8.9	8.2	8.2	8.2	8.2	14.1	14.1	14.1	14.1
Development Capacity	flowbits	27.2	27.3	27.2	27.3	17	17	17	17.1	19	19	19	19.1	29.8	29.8	29.8	29.8
Average Path Length		6.471	6.471	6.47	6.455	2.043	2.043	2.042	2.043	2.03	2.029	2.209	2.029	2.823	2.823	2.823	2.823
Biomass																	
Trophic Level I	gC/m2	2.2	2.2	2.2	2.2	4.143	4.143	4.143	4.143	4.241	4.241	4.241	4.241	5.092	5.092	5.092	5.092
Trophic Level II	gC/m2	8.22	8.232	8.23	8.233	7.974	7.974	7.97	7.988	11.42	11.42	11.43	11.42	8.45	8.45	8.451	8.461
Trophic Level III	gC/m2	1.833	1.835	1.826	1.834	0.563	0.563	0.567	0.551	0.422	0.422	0.416	0.42	0.363	0.363	0.362	0.353
Trophic Level IV	gC/m2	0.054	0.054	0.052	0.054	0.048	0.048	0.048	0.046	0.015	0.015	0.014	0.014	0.04	0.04	0.04	0.038
Trophic Level V	gC/m2	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0	0	0	0	0.001	0.001	0.001	0.001
Flow																	
		-	-	-	-												
Trophic Level I	gC/m2/day	3.122	3.123	3.123	3.117	3.494	3.494	3.494	3.506	2.778	2.777	2.777	2.783	6.738	6.738	6.738	6.737
Trophic Level II	gC/m2/day	7.103	7.104	7.104	7.104	2.023	2.023	2.023	2.023	2.657	2.657	2.657	2.657	2.471	2.471	2.471	2.471
Trophic Level III	gC/m2/day	1.777	1.777	1.776	1.777	0.018	0.018	0.018	0.018	0.023	0.023	0.023	0.023	0.022	0.022	0.022	0.022
Trophic Level IV	gC/m2/day	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002
Trophic Level V	gC/m2/day	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mean Trophic Level of Catch			2.94		3.14		2.56		2.68		2.64		2.8		2.66		2.59

Table 4.4: System Properties of Neuse River Estuary, NC, for all seasons and fishing scenarios. Treatments: N = base model, no fishing extraction or discards present; F = fishing extraction only; B = discards only; FB = fishing extraction and discards.

Year	1997								1998							
Month	June				Sept				June				Sept			
Treatment	N	F	B	FB	N	F	B	FB	N	F	B	FB	N	F	B	FB
Large Predators	0.096	0.099	0.355	0.355	0.001	0.001	0.148	0.274	0.075	0.075	0.365	0.335	0.0015	0.015	0.375	0.363
Sea Turtles	0.09	0.073	0.199	0.197	0.311	0.311	0.349	0.314	0.305	0.305	0.389	0.19	0.397	0.397	0.419	0.396
Gulls	0.528	0.386	0.597	0.596	0.298	0.298	0.42	0.414	0.315	0.319	0.521	0.465	0.377	0.377	0.569	0.505
Bluefish and large flounder	0.282	0.25	0.3	0.299	0.028	0.028	0.028	0.026	0.041	0.041	0.039	0.04	0.055	0.055	0.055	0.051
Jellyfish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelagic Fish	0.688	0.646	0.643	0.643	0.464	0.464	0.464	0.452	0.339	0.339	0.334	0.338	0.649	0.649	0.647	0.622
Demersal Fish	0.138	0.071	0.082	0.082	0.209	0.209	0.196	0.226	0.093	0.093	0.103	0.097	0.065	0.065	0.071	0.126
Blue Crabs	0.271	0.299	0.313	0.304	0.367	0.367	0.321	0.364	0.267	0.267	0.269	0.261	0.349	0.349	0.357	0.312
Brown/Pink Shrimp	0.242	0.222	0.222	0.222	0.254	0.254	0.254	0.254	0.275	0.275	0.275	0.275	0.3	0.3	0.3	0.3
White Shrimp	0.424	0.432	0.432	0.432	0.254	0.254	0.254	0.254	0.275	0.275	0.275	0.275	0.3	0.3	0.3	0.3
Oysters	0	0	0	0	0	0	0	0	0.01	0.01	0.01	0.01	0	0	0	0
Other Molluscs	0	0.147	0.147	0.147	0	0	0	0	0.01	0.01	0.01	0.014	0	0	0	0
Soft-bodied Benthos	0.204	0.205	0.205	0.205	0.126	0.126	0.126	0.126	0.133	0.133	0.133	0.133	0.211	0.211	0.211	0.211
Meiobenthos	0.17	0.181	0.181	0.181	0	0	0	0	0	0	0	0	0	0	0	0
Zooplankton	0.154	0.154	0.154	0.154	0.053	0.053	0.053	0.053	0	0	0	0	0	0	0	0

Table 4.5: Omnivory indices for consumer groups in the Neuse River Estuary, NC, by season and fishing treatment. Treatments:
N = base model, no fishing extraction or discards present; F = fishing extraction only; B = discards only; FB = fishing extraction and discards.

	Year	1997								1998							
	Month	June				Sept.				June				Sept.			
	Treatment	N	F	B	FB	N	F	B	FB	N	F	B	FB	N	F	B	FB
1	Large Predators																
2	Sea Turtles																
3	Gulls	12, 13	7	7, 11						7, 9	7	7		7			
4	Bluefish and large flounder																
5	Jellyfish																
6	Pelagic Fish			13	18	12	12	12						11, 12, 13	11, 12	11, 12, 13	6, 11, 12, 13
7	Demersal Fish	9, 11, 12, 14, 18	18	11, 12, 13	18									14	14	14	14
8	Blue Crabs		19	19	19												
9	Brown/Pink Shrimp																
10	White Shrimp																
11	Oysters																
12	Other Molluscs																
13	Soft-bodied Benthos																
14	Meiobenthos																
15	Zooplankton																
16	Phytoplankton																
17	Benthic Microalgae																
18	Free-living Bacteria																
19	Sediment Bacteria																
Total Positive MTI:		19	17	21	16	7	9	8	5	12	11	12	9	13	11	14	13

Table 4.6: MTI Results by year, season and fishing treatment. Consumer groups with positive, >0.1 mixed trophic impact (combined direct and indirect influence) on other groups. Treatments: N = base model, no fishing extraction or discards present; F = fishing extraction only; B = discards only;FB = fishing extraction and discards.

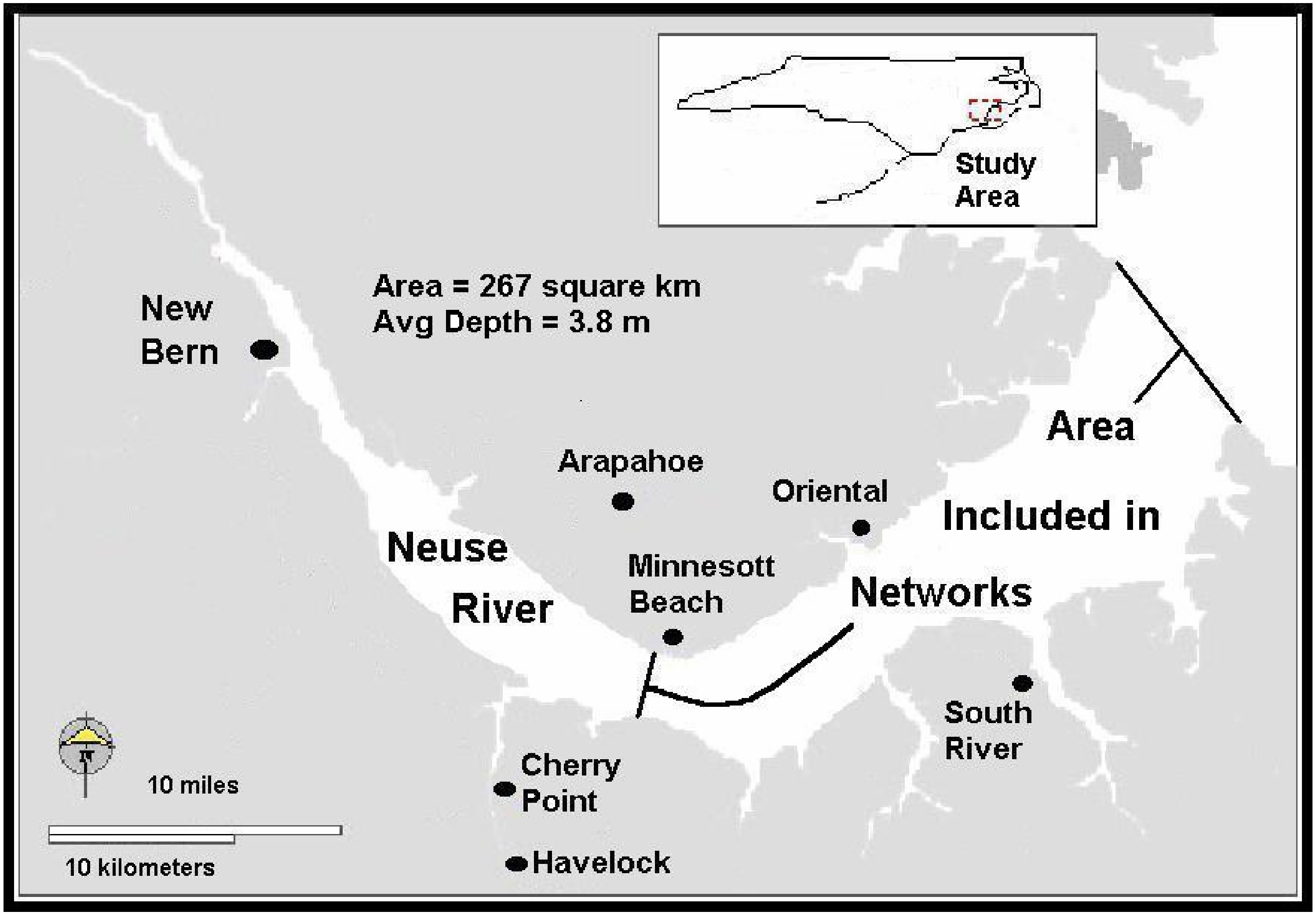

Figure 4.1. Mesohaline Neuse River Estuary, NC, model boundaries.

CHAPTER FIVE:

Multispecies Interactions in a Fishery Ecosystem and Implications for Fisheries Management: The Impacts of the Estuarine Shrimp Trawl Fishery in North Carolina

The goal of ecosystem-based management is the sustainability of ecosystem structures and function (Christensen et al. 1996). The current paradigm shift away from the management of a single species or habitat of concern towards an integrative management scheme that incorporates complex ecological interactions has emerged as scientists and managers recognize the need to incorporate human activities into conceptual and actualized models of food webs, communities, and other ecological units (Pew Ocean Commission 2003, USCOP 2004). However, despite increased support for the ideas of ecosystem management, practicality often demands that management remain mired in the centuries-old idea of single species management. Need for development of the scientific understanding to conduct ecosystem-based management of the estuaries of North Carolina, and to estuarine systems in general, is evident from the highly publicized debates that have raged recently over natural resource management and policy in states along the Atlantic and Gulf Coasts. Issues of significant concern in coastal areas are the demand for reduced nitrogen loading to rivers, which feed into estuaries along the coast, development of coastal areas that destroys wildlife habitat and weakens natural protection from storms and sea-level rise, and the overexploitation of a number of commercially and recreationally valuable fisheries.

However, the logistics required to examine every aspect of ecosystem interaction prevents scientists and managers from carefully testing each policy action for ecosystem effects. Models of ecosystems based on the most current scientific knowledge of interactions within the ecosystem can aid scientists and managers in making informed management decisions and moving towards ecosystem-based management.

Despite ongoing management efforts and research by the North Carolina Division of Marine Fisheries, there continues to be a strong movement among some recreational fishermen to achieve a ban on trawling in the inshore waters of the state in advance of the completion of management plans. If implemented, such a trawl ban would have tremendous economic and social consequences because of the high value of these shrimp fisheries (on average, $11 million per year, second only to the blue crab fishery in economic value) and the reliance of the majority of North Carolina's shrimp fishers on inshore trawling (NCDMF 1999). The perceived benefits of such a trawl ban are reduction in juvenile mortality of many fishes now killed as bycatch during trawling and protection of bottom habitat now disturbed by repeated passage of trawl nets. The formal population models for fisheries species of the Atlantic Coast estuaries which have included bycatch mortality have been limited to species of primarily commercial interest (weakfish, Atlantic croaker, menhaden), and the effects of bycatch mortality from trawling on recreationally important populations remains an open question. Additionally, our scientific understanding of the long-term consequences of disturbing the estuarine seafloor by repeated passage of trawl nets is inadequate (see Watling and Norse 1998 vs. Collie et al. 2000, Thrush and Dayton 2002) to confidently inform this debate and help formulate a more holistic approach to estuarine resource management. Furthermore, the possibility that bycatch from trawlers in estuarine waters is being utilized by commercially valuable species has not been considered or tested. The discards of small fish from the shrimp trawl fisheries in inshore waters may be important in sustaining the high production of blue crabs, the most valuable fishery in North Carolina. Knowledge of the role and importance of such interactions among different fisheries is critical to the development of wise and sustainable management.

The studies presented in the preceding chapters provide critical information for North Carolina managers seeking to improve management of shrimp and crab fisheries for the state, and for fisheries scientists in other areas in seeking to increase understanding of multispecies interactions in fisheries ecosystems. Specifically, the monitoring of the composition of bycatch in the shrimp trawl fishery in North Carolina (Chapter Two) demonstrates that collecting data on bycatch composition with attention to time of week, time of week, and tow duration can lead to increased understanding of when bycatch and bycatch:catch ratios are minimized. Through stratified sampling by time of week, time of night, and duration of tow, I demonstrated that shrimp catch is maximized after breaks in trawling (weekend breaks or breaks between trawling trips) while bycatch CPUE (catch per unit effort) did not change significantly with the timing of the trip. Furthermore, the differences in survival of various species that comprise the discards from the shrimp trawl fishery demonstrate that simply characterizing the bycatch is insufficient to obtain an accurate estimate of discard mortality and its possible effects on populations. When a stock assessment is conducted for species caught as bycatch in the shrimp trawl fishery, it is imperative that both bycatch quantity and survival be considered in the mortality estimation.

The demonstration of scavenger response to discards and the preference for blue crabs to feed on discarded carrion, as well as the potential for such feeding to change predation patterns on economically valuable bivalves (Chapter Three), can aid North Carolina managers in minimizing the effects of changes in management strategies on the potential catches of fish, blue crabs, and bivalves. The potential for decreases in the amount of shrimp trawler bycatch to have a negative impact on blue crabs and bivalves should be weighed against the benefits expected from such changes. Combining the Ecopath model (Chapter Four) with an economic model and with single-species models could aid in this exercise. The demonstration that carrion from trawler discards affects predation patterns on the natural prey of scavengers has lessons for managers of diverse fisheries world-wide. Discarded carrion in other fisheries may also create changes in the food web, and managers concerned about reducing discards should also investigate the potential for changes in populations of species that eat the carrion and their typical prey. Adaptive management (Walters and Holling 1990) which includes tests of the impact of reducing bycatch on other economically or ecologically valuable species is a way to simultaneously increase understanding of fisheries ecosystems and implement changes expected to benefit the system. Furthermore, many of the large fisheries on the Atlantic coast include the baiting of traps for crustaceans (lobsters, blue crabs, and stone crabs), and the availability of bait is likely to act similarly to discarded carrion in changing feeding patterns on alternate prey for organisms small enough to escape traps or that are discarded by fishers.

The pond experiments discussed in chapter three demonstrate that in the short term, blue crabs change their patterns of predation on their typical bivalve prey in the presence of food subsidies of discarded carrion. A review by Polis and Strong (1996) notes that most consumers that receive allochthonous inputs of food (spatial food subsidies) show a numerical response and that food subsidies can elicit changes in consumer-resource relations and food web dynamics. Because fisheries input of dead discards into the system is donor-controlled (consumers do not affect the renewal rate of the food input), feedbacks characteristic of predator-prey interactions do not apply. Populations that benefit from the subsidy become decoupled from productivity lower on their natural food chain and may have adverse effects on their usual prey, even driving densities below a level which could support consumers during non-subsidized times. Therefore, changes in trophic dynamics due to subsidies likely have far-reaching effects in estuarine systems where juvenile fish and crustaceans occur in high densities and interactions among species of fisheries interest are most common. Expanding the pond experiments to the field, especially as part of an adaptive management program, could further understanding of the actual effects of carrion availability on blue crab populations and test the hypotheses regarding consumer subsidization, which are much less tested than the theories of subsidization of primary producers by nutrient input to systems (Polis et al. 1997).

The Ecopath model (Chapter 4) combines the information on discard amounts from Chapter 2 and the diet information from Chapter 3, along with information from the literature on other food web components of the Neuse River Estuary, to analyze the effects that fishing may have on the whole system. The extensive sampling of the Neuse River Estuary has provided a unique opportunity to compare the effects of fishing by season and by the extent of disturbance from another anthropogenic impact, eutrophication. The effects of fishing are small compared to those from eutrophication on total system properties, but fishing and discarding does change the trophic structure by increasing connections in the food web and keeping carbon in the system for a longer time by retaining it as detritus rather than mobile demersal fish, and creating a more web-like trophic structure (which Odum [1969] considers more stable). The availability of carrion also seems to be more important when the system is stressed from eutrophication and the typical benthic invertebrate prey of fisheries species is depleted. This is the first set of models to examine individually the effects of discarding and fishery extraction on a system, and to compare them seasonally and between two years of differing disturbance by hypoxia.

Recommendations specific to the management of North Carolina's fisheries emerge from the studies in the preceding chapters. First, a substantial amount of biomass is lost to bycatch mortality in the shrimp fishery, and changes in the timing of shrimp fishing could reduce that amount of bycatch if that is a primary goal of management. Second, changes in the biomass of discards could have unanticipated effects on fisheries catches. Especially in times of food limitation for blue crabs, decreases in discard availability may decrease blue crab populations due to lack of food, increase blue crab feeding on bivalve prey (many of which are also fished), or increase blue crab cannibalism. Experimental and model results suggest that managers must balance the wasting of fisheries production of finfish against possible decreases in blue crab and bivalve fisheries production.

The exercise of creating the ECOPATH model and analyzing its results suggests that there are changes to the trophic structure of the system resulting from fishing that were, before now, unrecognized because of the lack of knowledge about the quantity of bycatch and the response of scavengers to that bycatch. It is possible that many other unanticipated effects of fishing remain to be suggested and tested. For example, the possibility that trawling disturbance in the Neuse damages benthic fauna and makes them easier for predators to access (as seen by Ramsay et al. 1998 in the Irish Sea) has not been tested, nor has there been a test of the hypothesis that the constant disturbance by trawling leaves large areas of the Neuse River Estuary system in a constant state of early succession, which would be advantageous to shrimp and other organisms that eat meiofauna.

This study combines monitoring, experimental ecology, and fisheries modeling in a way that demonstrates the importance of all three in reaching an understanding of the system. Fisheries modeling depends on monitoring for good data, but without experiments that demonstrated different feeding patterns with and without the availability of carrion (something that may be masked in the field due to the constant occurrence of trawling), the changes in diets in the presence of trawling may not have been recognized. Indirect interactions predicted by the model provide valuable hypotheses of indirect interactions in the system that can be tested experimentally in the future; for example, experiments examining how the presence of discards affects gull feeding on alternate prey would be particularly interesting, since gulls prey upon some of the other scavengers of carrion as well (an example of intraguild predation [Polis and Holt 1992]). This would test the hypothesis put forward by Huxel et al. (2002) as a result of their theoretical food web modeling, that subsidies affecting more than one consumer level are destabilizing, while subsidies affecting only one consumer level tend to be stabilizing.

Finally, this study shows the difficulties in management of satisfying multiple needs and weighing those needs against each other. Bycatch is considered one of the major problems associated with commercial fishing (Dayton et al. 1995), but this work suggests that its availability for years in the estuaries of North Carolina has altered feeding patterns of another commercially valuable species, the blue crab. Therefore, the desire for managers to reduce bycatch from the estuarine shrimp trawl fishery must be weighed against the possibility that negative effects on blue crabs or their bivalve prey may result. There are no easy answers, but science and management must openly confront the changes that humans have made to ecosystems at every level, from the obvious (effects on producers [eutrophication] to herbivores and consumers [over-fishing]) to the less obvious (effects on scavengers through discarding of bycatch and baiting, and destruction of the benthos by fishing gear), and manage systems based on the best possible understanding of those multiple impacts. The move towards ecosystem-based management has made it unacceptable to focus on a single species or fishery and assume that changes made to the management of it will not impact other species and fisheries.

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Appendix: Ecopath Input

For all models: Detritus Fate

Fate	Suspended POC	Sediment POC	DOC	Pelagic Carrion	Demersal Carrion	Export
Source						
Large Predators	0	0	0	0	0	1
Sea Turtles	0	0	0	0	0	1
Gulls	0.2	0	0	0	0	0.8
Bluefish/Large Flounder	0	0	0	0	0.1	0.9
Jellyfish	0.05	0.1	0	0	0	0.85
Pelagic Fish	0	0	0	0.1	0.25	0.65
Demersal Fish	0	0	0	0	0.25	0.75
Blue Crabs	0	0.25	0	0	0.2	0.55
Brown/Pink Shrimp	0	0.25	0	0	0.25	0.5
White Shrimp	0	0.25	0	0	0.25	0.5
Oysters	0	0.5	0	0	0	0.5
Mollusks	0	0.5	0	0	0	0.5
Soft-bodied Benthos	0	1	0	0	0	0
Meiobenthos	0	1	0	0	0	0
Zooplankton	0.25	0.75	0	0	0	0
Phytoplankton	0.5	0.5	0	0	0	0
Benthic Microalgae	0	1	0	0	0	0
Freeliving Bacteria	1	0	0	0	0	0
Sediment Bacteria	0	1	0	0	0	0
Suspended POC	0	1	0	0	0	0
Sediment POC	0	0	0	0	0	1
DOC	0	0	0	0	0	1
Pelagic Carrion	0	0	0	0	1	0
Demersal Carrion	0	1	0	0	0	0

For all models: All compartments utilize 100% of habitat.

For scenarios: N = no bycatch or fishing; F = Fishing only; D = Discarding only; FD = Fishing and Discarding

Biomass (gC/m2)	Jun-97	Sep-97	Jun-98	Sep-98	
Large Predators	0.001	0.001	0.001	0.001	
Sea Turtles	0	0	0	0	
Gulls	0.001	0	0.001	0.001	
Bluefish/Large Flounder	0.003	0	0.001	0.006	
Jellyfish	0.007	0.082	0	0.005	
Pelagic Fish	0.06	0.384	0.067	0.044	
Demersal Fish	0.074	0.367	0.22	0.214	
Blue Crabs	0.033	0.006	0.075	0.004	
Brown/Pink Shrimp	0.002	0.039	0.035	0.01	
White Shrimp	0	0.02	0	0.015	
Oysters	0.033	0.003	0.033	0.033	
Mollusks	6	6.01	9.84	6.03	
Soft-bodied Benthos	0.311	0.085	0.098	0.663	
Meiobenthos	1	0.558	1	0.558	
Zooplankton	0.436	1.03	0.484	1.27	
Phytoplankton	2.1	1.933	1.971	2.672	
Benthic Microalgae	0.1	0.1	0.1	0.1	
Freeliving Bacteria	1.45	1.41	1.47	1.62	
Sediment Bacteria	0.7	0.7	0.7	0.7	
Suspended POC	5.74	4.41	5.74	4.41	
Sediment POC	350	350	350	350	
DOC	24	2.6	2.72	2.98	
Pelagic Carrion	(0.001)	(0.001)	(0.001)	(0.001)	(only in D, FD scenarios)
Demersal Carrion	(0.002)	(0.004)	(0.002)	(0.004)	(only in D, FD scenarios)

All biomass inputs rounded to nearest one thousandth. Therefore, 0 input means value less than 0.001.

Production/Biomass per day	Jun-97	Sep-97	Jun-98	Sep-98
Large Predators	0.001	0.001	0.001	0.001
Sea Turtles	0.001	0.001	0.001	0.001
Gulls	0.014	0.005	0.014	0.144
Bluefish/Large Flounder	0.003	0.002	0.001	0.002
Jellyfish	0.002	0.002	0.002	0.002
Pelagic Fish	0.002	0.004	0.007	0.007
Demersal Fish	0.002	0.005	0.005	0.005
Blue Crabs	0.022	0.019	0.022	0.021
Brown/Pink Shrimp	0.015	0.015	0.015	0.015
White Shrimp	0.015	0.015	0.015	0.15
Oysters	0.014	0.014	0.014	0.014
Mollusks	0.13	0.004	0.013	0.005
Soft-bodied Benthos	0.023	0.011	0.026	0.014
Meiobenthos	0.11	0.084	0.011	0.084
Zooplankton	1.7	0.803	1.698	0.795
Phytoplankton	0.4	0.353	0.294	0.394
Benthic Microalgae	0.5	0.285	0.5	0.28
Freeliving Bacteria	0.917	0.922	0.925	0.92
Sediment Bacteria	1	1	1	1

Consumption/Biomass per day	Jun-97	Sep-97	Jun-98	Sep-98
Large Predators	0.006	0.006	0.006	0.006
Sea Turtles	0.006	0.006	0.006	0.006
Gulls	0.231	0.231	0.231	0.231
Bluefish/Large Flounder	0.019	0.016	0.01	0.016
Jellyfish	0.005	0.005	0.007	0.005
Pelagic Fish	0.029	0.031	0.079	0.07
Demersal Fish	0.026	0.036	0.036	0.035
Blue Crabs	0.104	0.1	0.104	0.106
Brown/Pink Shrimp	0.075	0.077	0.072	0.075
White Shrimp	0.075	0.077	0.075	0.075
Oysters	0.03	0.03	0.03	0.03
Mollusks	0.41	0.02	0.045	0.022
Soft-bodied Benthos	0.11	0.07	0.133	0.094
Meiobenthos	0.55	0.451	0.55	0.421
Zooplankton	3.394	1.602	3.409	1.614
Freeliving Bacteria	1.793	1.793	1.793	1.793
Sediment Bacteria	2.5	2.5	2.5	2.5

For all consumer compartments in all models, unassimilated:consumption is 0.2

Fisheries Removal in gC/m2/day:

	Jun-97	Sep-97	Jun-98	Sep-98	
Brown Shrimp	0.001	0.002	0.001	0.002	(for F and FD only)
White Shrimp	0	0	0	0	(for F and FD only)
Blue Crabs	0.002	0.001	0.002	0.001	(for F and FD only)

Discard Removal in gC/m2/day

Demersal Fish	0.006	0.006	0.003	0.003	(for D and FD only)

Discard Fate is always .25 to pelagic carrion, .75 to demersal carrion.

Diet composition, 6-97 N, F

	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19
		Predator																
1	Large Predators																	
2	Sea Turtles																	
3	Gulls																	
4	Bluefish/Large Flounder																	
5	Jellyfish																	
6	Pelagic Fish	0.8		0.25	0.05		0.02	0										
7	Demersal Fish	0.1		0.05	0.02		0.05	0.01	0.01									
8	Blue Crabs		0.2	0.1	0.03			0.04	0.01									
9	Brown/Pink Shrimp			0.01			0	0	0		0.02							
10	White Shrimp			0.05							0.02							
11	Oysters			0.27	0.05			0.01	0.07									
12	Mollusks		0.4	0.05	0.3			0.07	0.65									
13	Soft-bodied Benthos		0.4		0.3		0.22	0.69	0.12	0.2	0.19							
14	Meiobenthos				0.12			0.01	0.1	0.6	0.26			0.02	0.01			
15	Zooplankton					1	0.18	0.15										
16	Phytoplankton						0.28					0.5	0.22	0.45		0.19		
17	Benthic Microalgae								0.01	0.05	0.08		0	0.05	0.07			
18	Freeliving Bacteria						0.11	0					0.05			0.81		
19	Sediment Bacteria							0.01	0.01	0.03	0.03		0.13	0.25	0.22			
20	Suspended POC						0.12					0.5	0.3					1
21	Sediment POC				0.13		0.02	0.01	0.01	0.13	0.41		0.05	0.23	0.7		1	
22	DOC												0.25					
23	Pelagic Carrion																	
24	Demersal Carrion																	
	Import	0.1		0.22														

All inputs rounded to nearest hundredth.

Diet composition, 6-97 D, FD

	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19
		Predator																
1	Large Predators																	
2	Sea Turtles																	
3	Gulls																	
4	Bluefish/Large Flounder																	
5	Jellyfish																	
6	Pelagic Fish	0.72		0.2	0.05		0.02	0										
7	Demersal Fish	0.1		0.04	0.02		0.05	0	0.01									
8	Blue Crabs		0.19	0.08	0.03			0.04	0.01									
9	Brown/Pink Shrimp			0			0	0	0		0.02							
10	White Shrimp										0.02							
11	Oysters			0.04	0.05			0.01	0.07									
12	Mollusks		0.37	0.22	0.28			0.07	0.4									
13	Soft-bodied Benthos		0.37	0.04	0.28		0.22	0.68	0.13	0.2	0.19							
14	Meiobenthos				0.11			0.01	0.1	0.6	0.26			0.02	0.01			
15	Zooplankton					1	0.18	0.16										
16	Phytoplankton						0.28					0.5	0.22	0.45		0.19		
17	Benthic Microalgae								0.02	0.05	0.08		0	0.05	0.07			
18	Freeliving Bacteria						0.11	0					0.05			0.81		
19	Sediment Bacteria							0.01	0.01	0.03	0.03		0.13	0.25	0.22			
20	Suspended POC						0.12					0.5	0.3					1
21	Sediment POC				0.13		0.02	0.01	0.15	0.13	0.41		0.05	0.23	0.7		1	
22	DOC												0.25					
23	Pelagic Carrion	0.08	0.03	0.1				0.01										
24	Demersal Carrion		0.05	0.1	0.05				0.1									
	Import	0.1		0.18														

All inputs rounded to nearest hundredth.

Diet composition, 6-98 N, F

	Prey	Predator 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19
1	Large Predators																	
2	Sea Turtles																	
3	Gulls																	
4	Bluefish/Large Flounder																	
5	Jellyfish																	
6	Pelagic Fish	0.8		0.23	0.02		0	0										
7	Demersal Fish	0.1		0.05	0.03		0.08	0.03	0.03									
8	Blue Crabs		0.4	0.08				0.01	0.02									
9	Brown/Pink Shrimp			0.05			0.01	0	0.03	0.01	0.01							
10	White Shrimp																	
11	Oysters			0.03				0.02	0.02									
12	Mollusks		0.3	0.31	0.35		0.2	0.38	0.55									
13	Soft-bodied Benthos		0.1	0.05			0.08	0.13	0.05	0.15	0.15			0.02				
14	Meiobenthos				0.6		0.1	0.21	0.05	0.23	0.23			0.13				
15	Zooplankton					1	0.23	0.17				0.01	0.01					
16	Phytoplankton						0.09					0.09	0.03			0.02		
17	Benthic Microalgae							0.01		0.1	0.1		0.02	0.25	0.05			
18	Freeliving Bacteria						0.13					0.2	0.18			0.69		
19	Sediment Bacteria							0.01	0.06	0.2	0.2		0.03	0.25	0.5			
20	Suspended POC						0.08	0.01				0.6	0.41			0.1		1
21	Sediment POC							0.02	0.2	0.31	0.31		0.02	0.35	0.45		1	
22	DOC											0.1	0.3			0.19		
23	Pelagic Carrion																	
24	Demersal Carrion																	
	Import	0.1	0.2	0.2														

All inputs rounded to nearest hundredth.

Diet composition, 6-98 D, FD

	Prey	Predator 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19
1	Large Predators																	
2	Sea Turtles																	
3	Gulls																	
4	Bluefish/Large Flounder																	
5	Jellyfish																	
6	Pelagic Fish	0.72		0.2	0.02		0	0										
7	Demersal Fish	0.08		0.05	0.03		0.08	0.02	0.02									
8	Blue Crabs		0.35	0.08				0.01	0.02									
9	Brown/Pink Shrimp			0			0.01	0	0.02	0.01	0.01							
10	White Shrimp																	
11	Oysters			0.04				0.02	0.02									
12	Mollusks		0.28	0.22	0.35		0.2	0.39	0.54									
13	Soft-bodied Benthos		0.1	0.04			0.08	0.13	0.05	0.15	0.15			0.02				
14	Meiobenthos				0.6		0.1	0.21	0.05	0.23	0.23			0.13				
15	Zooplankton					1	0.23	0.15				0.01	0.01					
16	Phytoplankton						0.09					0.09	0.03			0.02		
17	Benthic Microalgae							0.01		0.1	0.1		0.02	0.25	0.05			
18	Freeliving Bacteria						0.13					0.2	0.18			0.69		
19	Sediment Bacteria							0.01	0.05	0.2	0.2		0.03	0.25	0.5			
20	Suspended POC						0.08	0.01				0.6	0.41			0.1		1
21	Sediment POC							0.02	0.15	0.31	0.31		0.02	0.35	0.45		1	
22	DOC											0.1	0.3			0.19		
23	Pelagic Carrion	0.05	0.03	0.1				0.03	0.1									
24	Demersal Carrion	0.05	0.05	0.1														
	Import	0.1	0.2	0.17														

All inputs rounded to nearest hundredth.

Diet composition, 9-97 N, F

	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19
		Predator																
1	Large Predators																	
2	Sea Turtles																	
3	Gulls																	
4	Bluefish/Large Flounder																	
5	Jellyfish																	
6	Pelagic Fish	0.7		0.23	0.03		0.04	0.01										
7	Demersal Fish	0.3		0.05	0.02		0.13	0.01	0.15									
8	Blue Crabs		0.3	0.08			0.01	0	0.01									
9	Brown/Pink Shrimp			0.05			0.02	0.02	0.03	0.02	0.02							
10	White Shrimp						0.01	0.01	0.02	0.02	0.02							
11	Oysters			0.03				0	0.01									
12	Mollusks		0.4	0.31	0.35		0.08	0.45	0.49									
13	Soft-bodied Benthos		0.1	0.05			0.04	0.01	0.01	0.05	0.05			0.02				
14	Meiobenthos				0.6		0.06	0.1	0.01	0.25	0.25			0.12				
15	Zooplankton					1	0.2	0.17								0.05		
16	Phytoplankton						0.31					0.6	0.22			0.3		
17	Benthic Microalgae						0.01	0.08	0.02	0.12	0.12			0.3	0.1			
18	Freeliving Bacteria						0.01									0.6		
19	Sediment Bacteria						0.01	0.05	0.05	0.22	0.22			0.28	0.45			
20	Suspended POC						0.04					0.4	0.78			0.05		1
21	Sediment POC						0.04	0.11	0.2	0.33	0.33			0.28	0.45		1	
22	DOC																	
23	Pelagic Carrion																	
24	Demersal Carrion																	
	Import		0.2	0.2														

All inputs rounded to nearest hundredth.

Diet composition, 9-97 D, FD

	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19
		Predator																
1	Large Predators																	
2	Sea Turtles																	
3	Gulls																	
4	Bluefish/Large Flounder																	
5	Jellyfish																	
6	Pelagic Fish	0.69		0.19	0.03		0.04	0.01										
7	Demersal Fish	0.26		0.02	0.02		0.13	0.01	0.05									
8	Blue Crabs		0.22	0.05			0.01	0	0.01									
9	Brown/Pink Shrimp			0.05			0.02	0.02	0.03	0.02	0.02							
10	White Shrimp						0.01	0.01	0.02	0.02	0.02							
11	Oysters			0.03				0	0.01									
12	Mollusks		0.39	0.28	0.35		0.08	0.46	0.49									
13	Soft-bodied Benthos		0.08	0.05			0.04	0.01	0.01	0.05	0.05			0.02				
14	Meiobenthos				0.6		0.06	0.1	0.01	0.25	0.25			0.12				
15	Zooplankton					1	0.2	0.17								0.05		
16	Phytoplankton						0.31					0.6	0.22			0.3		
17	Benthic Microalgae						0.01	0.07	0.02	0.12	0.12			0.3	0.1			
18	Freeliving Bacteria						0.01									0.6		
19	Sediment Bacteria						0.01	0.05	0.05	0.22	0.22			0.28	0.45			
20	Suspended POC						0.04	.				0.4	0.78			0.05		1
21	Sediment POC						0.04	0.08	0.15	0.33	0.33			0.28	0.45		1	
22	DOC																	
23	Pelagic Carrion	0.05	0.02	0.05				0.02										
24	Demersal Carrion		0.06	0.09					0.15									
	Import		0.22	0.19														

All inputs rounded to nearest hundredth.

Diet composition, 9-98 N, F

		Predator																
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19
1	Large Predators																	
2	Sea Turtles																	
3	Gulls																	
4	Bluefish/Large Flounder																	
5	Jellyfish																	
6	Pelagic Fish	0.65		0.19	0.03		0.01	0.02										
7	Demersal Fish	0.25		0.04	0.03		0.18	0.02	0.1									
8	Blue Crabs		0.09	0.07				0.01	0.01									
9	Brown/Pink Shrimp			0.04			0.03	0.01	0.01									
10	White Shrimp						0.04	0.01	0.01									
11	Oysters			0.02			0.01	0.02	0.03									
12	Mollusks		0.28	0.25	0.35		0.03	0.15	0.55									
13	Soft-bodied Benthos		0.28	0.04			0.2	0.61	0.1	0.17	0.17			0.05				
14	Meiobenthos				0.6			0.02		0.22	0.22			0.2				
15	Zooplankton					1	0.15	0.12										
16	Phytoplankton						0.2					0.4	0.1			0.05		
17	Benthic Microalgae								0.03	0.1	0.1		0.01	0.1	0.05			
18	Freeliving Bacteria						0.05					0.2	0.1			0.07		
19	Sediment Bacteria						0.02		0.03	0.2	0.2		0.01	0.33	0.48			
20	Suspended POC						0.05	0.01				0.4	0.79			0.15		1
21	Sediment POC						0.05		0.05	0.31	0.31		0.01	0.33	0.48		1	
22	DOC															0.74		
23	Pelagic Carrion	0.1	0.03	0.1				0.01										
24	Demersal Carrion		0.05	0.1					0.1									
	Import		0.28	0.16														

All inputs rounded to nearest hundredth.

	Diet composition, 9-98 D, FD	Predator																
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19
1	Large Predators																	
2	Sea Turtles																	
3	Gulls																	
4	Bluefish/Large Flounder																	
5	Jellyfish																	
6	Pelagic Fish	0.7		0.23	0.03		0.01	0.02										
7	Demersal Fish	0.3		0.05	0.03		0.18	0.02	0.11									
8	Blue Crabs		0.1	0.08				0.01	0.01									
9	Brown/Pink Shrimp			0.05			0.03	0.01	0.01									
10	White Shrimp						0.04	0.01	0.01									
11	Oysters			0.03			0.01	0.02	0.03									
12	Mollusks		0.3	0.31	0.35		0.03	0.16	0.56									
13	Soft-bodied Benthos		0.3	0.05			0.2	0.61	0.1	0.17	0.17			0.05				
14	Meiobenthos				0.6			0.02		0.22	0.22			0.2				
15	Zooplankton					1	0.15	0.13										
16	Phytoplankton						0.2					0.4	0.1			0.05		
17	Benthic Microalgae								0.05	0.1	0.1		0.01	0.1	0.05			
18	Freeliving Bacteria						0.05					0.2	0.1			0.07		
19	Sediment Bacteria						0.02		0.06	0.2	0.2		0.01	0.33	0.48			
20	Suspended POC						0.05	0.01				0.4	0.79			0.15		1
21	Sediment POC						0.05		0.06	0.31	0.31		0.01	0.33	0.48		1	
22	DOC															0.74		
23	Pelagic Carrion																	
24	Demersal Carrion																	
	Import		0.3	0.2														

All inputs rounded to nearest hundredth.