

HABITAT USE AND MOVEMENT OF SUBADULT RED DRUM, *SCIAENOPS*
OCELLATUS, WITHIN A SALT MARSH-ESTUARINE SYSTEM

by

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(Under the Direction of Ronald T. Kneib)

ABSTRACT

Ultrasonic telemetry was used to measure temporal and spatial patterns of movements in subadult red drum *Sciaenops ocellatus*, within a salt marsh-estuarine system. In summer and autumn 2001 and 2002, 31 individuals (30.8 cm \pm 4.3 S.D. total length) were captured by hook and line, surgically implanted with ultrasonic transmitters and released within the upper reaches of the Duplin River estuary, Sapelo Island, Georgia. A stationary array of 10 receivers/data loggers recorded 125,198 fish detections. The data showed that fish exhibited a high degree of site fidelity and a variety of individual movement patterns, ranging from little or no movement to regular forays related to tidal and diel cycles. With the exception of a floating dock structure, no clear patterns of orientation toward specific natural habitat features (e.g. intertidal creek channels, oyster reefs, etc.) or potential prey resources could be demonstrated. Although the study was conducted within a National Estuarine Research Reserve, unrestricted recreational angling was a known, or suspected factor in the loss of ~42% of tagged fish in 2002.

INDEX WORDS: Red Drum, *Sciaenops ocellatus*, Ultrasonic Telemetry, Salt Marsh, Estuary, Essential Fish Habitat, Habitat Utilization, Fish Movement

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B.S., Plymouth State College, 1996

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial
Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2003

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DEDICATION

This work is dedicated to my late Grandfathers, Malcolm Dresser and John Kelly, both passionate recreational fishermen.

ACKNOWLEDGEMENTS

The completion of this work was made possible with the help of the following people: Ron Kneib who served as my major professor and contributed greatly to the development of this project. Steve Newell for supplementing additional expenses for this project. Cecil Jennings and Cathy Pringle for serving on my advisory committee. Mary Price, Laura Cammon, Lori Hendricks, Ryan Harlick and the entire UGAMI staff for their logistical support. Spud Woodward and Dorset Hurley of the Georgia DNR provided valuable input and feedback to the project. Kevin Dresser provided valuable tech-support. Larry Spencer, Chris Chabot, and Len Reitsma challenged and motivated me as an undergrad to pursue graduate school. Don Buso and Gene Likens opened many doors for me while working at Hubbard Brook, perhaps the best job I'll ever have. Thank you to my family for all of their support of my career choice.

Most importantly I owe a great debt to my wife Heather, who unselfishly tolerated my ambitions and made many personal sacrifices, allowing me to reach my goals – I can't thank you enough for your support, and for dealing with my uncharacteristic stress these past 2+ years.

This thesis is based upon research supported by the National Science Foundation under Grant #: 9629621 and the University of Georgia Marine Institute. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the National Science Foundation or the University of Georgia.

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INTRODUCTION

Estuarine salt marshes of the world, and in particular the Southeastern United States, have been credited with providing essential nursery (Weinstein 1979), refuge (Boesch & Turner 1984), and feeding (Sogard & Able 1991, Rozas & Minello 1998) habitat for numerous fish species that use marsh resources at some point in their life cycle. The concept that many coastal marine fishes are estuarine dependent was initially accepted as a tenet of estuarine ecology based mainly on the work of Gunter (1938). Recent researchers have sought quantitative justification for the through direct measures of habitat use (Baltz et al. 1993, Smith & Able 1994,) and by measuring the abundance and density of various developmental stages of marine fish species within salt marsh/estuarine habitats (Kneib 1993, Stunz 2002a).

Role of nekton in estuaries

Fishes and other nekton, like all organisms that use the intertidal and shallow subtidal habitats of salt marsh ecosystems, are exposed to a suite of variable environmental (tidal/diurnal cycles, water chemistry), physical (structure and morphology of habitat), and biological (physiological tolerances, predation, competition) conditions that have shaped their life history traits. Changes in these conditions at different temporal and spatial scales influence the movement of nekton within and between estuarine habitats during different stages in their life cycles. Some estuarine-resident species (e.g., the killifish, *Fundulus heteroclitus*) spend their entire lives in shallow near-shore or intertidal estuarine habitats. While others move in-out of intertidal and subtidal habitats

on temporal cycles that are entrained by tides or diel variables; a subset of the latter (e.g., estuarine transients) enter and leave the estuary on broader seasonal cycles (see Kneib 1997, 2000). Movements of nekton and resulting habitat use can also exhibit variation between individuals of the same species. Individuals within a species or life stage may also exhibit variation in movements as a response to different biotic and abiotic stimuli. For example, fishes and decapod crustaceans commonly move within the estuary in response to localized hypoxic events (Hackney et al. 1976), changing salinity (Kanandjembo et al. 2001), or predation intensity (Rountree & Able 1993).

An important consequence of nekton movements at different scales between habitats within estuaries and adjacent coastal environments is the transfer of production in the form of fish and crustacean biomass. Transfers of living biomass from the most productive estuarine habitats (e.g., intertidal salt marshes or mangroves) via nekton populations to the open estuary or coastal ocean is an important component in the overall functioning of estuaries in the coastal landscape (Kneib 1997, 2000, Deegan et al. 2000)

The exact mechanism(s) by which the productivity of tidal wetlands is transferred to adjacent estuarine and coastal ocean waters is unclear and has long been a topic of debate (Teal 1962, Nixon 1980, Odum 1980). However, fishes and nektonic crustaceans that use marsh resources directly or that feed on species or life stages with direct access to intertidal resources are likely to have an important functional role in facilitating this transfer of energy across the landscape at different spatial scales (Kneib 1997).

Kneib (1994, 1997) proposed the “trophic-relay” conceptual model to describe this for the salt marsh/estuarine ecosystem. The model shows different life stages of both resident and transient species of nekton moving marsh production through spatially-

explicit trophic links and by direct migration/dispersal that occur at multiple temporal and spatial scales. In this proposed scenario, predatory fishes utilize subtidal channels as staging areas, or marsh access points during flood-tide stages, and intertidal creeks at some point in the ebbing tide to forage on prey species retreating from the marsh surface with the receding tide (Kneib 2000, Tupper & Able 2000). Biotic transport of energy via movement of nekton from the estuary to the open ocean has also been demonstrated for gulf menhaden *Brevoortia patronus* (Deegan 1993), pinfish *Lagodon rhomboides* (Irlandi and Crawford 1997), white shrimp *Litopenaeus setiferus* (Webb & Kneib 2002), as well as for yellow perch *Perca flavescens*, northern pike *Esox lucius*, and other fish species of the Great Lakes estuaries by Brazner et al. (2001). Moreover, it has been suggested that marsh and tidal creek edge is a primary feeding habitat for predatory sciaenids (Baltz et al. 1993, Minello et al. 1994, Peterson & Turner 1994). Preference for habitat edge in these cases may be a function of refuge or foraging value (Boesch & Turner 1984) for estuarine species that rely on resources associated with the intertidal marsh. Direct observation of movements between habitat types is lacking for most nekton species, so the functional links between intertidal and subtidal estuarine production and the role that transient marine nekton may serve has not been fully validated.

In order to test concepts presented in models such as the trophic relay (Kneib 1997, 2000), we must have detailed information on species-specific behavior, movements, and habitat use within the estuarine/salt marsh landscape. Previous work on the trophic relay model has focused on movements of nektonic prey species that exhibit seasonal migration to the coastal ocean as well as tidal movement between creek channels and the intertidal marsh plain (Webb 2000, Webb & Kneib 2002). However,

there are few studies of movements in the larger transient predators that would complete the proposed production link between marshes and the coastal estuary outlined in the trophic relay model.

This study attempts to fill key information gaps involving habitat use and mechanisms of energy flow between landscape components (salt marsh → subtidal estuarine ecosystem), by tracking the movements of subadult red drum (*Sciaenops ocellatus*), a large predatory fish that associates closely with marsh habitats as subadults. Ultrasonic telemetry transmitters and a network of hydrophone dataloggers were used to obtain previously unknown data on this species' movements and habitat use of subtidal and intertidal creeks within the salt marsh landscape.

The research focused on answering the following questions: 1) Are there general temporal or spatial patterns of habitat use by subadult red drum within subtidal and intertidal salt marsh creeks? 2) If so, are those patterns related to accessible habitat structure, diel/tidal cycles, or available prey resources? 3) How much individual variation in movement or habitat use is expressed within populations of subadult red drum? 4) Is there strong site-fidelity among individuals within the tidal estuary?

Red drum, Sciaenops ocellatus (Linnaeus, 1766)

The red drum *Sciaenops ocellatus* (synonyms: *Sciaenops ocellata*, common names: redfish, channel bass, spot-tail bass, puppy drum) is a perciform fish in the family Sciaenidae, one of the most common groups of fishes in nearshore/inshore estuarine subtropical waters worldwide. On the Atlantic & Gulf coasts of the southeastern United States, red drum are found from Virginia to northeastern Mexico but rarely occur north of

Maryland (Yokel 1966). The northernmost record of red drum is a single fish caught in a trap in Buzzards Bay, Massachusetts, in 1894 (Yokel 1966).

In Georgia, spawning occurs during late summer and early autumn (Aug – Nov) in aggregations within nearshore coastal waters (Welsh & Breder 1923, Boothby & Avault 1971, Setzler 1977). Upon fertilization, eggs float to the surface and develop quickly, often hatching in little more than 24 h (Wenner 1992). Larvae are transported into the estuary and passively distributed via tidal currents throughout the complex network of creeks within the estuarine-salt marsh system (Setzler 1977, Wenner 1992). Following settlement in these shallow polyhaline habitats, juvenile red drum overwinter in the deeper waters of the estuary and typically remain in these nursery areas for up to a year (Wenner 1992).

Young red drum grow quickly, reaching lengths > 25 cm by Age 1 and may grow to 80 cm at sexual maturity within 3-5 yrs (Wenner 1992, Woodward 1994). Recruitment into the subadult age class begins at about ten months and lasts until sexual maturity. Compared to other sciaenid species, which mature in 1-3 yrs, red drum are slow to reach reproductive age and the subadult age class includes individuals up to 5 y of age (Johnson 1978). Red drum in this life stage inhabit mainly the subtidal estuary, sometimes making forays onto the intertidal marsh plain on flood tides and perhaps some limited movement outside of the natal estuary (Wenner 1992). Tagging studies conducted by the Georgia Department of Natural Resources (GA-DNR) found that most (86% of 271-tagged individuals) subadult red drum were recaptured within 5 km of the release location. However, a small portion (4%) moved a distance greater than 30 km, with a single individual moving a distance of 168 km over a 76 d period (Woodward 1994). Overstreet

(1983) reported that of 88 subadult red drum tagged in the Gulf of Mexico, 10 were recaptured within 1 to 464 days less than 4 km from their release site, and another 10 were recaptured within 4 to 316 days, 4 to 33 km from their release site. In the same study, a single adult red drum, over a period of 752 days, moved 778 km west where it was recaptured at Galveston, Texas (Overstreet 1983). Osburn et al. (1982) reported that between 52% and 81% of tagged red drum in Texas bays moved less than 10 km from their release location.

The diet of subadult red drum includes fiddler crabs, mud crabs, and blue crabs, penaeid and palaemoneid shrimps, and fishes including juvenile spot, white mullet, menhaden, and adult mummichogs (Boothby & Avault 1971, Overstreet & Heard 1978, Wenner 1992, Llanso et al. 1998, Scharf & Schlicht 2000). Analyses of red drum gut contents in the southeastern U.S. indicate that decapod crustaceans are primary components in the diet of most size classes, but fishes become increasingly important prey items of subadult and adult red drum (Table 1). At sexual maturity (~3-5 years of age), red drum typically emigrate from their juvenile/subadult nursery habitat and begin to associate with deeper-waters, particularly near channels and inlets (Wenner 1992).

Historically, red drum have not supported a large commercial fishery on the U.S. Atlantic coast, comprising only a small proportion of fisheries landings (ASMFC 1999). The commercial fishery that currently exists (sale of red drum permitted in Virginia, North Carolina, and Georgia) is sustained mostly from by-catch resulting from trawling for other commercially targeted species (i.e., shrimp). Harvest of red drum (recreational or commercial) within the exclusive economic zone (EEZ) (United States federal regulatory jurisdiction covers all waters within 3 - 200 nautical miles of the coast) of the

U.S. Atlantic coast has been prohibited since 1989 (GA-DNR 2002). Since 1992, total reported commercial landings of red drum have averaged < 1,000 lbs/yr, although it is recognized that an undocumented market for red drum, sold directly to restaurants, exists in coastal Georgia (GA-DNR 2002).

While commercial catches have remained low since the 1950's, the recreational fishery for red drum has grown substantially throughout the southeastern U.S. during the past two decades. Since 1981, when recreational catch records began, recreational landings accounted for ~85% of the annual harvest of 1,672,211 lbs (ASMFC 1999) (Fig. 1). In Georgia, and throughout the southeastern U.S., red drum is among the top five sport fishes targeted by recreational anglers (Pafford & Nicholson 1989, <http://www.state.ga.us/dnr/coastal/2000data.html>). According to the Coastal Conservation Association (CCA), recreational anglers spent \$27 million in North Carolina fishing for red drum in 1998, while the total commercial fishery value for that state between 1972 and 1997 was only \$1.8 million (http://www.joincca.org/html/asfmc/asmfc_reddrum.htm). In Georgia, the DNR estimates that recreational anglers currently spend over \$30 million each year targeting red drum *and* spotted seatrout *Cynoscion nebulosus* (GA-DNR 2002)

Recreational fishing pressure on red drum in most states of the southeastern U.S. has targeted a portion of the subadult population through the enforcement of slot limits on legal size. In Georgia, a slot limit of 14 to 27 inches (35.6 to 68.6 cm) for red drum was enforced between 1993 and 2002. Catch surveys have indicated that most red drum taken in the recreational fishery are from the lower end of the slot (Figure 2). Stock assessments for the southeast have demonstrated that mortality resulting from recreational fishing

pressure on subadults may limit recruitment to the adult population (Vaughan 1996). While the taking of subadults from the population may have detrimental impacts on recruitment into the adult population, the upper limit of the slot (27 inches) was designed to ensure that some proportion of sexually mature individuals were not harvested and the larger more fecund individuals contributed to spawning. Prior to the implementation of these regulations in the early 1990's, red drum was overfished; with a Spawning Potential Ratio (SPR) of < 5% (Woodward, personal communication). SPR is a species-specific measure of what proportion of the population recruits into the adult spawning stock. Where this percentage falls below the target SPR, currently 40% for red drum, a species is considered overfished.

During 2002, in an effort to increase the realized SPR to the target SPR of 40%, the Atlantic States Marine Fisheries Commission (ASMFC) amended the interstate fishery management plan to reduce the maximum size limit for red drum from 27 to 23 inches, creating a new legal size slot-limit of 14 to 23 inches. This maximum size limit reduction theoretically achieves the target 40% SPR by allowing escapement of larger (> 23 in) individuals from the recreational fishery and recruitment into the spawning stock. (Woodward, personal communication). Recent work by Conover et al. (2002) supports the idea that limiting the harvest of adults of a fish population may benefit a species by increasing genetic variation and the long-term sustainable yield of the stock. In Georgia, the size distribution of red drum harvested by recreational anglers appeared to shift toward a greater proportion of fish larger than 14 inches in response to enforcement of the previous slot limit (Fig. 2), but the difference in size distributions was not statistically significant (Kolmogorov-Smirnov two sample test, $p = 0.376$). In Florida, a 14 to 27 inch

slot limit has been enforced since 1987. Since then, there has been a shift at the upper end of length frequencies from larger (>27 inches), to smaller individuals (< 27 inches) and the number of older adult fish has increased, suggesting improved escapement from the recreational fishery (Murphy 2001). The new narrower slot in Georgia will surely test whether adequate numbers of adults will be recruited and maintain a stable spawning population.

Given the increasing recreational fishing pressure, and consequential economic importance of harvesting the subadults of this species, it is important to understand the habits and habitat requirements of this life stage so that essential habitat can be defined and protected as part of the continuing efforts to effectively manage the fishery.

To date, most research on red drum has focused on feeding (Boothby & Avault 1971, Bass & Avault 1975, Overstreet & Heard 1978, Fuiman & Ottey 1992, Llanso et al. 1998, Scharf & Schlicht 2000, Leiner et al. 2000), spawning (Murphy & Taylor 1990, Nicholson & Jordan 1994, Nicholson et al. 1996, Murphy & Crabtree 2001, Stunz & Minello 2001, Collins et al. 2002, Vaughn & Carmichael 2002), and general biology & life history (Yokel 1966, Simmons & Breur 1962, Overstreet 1983, Wenner 1992) of red drum in the southeastern U.S. Other work on this species has contributed to the understanding of red drum growth (Murphy & Taylor 1990, Stunz et al. 2002a), habitat use (Osburn et al 1982, Adams & Tremain 2000, Stunz et al. 2001), mortality (Murphy & Taylor 1990, Ross et al. 1995, Latour et al. 2001) and density (Stunz et al 2002b). However, there is a paucity of information critical to defining essential fish habitat (EFH) for juveniles and subadults of this species within the Southeast Atlantic Bight (SAB), including specific habitat requirements and movements within the estuarine nursery.

Attempts to monitor habitat use of red drum using conventional (Osburn et al 1982, Overstreet 1983, Adams & Tremain 1999) and ultrasonic (Nicholson & Jordan 1994, Nicholson et al. 1996, Woodward & Nicholson 1997) tagging methods have not addressed the use of specific habitats within estuarine habitats across diel and tidal cycles.

Background of ultrasonic telemetry

Innovative techniques and developments in sampling methods have been employed for sampling within salt marsh and estuarine environments (see reviews by Kneib 1997, Rozas & Minello 1997). However, the structure and morphology of tidal creeks within the salt marsh have proven challenging to most workers, forcing sampling efforts to focus on a particular depth/location (marsh surface, edge, open water), or the use of multiple gear types within the same study (i.e., one gear/method for shallow areas and another for deeper areas). Furthermore, the constraints of sampling gear have limited the types of questions that could be addressed regarding habitat use and movement at different spatial and temporal scales.

Ultrasonic telemetry technology, developed in the 1960's (Henderson et al. 1966), has since evolved into a useful tool for addressing ecological and basic life history questions regarding fish populations that otherwise would be difficult to answer. Data from conventional tagging techniques (e.g., visible external tags) is limited to location of the fish at the point of initial capture. Furthermore, collection of data (recaptures) is often fishery-dependent, that is, cooperation of the recreational and commercial fishing

community is critical. Ultrasonic and radio telemetry allows the collection of more specific types of data (e.g., movement, habitat use) *in situ* and without these limitations.

Ultrasonic transmitters typically operate in the 50 to 100 kHz range, which is far beyond the 3 kHz upper limit of sound detection for most teleost fishes (Fay 1988). Recent work by Mann et al. (1997, 1998), suggests that American shad *Alosa sapidissima*, and perhaps other clupeid species, respond to sound in the ultrasonic range up to 180 kHz; however, there is no evidence to suggest that red drum can detect sound at ultrasonic frequencies. Red drum commonly produce low-frequency sound (drumming), so logically their capacity to perceive sound would be restricted to lower frequencies.

Recent developments in technology have allowed for smaller transmitter sizes, longer battery life, and reduced impact on the natural behavior of the organism being studied. A significant advantage of tracking individual fish with telemetry compared to other means of sampling is that real-time data can be obtained on the use of, and movements among, specific locations or habitats within the detection range of a particular array of hydrophone receivers. Data from conventional sampling methods (trawl, traps, hook/line) provides this information only for the short time interval during which the samples are collected (daily, weekly, monthly). Current technology allows for the continuous tracking of any number of individual organisms for up to several months, with the principal limiting factor being the battery life of the transmitter.

Ultrasonic telemetry transmitters, or “pingers” have not been used extensively with red drum. To date, ultrasonic telemetry applications in red drum has been limited to developing a transmitter attachment technique (Carr & Chaney 1976), movement of adults (Woodward & Nicholson 1997), identifying spawning locations of adults

(Nicholson & Jordan 1994, Nicholson et al. 1996), and the assessment of stock enhancement programs (Parkyn et al. 2001, Sherwood et al. 2001, Neidig et al. 2002).

For other fish species, ultrasonic telemetry has been widely employed in addressing questions concerning the diel distribution and movement of salmonids *Oncorhynchus sp.* (Candy & Quinn 1999, Baldwin et al. 2002), white grunt *Haemulon plumieri* (Tulevech & Recksiek 1994), tautog *Tautoga onitis* (Arendt et al. 2001), American eel *Anguilla rostrata* (Helfman et al. 1983), coelacanth *Latimeria chalumnae* (Hissmann et al. 2000), and the leafy seadragon *Phycodurus eques* (Connolly et al. 2002). This approach also has been applied successfully to address issues concerning habitat use in striped bass *Morone saxatilis* (Haeseker et al. 1996, Tupper & Able 2000), Atlantic croaker *Micropogonias undulates* (Miller & Able 2002), and red snapper *Lutjanus campechanus* (Szedlmayer 1997). Ultrasonic telemetry was used to determine home range of, lingcod *Ophiodon elongatus* (Matthews 1992), and cunner *Tautoglabrus adspersus* (Bradbury et al. 1995). Additionally migrations of, striped bass *Morone saxatilis* (Carmichael et al. 1998), steelhead trout *Oncorhynchus mykiss* (Skalski et al. 2001), and Atlantic salmon *Salmo salar* (Potter 1988, Lacroix & McCurdy 1996) have been monitored using ultrasonic telemetry systems.

Objectives

In the present study, I applied some of the most advanced ultrasonic telemetry technology currently available in an attempt to meet the following specific objectives: (1) Characterize the habitat use and movements of subadult red drum inhabiting the upper reaches of the Duplin River tidal marsh-estuarine complex adjacent to Sapelo Island,

Georgia. (2) Determine whether subadult red drum exhibit site fidelity or preference associated with specific types of component habitats (e.g., oyster reef, intertidal/subtidal creek channels, subtidal marsh edge) within the marsh/estuarine landscape. (3) Determine whether the movements of subadult red drum are related to the abundance of potential nektonic food resources associated with the mouths of intertidal and subtidal creek channels that dissect the tidal marsh landscape. (4) Determine whether subadult red drum movement patterns are consistent with the trophic-relay model of secondary marsh productivity transfer.

METHODS

Study areas and site descriptions

All transmitter data and nekton samples were collected from tidal creek systems associated with the upper reaches of the Duplin River within the Sapelo Island National Estuarine Research Reserve (SINERR), located on the landward side of Sapelo Island, which is one of a continuous chain of 13 barrier islands located in Georgia, USA (Fig. 3). The SINERR is representative of the uninterrupted strip of salt marsh (8 – 12 km wide) that separates Georgia's barrier islands from the mainland (Ragotzkie & Bryson 1955). The Duplin River, an elongated estuarine tidal bay opening into Doboy Sound, is inundated twice daily by tides with a mean range of 2.1 m (Wadsworth 1980). Typical of the polyhaline portions of estuaries along the southern U.S. Atlantic coast, the dominant vegetation of the salt marsh surface is smooth cordgrass, *Spartina alterniflora*. Approximately 10 km² of the ~11 km² Duplin River drainage consists of tidal salt marsh, dissected by abundant sinuous intertidal and subtidal creeks characterized by mean monthly water temperatures with an annual range of 10 – 30°C, and salinity ranging from 15 – 30 psu (Wadsworth 1980, Webb & Kneib 2002).

Study areas on the Duplin River (Fig. 4), which included the upper reach (Upper Duplin) and a tributary creek (Stacey Creek) comprised a variety of different component habitat features (intertidal mud-flat creek [IMF], subtidal creek [SUB], edge [DE], open water, or dock) of special interest, some of which contained oyster reefs (designated by an “R” following the site name). Different combinations of these habitat sites were selected as semi-permanent tracking stations for deploying hydrophone

receivers/dataloggers (2001, 2002) and sampling stations for assessing abundance of nektonic prey (2002). A floating dock structure (DOCK) located within the Upper Duplin study area was also the focus of red drum tracking efforts in this study. All sampling in this study was conducted from May through November of both years (Fig. 5).

Ultrasonic receiver array and transmitters

Movements of red drum were tracked using an array of 10 semi-stationary hydrophone receivers/dataloggers (Vemco® Ltd., model VR1) designed to detect, identify, and record individually-coded signals from small (3.5 x 0.8 cm, 3.5 g in water) ultrasonic telemetry transmitters, or “pingers” (Vemco® Ltd., model V8B-2L-R256) that were internally implanted in subadult red drum. Costs of receivers (ca. \$1000 each) and pingers (ca. \$300 each) limited the aerial extent of the estuary that could be covered and the number of fish that could be tagged. Positions of the hydrophone receivers within the array were adjusted during the preliminary stages of fish-tracking (2001) in such a way as to fine-tune the detection of tagged fish. The principal locations of the hydrophone receivers within the landscape are shown for the Stacey Creek and Upper Duplin study areas in Fig. 4.

The surgically implanted transmitter (Fig. 6) produced a continuous pulse of coded pings (69 kHz) at 45 to 75 sec intervals. Transmission of signal at this frequency (69 kHz) combined with the unique coded string of pulses from each transmitter, minimized the likelihood of interference or signal collision with other sound-producing devices/organisms such as electronic fish finders, snapping shrimp, and concurrent telemetry studies within the environment (Arendt et al. 2001).

A total of 31 pingers were implanted in the course of the two-year investigation, with no more than 10 individuals at large simultaneously. Once activated, the pinger's lithium batteries had a life-expectancy of 90 - 110 d. Within that period, signals from individual fish were detected, decoded, identified, and recorded with the time of detection by the hydrophone receivers whenever a transmitter was within range. Preliminary field tests determined the detection range in open water to be 200-400m in the tidal creeks of the SINERR. Hydrophone receivers operated on a single Lithium C-cell battery with a life-expectancy of 180 d. Data were downloaded in the field from each receiver via a magnetically-coupled probe attached to a PC interface and a Dell Latitude LSH400ST notebook computer using interface software provided by Vemco Ltd., Inc. During the course of this study another telemetry project, tracking the movements of blue crab, was ongoing within the SINERR. The blue crab transmitters operated at 65 to 85kHz, a range that included the 69 kHz signal of the transmitters in this study (Wrona, personal communication).

Mobile hydrophone survey

During this study it became clear that tracking fish outside the range of the stationary hydrophone array would provide useful data, especially when tagged fish remained outside the detection range of the receiver array for prolonged periods. In spring 2002, a mobile omni-directional hydrophone (Vemco model VH40) and tracking system (Vemco model VR28) unit was ordered. When the unit arrived in September 2002, it was used to locate and track individual fish during tidal stages associated with movement and dispersal of red drum. From September through November 2002 several

attempts were made to locate and track tagged fish within and outside of the study area, from a 16' Boston Whaler ®-type skiff powered by a 50 hp outboard motor.

Two strategies were used in these searches. The first approach involved randomly searching tidal tributaries of the main Duplin River channel. In the second strategy, I initially located tagged fish at sites they were known to frequent at low tide and then attempted to follow them as they moved with the flooding tide. Maintaining continuous contact with fish that entered dense intertidal vegetation or moved rapidly in sinuous tidal creek channels often was difficult.

Capturing red drum for tagging

Hook-and-line methods were used to capture individual fish to be implanted with a transmitter. All fish were captured within the Upper Duplin study area, adjacent to the “Hunt Camp Dock” (referred to as the DOCK site in this study) (See Fig. 4). Size 2/0 circle-type hooks were fished with live bait (mummichog, white mullet, or white shrimp) and tied to a weighted casting-float rig set on 8-10 lb test monofilament line, as described in Wenner (1992). These hooks are self-setting and result in more lip-hooked fish compared to other hook types, a feature desirable for attaining high post-hooking survival rates (Nicholson & Jordan 1994).

Previous work has demonstrated that hook-and-line methods of capture yielded greater post-capture survival rates than other methods. Mouth-hooked spotted seatrout (*Cynoscion nebulosus*), a closely related sciaenid fish exhibited survival rates of 98%, compared to only 72% survival for gill nets (Murphy et al. 1993). In Georgia and Texas, hook-caught red drum (20-84 cm total length) exhibited post-hooking survival rates of

90-97% in laboratory tanks or field mesocosms (Jordan and Woodward 1992, Matlock et al. 1993). Survival rates probably are even greater under field conditions where released fish do not encounter the stress of laboratory conditions.

Surgical procedures for implanting transmitters

Transmitters were surgically implanted within the peritoneal body cavity as described in other studies (Hart & Summerfelt 1975, Bidgood 1980, Summerfelt & Smith 1990, Winter 1996, Thoreau & Baras 1997, Baras & Jeandrain 1998). Fish caught by hook and line were quickly landed and placed directly into a covered, aerated 50-L cooler containing an anesthetic bath of 70 mg L⁻¹ tricaine methanesulfonate (MS-222) Finquel® (Argent Chemical Laboratories). The anesthetic solution was prepared prior (< 1 h) to capture of fish by adding 1.05 g of crystallized MS-222 to 15 L ambient Duplin River water. When *stage-4* anesthesia (loss of equilibrium, slow opercular rate, loss of spinal reflexes) as defined by Summerfelt & Smith (1990) was achieved, the fish was carefully removed from the bath, measured on a board, weighed with a hanging scale, and placed onto a rigid, foam-cushioned surgical platform equipped with a re-circulating anesthesia pump, (Fig. 7), which was modified from a design by Courtois (1981). This simple and efficient design was constructed from a Styrofoam cooler, plastic screening, foam insulation, plastic tubing/connectors, and a standard 500 gal hr⁻¹ (31.5 L min⁻¹) bilge pump. The pump tubing was retrofitted with a flow-reduction bypass, which slowed the flow velocity into the fish to approximately 15 L min⁻¹. The flow-through set-up maintained anesthesia during the 4 min. surgical procedure, while continuously irrigating the gills with oxygenated water. Transmitters and surgical instruments were disinfected in

a bath of Betadine® solution prior to surgeries. No prophylaxis or topical disinfectants were applied directly to the incision site so that the integrity of the mucous layer and living epithelium would be minimally compromised (Summerfelt & Smith 1990).

A transmitter was inserted into the body cavity through an approximately 1-cm long incision, made with a #20 scalpel blade, along the ventral line midway between the pelvic fins and anus. Scalpel blades were used once and discarded after each surgical procedure. At insertion, the transmitter was pushed slightly anterior to the incision so that it was held securely between the body wall and gas bladder. All surgeries were completed without bleeding. To minimize surgery time, handling time, and overall stress on the fish, the incision was not closed with sutures, staples, or adhesive. Baras & Jeandrain (1998) demonstrated on European eels *Anguilla anguilla* that small incisions (< 1 cm) healed faster than those closed with sutures, and yielded survival rates similar to a non-incision control group. Upon completion of surgical procedures, fish were transferred into another 50-L cooler containing aerated ambient Duplin River water. Fish were observed until self-righting and normal swimming behavior resumed (within 2 min). They were held for an additional 10 min to ensure full post-anesthesia/surgery recovery, and then released back into the Duplin River within the study area.

In laboratory trials, five red drum were implanted with dummy transmitters, (same size, shape and weight but without the electronics of an active transmitter). The incisions closed within 3 d, and healed with visible scar tissue within 10 d. One of the laboratory fish died within 10 min post-surgery, likely as a result of injuries sustained during transport from surgical table to lab tank (fish dropped onto lab floor). After ~30 d the remaining 4 fish were sacrificed. No signs of infection were observed internally or

externally adjacent to the incision site. Dummy transmitters were encapsulated in connective tissue between the body wall and peritoneum. All of the implanted lab-trial fish retained their tags and did not exhibit transintestinal or body wall expulsion of transmitters, a phenomenon that has been observed for rainbow trout *Oncorhynchus mykiss* (Chisholm & Hubert 1985), channel catfish *Ictalurus punctatus* (Summerfelt & Mosier 1984, Marty & Summerfelt 1986), and African catfish *Heterobranchus longifilis* (Baras & Westerloppe 1999).

Sampling for potential prey

Abundance of potential nektonic prey species was assessed in different habitat types using cast nets and minnow traps during 2002 (May through July). Standard, dual-funnel (2.5 cm diameter opening) galvanized steel mesh (0.64 cm) minnow traps as described in Kneib & Craig (2001), were freshly baited (wet, “seafood-flavor” canned cat food secured inside a film canister with drilled-out ¼ inch holes), and deployed for 30 min intervals. Three traps were fished simultaneously; two traps along the edges of the creek and one trap in the middle of the creek. For DE sites, traps were placed along the edge only, 1m, 2m, and 3m from edge, respectively. Sites were marked with a PVC stake/buoy. Traps were baited to promote maximum capture of any prey species present; especially to capture those species that otherwise might not enter traps. During each sampling period, cast net samples, 10 quality casts per site, were obtained as described by Webb (2000). A cast was considered to be a quality cast when the net was $> \frac{3}{4}$ open upon hitting the surface of the water. If a cast did not meet this requirement, another attempt was made.

Samples obtained from both traps and nets were immediately placed on ice and transported to the lab for identification, enumeration, and measurement of the catch. Collection of potential prey were made six times at each of the 10 sites across three tidestage-groups (low, mid, high) for a total of 180 sampling events between May-July 2002. To avoid biasing the order of sampling, a random number (1 – 10) was assigned to each site to determine the sampling order within a given tidestage. After all ten sites were sampled; each was re-assigned a new random number that determined the order for the next round of sampling.

Environmental parameters

Temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), and salinity (psu) were measured during May – July 2002 concurrent with potential prey sampling efforts at all sites using a YSI® Model-85 portable temp/oxygen/salinity meter. These measures were included to provide further site characterization of the monitored habitat types [DE, SUB, IMF].

Data processing & analysis

Data obtained from the hydrophone receivers were retrieved at intervals ranging from one week to one month. Raw ASCII-text files were offloaded using software provided by the manufacturer from the field receivers to a Dell® Latitude LSH400ST notebook computer. These files were converted into Excel® spreadsheet format, where data were examined visually for integrity and errors. To avoid overlap of data between sites and to ensure that each ping detected by the hydrophone was in fact a unique detection, an algorithm was pre-programmed in the datalogger by the manufacturer that

filtered out any detection not positively identified and decoded. Given the proximity of receivers within the study area, and potential for signal overlap between sites, another post-processing data-filtering tool was employed to eliminate simultaneous detections of a single transmission at multiple sites (overlap). Data were filtered for detections with an interval < 45 seconds since its previous detection (45 sec is the minimum time interval between unique signals from a given transmitter). These data points were removed from the original dataset and stored in unique files that represented a tagged fish occupying physical space between two or more receiver locations. The data that remained after filtering represented transmitter detections unique to that particular site (e.g., detections at site SUB3 exist only at SUB3 and not SUB2, SUB1). A 24 h time delay from the time the fish was released back into the environment was incorporated into the post-processing of data to ensure that the observed detections were not influenced by potential complications or stress from the surgical procedure.

The data were apportioned into three study periods, each separated temporally and by unique cohorts of individual tagged fish: 1) Upper Duplin summer 2001 [$n = 9$ fish], 2) Upper Duplin and Stacey Creek autumn 2001 [$n = 10$ fish], and 3) Upper Duplin summer-through-autumn 2002 [$n = 12$ fish]. Individual patterns of occurrence and detections for all tagged fish within each of the three study periods are presented in the appendices.

To graphically distinguish observed differences in the number and pattern of detections between tides, I divided the tide cycle into two groups: 1) Onset times for high and low tides, and 2) groups of high, mid, & low tides. Fig. 8 shows the approximate locations of each of these tide groups within a hypothetical tide cycle. The first grouping

of tides (Fig. 8A) uses the *onset* time of high tide vs. the *onset* time of low tide. The onset time of high and low tide was taken as the mid-point between consecutive tidal maxima and minima as follows:

$$ONSET_{H1} = H_1 - L_1 / 2 \quad \text{and} \quad ONSET_{L2} = L_2 - H_1 / 2$$

Where: H1 = time of first high tide maximum in a series
 L1 = time of first low tide minimum in a series
 H2 = time of second high tide maximum in a series
 L2 = time of second low tide minimum in a series

Tide onset times were used to graphically display detection patterns between tide stages (see appendices). For the second tide grouping, the tide cycle was separated into three distinct units – high (H), mid (M), and low (L). Preliminary observations indicated that the trajectory (flood vs. ebb) of the tidal flow did not influence detection frequency of tagged fish; therefore flood and ebb stages of high, mid, and low tides were combined (Fig. 8B).

All statistical procedures and graphical analyses were performed using the software packages SYSTAT® v.10, and SIGMAPLOT 2001® v.7.0 © 2000, SPSS Inc. Data management and filtering used VEMCO® VR1-PC tracking software, and EXCEL 2000® v.9.0 © 1985-1999, Microsoft Corp. Tide data (time, water level) were obtained using TIDE® tidal prediction software, Micronautics, Inc.

The analytical problems associated with telemetry tracking data (i.e., low sample number, high degree of natural variation, high amount of zeros in the dataset), described by Aebischer et al. (1993), make it difficult to apply statistically rigorous parametric hypothesis testing to the data sets. Still, certain individual patterns of movement were easy to demonstrate simply by using a graphical presentation of the data. A two-sample

Kolmogorov-Smirnov test was performed to test for homogeneity in the frequency distributions of tagged fish within the Upper Duplin study area. Two sample t-tests were used to compare inter-annual differences in size of fish and number of days at-large. Two-way analysis of variance (ANOVA) was used to test the effects of site type and tidestage on temperature, dissolved oxygen, and salinity between sites and between tides during 2002. In all tests, $\alpha = 0.05$ was used as a critical value for accepting or rejecting null hypotheses.

Neither the raw nor transformed abundance data from nekton sampling met the assumptions of normality or variance homogeneity, required for the application of standard parametric tests. For these data I used the Scheirer–Ray–Hare extension of the Kruskal–Wallis ANOVA (Sokal & Rohlf 1995) to test for effects of site type and tidestage on the ranked data. This test uses the ratio of the sum of squares to the mean square error to calculate a statistic (H), which is distributed as a chi-square variable, and is effectively similar to the statistic “F” used in parametric ANOVA. Tagged fish at-large for less than 24 hours post-surgery/release (see Table 3) were assumed to have died due to stress associated with handling and surgical procedure, and were excluded from statistical and graphical analyses.

RESULTS

Fish size

During the study period (June 2001 – December 2002) a total of 31 sub-adult red drum (n=19 in 2001 and n=12 in 2002) were tagged with ultrasonic transmitters and released within the study area. Twenty-seven of the tagged fish were initially below the State of Georgia minimum legal size of 35.6 cm total length (TL). Because all fish tagged within a given year, regardless of season, were from the same cohort (spawned August – November of previous year), they can be considered a random group of the subadult population for the season in which they were tagged. Fish tagged during late summer/autumn were larger than fish tagged during early summer because the mean individual size within the cohort had increased because of growth within the intervening interval. The average initial size for both years combined was 30.8 (\pm 4.3 S.D) cm TL and 330.2 (\pm 135.8 S.D.) g wet weight. The mean lengths of individuals tagged during 2001 (30.27 ± 4.348 S.D) and 2002 (31.76 ± 4.344 S.D.) were not significantly different ($t = -0.930$, $p = 0.360$, $\alpha = 0.05$). Individual fish captured in both years fit a common length-weight relationship reasonably well (Fig. 9). Table 3 summarizes the length, wet-weight, tagging date, release site, number of days at large, and suspected cause of fish loss from the study area for all 31 tagged fish.

Surgical implants

Surgical procedures took place without incident and within the constraints and recommendations provided in the literature. Table 2 summarizes the recommended

values for surgical parameters along with the observed values for this study. Average duration of surgical procedures was 4.1 ± 1.34 (S.D.) min. All fish surgically implanted with transmitters survived the procedure and initial ~10 min recovery period prior to release.

Ultrasonic tracking

Summaries of daily detections for individual tagged fish show considerable variability among individuals and between years (Fig. 10). Specific causes for loss of tagged fish (i.e., abrupt cessation in detections or movement), were not always known but likely to be one, or a combination, of the following: 1) death caused by post-surgical complications, 2) removal by recreational angling, 3) predation by bottlenose dolphin *Tursiops truncatus* or other large estuarine predator, or 4) active/passive dispersal or emigration from the study area.

A detection day was defined as a 24-h period in which an individual was detected by at least one receiver. Individual fish varied in the number of detection days, and the temporal pattern of detections. Some individuals were detected within the study area at least on a daily basis, whereas others appeared to be more sporadic in their movement in/out of the study area. Re-emergence of a fish that was considered “lost” from the study area for several days occurred in both years, but was more prevalent in 2001.

The number of days that tagged fish remained at-large within the study area (i.e. the time period between release date and date of last known detection) varied considerably among individuals and ranged from 1 to 101 d. However, the mean was 39.1 ± 34.4 (S.D.) days for both years combined. Three of 31, or 9.7%, tagged fish

exhibited total tracking records of < 24hr and were assumed to have succumbed to stress/mortality resulting from surgery and/or hooking mortality. Such an assumption is consistent with expected post-hooking mortality rates of 8% for red drum in Georgia (Jordan & Woodward 1992). Included under this assumption, for purposes of this study, was the likelihood that a fish recovering from post-hooking/post-surgical stress may have been more susceptible to predation via bottlenose dolphin or other estuarine predator, resulting in an apparent “post-surgical mortality”. For the 28 fish ($n_{2001} = 18$, $n_{2002} = 10$) that presumably survived the 24 hour post-surgery “critical period”, the adjusted mean number of tracking days for both years was 43.2 days (± 33.7 S.D.) and ranged from 5 to 101 days at large within the study area(s). For this subset of “survivors”, the average number of days at large was significantly greater ($t = -2.052$, $p = 0.049$, $t = 0.05$) in 2002 (59.8 ± 36.59 S.D.) than in 2001 (34.0 ± 29.07 S.D.). With the exception of two cases, where recreational anglers re-captured tagged fish (#24, #28) and returned the transmitters along with information on location of capture, it was impossible to determine the fate of a tagged fish with certainty. Angler re-captures of tagged fish accounted for the removal of 3 of 12 tagged fish from the study area during 2002, but angler removal was not confirmed during the previous year. Re-capture efforts were not attempted as part of this study.

A total of 35,356 and 13,988 detections from 15 fish were recorded within the Upper Duplin study area (UD) during summer and autumn 2001, respectively. There were 10,520 detections recorded from 7 fish (4 in-site releases, 3 “visitors” from the UD-released cohort) within the Stacey Creek study area (SC) during autumn 2001 and 65,334 detections from 12 fish within the UD during summer/autumn 2002. Fig. 11 shows the

total detections for individual fish by habitat type or location within each study area and season. During summer 2001 in the Upper Duplin study area 70.2% of detections occurred at the DOCK site, 27.9% at SUBX, 1.1% at IMF1, and 0.8% at SUB3. In the same study area during autumn 2001, the DOCK site again accounted for a substantial number of detections (43.9%), but there were relatively fewer at SUBX (0.6%) and SUB3 (1.4%) and many more at IMF1 (54.1%).

At the Stacey Creek study area, by far the most detections (92.3%) occurred at MID, followed by the UPPER site (4.6%), SC/DUPLIN (1.9%), and the LOWER site (0.7%). Note that the group of fish tagged in summer 2001 does not overlap temporally with the autumn 2001 group and that none of the summer 2001 fishes were detected in autumn 2001 (Fig. 10).

During the 2002 monitoring (a new cohort of tagged individuals) in the Upper Duplin study area, the previous DOCK station was represented by receivers relocated to three surrounding habitat types (DER1, SUBR1, and IMFR2) in an attempt to improve the resolution of detections in that area. Together these new locations accounted for 90.6% of all detections in 2002, confirming a previous suspicion that fish were exhibiting strong fidelity for this area of the receiver array.

The affinity of tagged fish for habitats in the vicinity of the floating dock structure (includes habitat sites: DOCK [2001], and DER1, SUBR1, & IMFR1 [2002]) within the Upper Duplin study area is clearly shown in Fig. 11. Given the overall lack of shading and overhead structure within this system, the dock may have served as an important refuge from predation (see Helfman 1981). The Hunt Camp Dock at Moses Hammock (DOCK) is known as a local “hot-spot” for red drum, and other common sport fishes

(e.g., spotted seatrout) within the SINERR. Affinity of fish for this dock is also evident in Fig. 12, which shows the total log-transformed detections in 2002 by habitat site vs. distance from original capture site. This relationship was significant, with an $r^2 = 0.470$, and p -value = 0.029.

Aggregation & dispersal

Subadult red drum did not show an exclusive affinity to shoaling (unorganized groups) or aggregation (mutual attraction to food or other resources) within the study area. Instead, these behaviors appeared limited to specific areas, especially during low and mid tides. In particular, shoaling aggregations of tagged fish seemed to occur in the vicinity of the DOCK site in both years (Figs. 13-16). Fig. 13 shows changes in the number of tagged fish ($n = 5$) at the DOCK site (see map in Fig. 4, lower panel) with tidestage during July 2001, over a period of 19 tidal replicates (~10 d). The most striking feature of the pattern is the shift in the number of fish present at low tide (3-4 individuals) compared to high tide (1-4 individuals). Typically (84% of low tides) there were 4 individuals present in the vicinity of the DOCK site during low tide, whereas at high tide there were occasions (21% of high tides) when only one fish was present at this site. At no time during this period were all five fish entirely absent or present but there was *always* at least one fish present occupying this site throughout the tidecycle.

Kolmogorov-Smirnov pairwise comparisons of these distributions indicated that the high tide distribution was significantly broader than low tide ($D_{MAX} = 0.474$, $p < 0.001$). But the mid tide distribution did not differ from either of the other tide stages (Kolmogorov-Smirnov tests, $p > 0.05$).

Fig. 15 shows the same distributions plotted for 2002 fish ($n = 7$) during August-September 2002, over a period of 58 tidal replicates (~30 d). Since a hydrophone receiver was not located exactly at the DOCK site during 2002, data were pooled from the 3 receivers (DER1, SUBR1, IMFR2) located within the detection range of the DOCK site. The most striking feature of these distributions of detections was again the shift in number of fish present at low tides compared to high tides – 3 fish were present for 24% of low tides and 26% of mid tides, whereas only 0-1 fish were present for 55% of high tides. A dissimilarity with the previous year's data was that there were occasions (8-30%) in 2002 at all tides when tagged individuals were entirely absent from the DOCK vicinity. Never were all seven fish entirely present together at this site. Kolmogorov-Smirnov pairwise comparisons of these distributions revealed that the high tide distribution was significantly narrower and shifted towards fewer fish present than in low and mid timesteps ($D_{MAX} = 0.347$, $p < 0.001$).

Most fish were located within the lower part of the study area (DOCK site) at all tides and fish were never detected within the upper part of the study area at low tide in 2001 (Fig. 14). However, tagged fish occupied the UPPER sites at other tide stages (84% of mid tides and 18% of high tides). This again, supports the notion that individuals dispersed away from the DOCK vicinity to move upriver with the flooding tide and returned on the ebb tide. The same broad-scale spatial differences in frequency distributions with respect to tidal stage were present in the 2002 detection data (Fig. 16), which showed only one fish rarely (<1% of low tides) present within the UPPER sites during low tide, 1-2 fish present on 13% of mid tides, and 42% of high tides. Results of Kolmogorov-Smirnov pairwise comparisons of these distributions revealed that the

frequency distributions of tagged fish located at the UPPER sites were significantly different from the DOCK sites during high ($D_{MAX} = 0.342$, $p < 0.001$), mid ($D_{MAX} = 0.797$, $p < 0.001$), and low ($D_{MAX} = 0.914$, $p < 0.001$) tides. These differences were seen where the distributions became narrower and shifted towards fewer numbers of fish present at the UPPER sites from high tide to low tide. The DOCK site distributions exhibited the opposite; became broader and shifted towards a greater numbers of fish present from high tide to low tide. The mid tide distributions for both sites reflect the transition between low and high tide distributions.

Dispersal of the aggregations in the vicinity of the DOCK site occurred during the flooding tide. During 2001, when only four receiver sites provided detections, details of the dispersal pattern could not be defined. However, with the repositioning of 10 receivers within the array in 2002, dispersal locations became evident for some cases by examining their “fish-tracker” plots (see appendices). Detections were frequent enough to define a tidal pattern was evident in 8 of 12 Upper Duplin fish during 2002. Typically one of the following dispersal patterns was evident on the flooding high tide; Upriver movement occurred in 4 of 10 fish which moved beyond site SUB3 during 45% of all possible tidecycles. Downriver or on-marsh movement into unmonitored locations occurred in 6 of the 10 fish on 21% of all possible tidecycles. Figure 17 shows these dispersal patterns for fish #21 (upriver dispersal), fish #28 (day-night alternating upriver dispersal), and fish #27 (downriver/on-marsh dispersal into unmonitored areas)

The timing of sunset with high tide was an apparent factor in determining whether a fish ventured upriver on the flooding tide. When high tide occurred during daylight, the fish moved upriver, however when high tide occurred after sunset, the fish remained in

the vicinity of the DOCK site (Fig. 17b). This alternating pattern occurred for 47% of all upriver movements beyond site SUB3 during 2002. Furthermore, as the timing of high tide crossed over from a daylight high tide to a nighttime high tide, the fish did not move for the next two consecutive tidecycles, as both flooding tides were initiated during the night. With the next daylight high tide, the fish resumed the pattern of moving on alternate flood tides.

Another underlying pattern within the fish exhibiting upriver movement was the “site-skipping” behavior observed for 4 of 12 fish, illustrated for fish #28 in Fig. 17b. Upriver movements for these fish did not follow a path directly up and down the main channel, instead they consistently bypassed sites DE2 and SUB3 en-route to upriver locations, and then again on the return ebb-tide trip. This “site-skipping” was likely the result of taking an alternative path through the flooded intertidal marsh, rather than following the broad bend in the main river channel at the DE2 and SUB3 sites. (Fig. 4).

Six of 12 fish did not move upriver on their flood-tide dispersals, and were suspected to have moved either downriver, into some adjacent intertidal creek system, or onto the flooded marsh surface. Figure 17c shows an example of this suspected dispersal pattern into unmonitored areas; the period during which the fish is not detected, overlaps closely with the period of a tidecycle.

Individual variation

There was substantial individual variation in fish movement and habitat use over the course of the study, but summaries of the occurrences for specific habitat use and movement patterns are given in Table 4 for Upper Duplin fish in 2002, the focal point for

this study. Habitat use and movement patterns included the following: 1) Low-tide aggregation at the DOCK site, 2) High tide upriver dispersal, 3) High tide dispersal to some unmonitored downriver or unknown site, 4) High tide dispersal mediated by an underlying diurnal pattern, and 5) “Site-skipping” during upriver dispersal. These patterns are depicted in Fig. 17. This individual variation is further documented in the attached appendices containing the detailed habitat use and movement information for all thirty-one individuals tagged during both years. I’ve highlighted some of these observations during the course of the study below.

Fish #'s 1, 2, and 3, which demonstrated strong low tide aggregations at the DOCK site and infrequent movements between sites within the Upper Duplin study area. Fish #'s 2 and 3 each exhibited a hiatus from the study area, 30 d and 10 d respectively, when the locations of these fish were unknown. Fish #4, was anomalous because it exhibited strong low tide use of site SUBX, and was not ever detected at the DOCK site. Fish #4 accounted for most (99%) of the total detections at this site SUBX during summer 2001. Fish #5 exhibited no emergent pattern of movement over a 26-d tracking period. Fish #'s 6, 8, 9, and 10 were at large in the study area for a considerable time (19 to 35 days), however their detection by any receiver in the array was a rare occurrence, each with fewer than 250 detections for the entire observation period (Appendix A, B).

During Autumn 2001, tagged fish were considered in two distinct sub-groups based on the area of their release: 1) Upper Duplin fish – six fish caught/released within the Upper Duplin study area, and 2) Stacey Creek fish – four fish caught within the Upper Duplin study area and released (transplanted) within the Stacey Creek study area (Table 3, Appendices C - F). Perhaps the most interesting finding of this phase of the

project was that three (#'s 11, 13, and 14) of the non-transplant, Upper Duplin fish were also detected within the Stacey Creek study area (Appendix F), a straight-line distance of ~2 km. The reverse was not observed; Stacey Creek fish were not detected within the Upper Duplin study area. Fish #12 (Upper Duplin release) exhibited strong preferences for the DOCK site during low tide. Fish #15 (Stacey Creek release) exhibited strong preferences for SC-MID during high tide. Fish #15 seemed to require additional time to acclimate to the new surroundings in Stacey Creek, taking ca. 10 d post-transplant before demonstrating a clear pattern of movement with tide stage (Appendix E).

Four fish from the Upper Duplin study area (#'s 11, 14, 17, and 18) had very short tracking periods (5 to 6 d). Fish #19, transplanted into Stacey Creek, also exhibited a short (< 6 d) tracking period. Why these fish were lost from the study areas in such a short time is unclear, but, given the extent of movement demonstrated by other individuals in this cohort, the fish simply may have emigrated from this portion of the Duplin River drainage, into an adjacent drainage (such as the Mud River, or New Teakettle Creek – see Fig. 1) and never returned to the study area. Fish # 20 was at large < 24 hours and presumably succumbed to post-surgical mortality (Appendix F).

Four fish (#'s 21, 23, 28, and 33) during 2002 exhibited frequent upriver dispersal on the flooding tide, followed by a return to their low tide “staging area” in the vicinity of the DOCK on the ebbing tide. These fish exhibited movements mediated by the time of sunset related to the time of high tide; where flood tides occurred close to sunset however, movement occurred only when the flood tide began prior to sunset. Rarely, was any between-site movement *initiated* after sunset. Fish #28 exhibited the strongest

upriver movement and diurnal patterns of these fish. Diurnal patterns were also observed for fish #'s 27 and 30, which dispersed to some unmonitored site(s) during high tide.

Fish #'s 21 and 33 exhibited similar overlapping habitat use and movement patterns (low tide DOCK aggregations, high tide upriver dispersal). These individuals also exhibited a “site skipping” behavior (Fig. 17c), where the fish frequently traveled from site SUB3 to site IMFR2 without passing by intermediate site DE2. This likely occurred when the fish made forays into unmonitored intertidal creeks or across the submerged densely-vegetated marsh surface. This “site-skipping” behavior, particularly in the vicinity of DE2, was observed for all four Group-III fish (#'s 21, 25, 28, and 33) in the Upper Duplin study area during 2002 (Appendix H). Since site DE2 is at a significant bend in the Duplin River (Fig. 4), it is likely that an alternative creek or marsh surface route provided a more direct path leading back to the low tide DOCK habitat, while at the same time reducing the fish's exposure to predation out in the open channel of the Duplin River. Individuals that exhibited strong habitual site fidelity, while undergoing tidal movements or in stationary positions, may have been predisposed to greater risk from angling mortality.

Mobile tracking data

During September through November 2002 several attempts were made to locate and track 8 tagged fish from the summer/autumn 2002 cohort (only 8 of the 12 tagged fish - #'s 21, 24, 25, 26, 27, 30, 31, and 33 were at-large during this period). A total of 16.5 hours were spent searching for these fish within, and adjacent to, the Upper Duplin study area at all timesteps. I successfully located and tracked each of the 8 at-large fish at

least once – mostly in the vicinity of the DOCK site during low tide. Attempts to follow an individual as it moved with the flooding tide were mostly unsuccessful. The 45 to 75 sec interval between “pings” emitted from the transmitter precluded active tracking while a fish was moving. Only on one occasion was an individual fish tracked for more than a few minutes. Fish # 31 was located and tracked for 45 min on 20 September 2002 as it moved on a flooding tide ca. 200 m upriver from an oyster reef near the DOCK site to an intertidal creek near the IMFR2 site, remaining close (< 5 m) to the Duplin River/marsh edge the entire time. The signal of this fish was lost once it entered the intertidal creek where it may have gained access to the now flooded vegetated marsh surface.

Angler re-captures

During 2002, three pingers (#24, #28, and one unknown #) were recovered from fish caught by anglers. An additional two tagged fishes were suspected to have been removed from the study area by recreational fishing activity within and adjacent to the 2002 Upper Duplin study area. There was not evidence for angler recoveries during 2001. All confirmed and suspected angler-caught fish were likely taken as legal-size fish at the time of re-capture. Fish #24 was caught on 2 Nov 2002 in Dobby Sound, adjacent to a subtidal creek (Oakdale Creek) near the confluence of the Duplin River at the south end of Sapelo Island, a location approximately 8.5 km straight-line distance from its last known location within the Upper Duplin study area. This fish’s last detection was recorded on 5 Oct 2002 at the DER1 site (most downstream site in the study area). Details of this individual’s movements during the ~28 d that elapsed between the time it left the study area and was ultimately captured are unknown but, the behavior certainly

demonstrates the potential for subadult red drum to move substantial distances after exhibiting a considerably degree of site fidelity (see Appendices G and H).

Fish #28 was caught during a mid-ebb tide on 21 Nov 2002 at the Hunt Camp Dock (Fig. 4). This fish's last detection was recorded at 11:31 EST on 21 Nov 2002, which closely approximates the time of capture as confirmed by the angler. Prior to its capture, this individual was the last remaining tagged fish of the 2002 group. Its removal from the study area consequently marked the end of monitoring for the 2002 field season within the Upper Duplin study area. An additional fish from the 2002 tagged cohort was also a confirmed angler capture, but the I.D.#, location caught, etc. was unavailable because the tag was discarded by the angler prior to reporting the capture.

Strong circumstantial evidence implicated angling mortality in the loss of two other tagged fish (#s 21 and 33) in 2002. Both Group-II fish, which had earlier made extensive tidal forays between the DOCK site and other upriver locations, were last detected in the vicinity of the Hunt Camp Dock (SUBR1 and IMFR2, respectively) within ~20 min of each other (14:01 and 14:20 EST, 23 Sep 2002). The next recorded detections for these fish were at site DER1 (~75 m down-river of the Hunt Camp Dock) at 16:36 EST and 16:04 EST, respectively. Subsequent detections of these tags indicated their continuous residence at DER1, with no movement detected for the next 74 d after which the study was terminated (6 Dec 2002). A sample of the detection records for these tags from 20 to 26 Sep 2002 (Fig. 17) demonstrate the proposed scenario that both fish were caught by a recreational angler at or around the Hunt Camp Dock at approximately the same time. These fish were likely within the legal slot-limit size (#33 was legal size at tagging, and #21 would have been expected to reach legal size prior to 23 Sep), so were

killed, cleaned on-site, and the entrails (with pingers) discarded into the Duplin River near the point of capture.

Nekton prey abundance

Table 5 lists all nektonic organisms collected with a combination of hook and line, cast net, and minnow traps within the Upper Duplin study area during 2002. White shrimp *Litopenaeus setiferus*, daggerblade grass shrimp *Palaemonetes pugio*, and white mullet *Mugil curema* were the most abundant species collected and represented approximately 32%, 27%, and 12% of total catch, respectively. Overall, the abundance of crustaceans (2811) was greater than that of fishes (1077) within the Upper Duplin study area.

Tables 6 and 7 list the mean abundance (\pm S.D.) for fishes and crustaceans, respectively. Note that many of the sampling efforts resulted in zero catch, especially during high tides. Few statistically significant differences were detected in the mean ranked abundance of prey fishes and crustaceans among groups defined by either tide stage (Fig. 19) or site/habitat type (Fig. 20). Mean ranked prey abundance was significantly higher at low tide than at either mid or high tides (KW-ANOVA, $H = 29.681$, $p < 0.001$), but there were no detectable differences in potential prey abundance among habitat types.

There were few obvious or notable temporal or spatial trends in values of the environmental variables associated with the prey sample collections with the exception of a slight increase in temperature during July and a sharp drop in salinity on 23 Jun 2002 following a brief period of heavy rainfall (Fig. 21). As a rule, neither mean salinity nor

mean dissolve oxygen levels varied significantly with tide stage in the shallow habitats sampled here, but water temperature was significantly greater at low tide than at other times (Fig. 22). However, the greatest difference was barely greater than one degree C (mean \pm SE water temperature in $^{\circ}$ C at low tide was 29.5 ± 0.3 compared to 28.3 ± 0.3 and 28.6 ± 0.3 at high and mid tides, respectively).

DISCUSSION

The principal rationale for this study focused on the potential role of sub-adult red drum as transient predators within the context of a trophic relay model (*sensu* Kneib 2000) to explain the movement of intertidal marsh production to the open estuary *via* a series of predator-prey interactions across the estuarine marsh landscape. However, the findings of this study do not support the functional role of red drum in the trophic relay as hypothesized by Kneib (1997, 2000) for large transient predators. The presumed on-marsh feeding by a portion (59%) of the tagged fish in this study suggests an alternative, more direct link between the vegetated marsh and subtidal portions of the estuary. In this alternative trophic-relay scenario, red drum do not utilize subtidal channels as principal foraging areas to access prey organisms moving off of the marsh during the ebbing tide, but rather they move onto the marsh surface directly during the flood tide where they likely feed on fiddler crabs and other marsh prey resources, then return to their subtidal aggregation areas. Although stomach contents for these individuals was not available as direct evidence of relative biomass accumulation within various subtidal and intertidal habitats, these subadult fish do exhibit high growth rates of 32 mm mo^{-1} (Wenner 1992) while undergoing the observed movement patterns. Although there is empirical evidence for red drum feeding on marsh resident species (Wenner 1992), additional data are needed to support this alternative trophic relay scenario.

Previous studies using ultrasonic telemetry on red drum have been limited to developing a transmitter attachment technique (Carr & Chaney 1976), movement of adults (Woodward & Nicholson 1997), identifying spawning locations of adults

(Nicholson & Jordan 1994, Nicholson et al. 1996), and the assessment of stock enhancement programs (Parkyn et al. 2001, Sherwood et al. 2001, Neidig et al. 2002). The present study is the first to apply ultrasonic telemetry to track subadult red drum within Georgia's tidal marsh creeks. The continuous tracking of individual red drum within the study areas provided new insights into the habits and habitat use of subadult fish in the Duplin River estuarine system. I have included the complete records of "scatter plot" and "fish-tracker" time series plots in the appendices (A – H) of this volume with the hope that answers to new questions can be gleaned from the data in the future.

Subadult red drum exhibited strong site fidelity within estuarine tidal creeks and have an affinity for structure. Fishes often use structure, particularly overhead structure, to conceal their presence from both potential predators and prey (Helfman 1981). The low-tide shoaling aggregations of red drum in the vicinity of the Hunt Camp Dock in this study could be related to the visual advantage gained by those fishes using this habitat resource. A portion of the tagged population did leave the dock area for some length of time, suggesting that this area may not always be ideal or suitable habitat, or that the subadult population comprises individuals with differing levels of site fidelity or homing.

Most individuals exhibited some type of a tidal pattern in their movements within the study areas. Perhaps the observed flood-tide dispersal forays (upriver or some unmonitored site) allow the fish to take advantage of some resource (food or habitat) that may not be accessible at low tide, i.e., intertidal creek channels or rivulets (Rozas et al. 1988) and perhaps the vegetated marsh surface itself (Wenner 1992, Collins et al. 2002). Many species of resident and transient estuarine nekton, including red drum, are known

to leave the subtidal estuary to use resources available to them on the vegetated marsh plain only on flood tides (Kneib 1997, Montague & Weigert 1990).

Collectively, the figures in Appendices A-H show a tidal pattern of individual movements within the Upper Duplin study area, particularly during summer-autumn 2002, when the stationary hydrophone receiver array was fine-tuned to detect movements of tagged fish that ‘homed’ to the area around the Hunt Camp Dock. For those individuals that frequently moved away from the dock area, the timing of their movements closely followed the flooding tide. Although the fish had access to intertidal creeks and marsh surface habitats, they often remained in the main channel of the Duplin River. As water levels receded with the ebbing tide, the fish generally returned to the same low tide habitat where they were initially captured and tagged – most often the DOCK site. When fish moved into intertidal creeks or across the marsh surface, they were outside the detection range of the stationary receiver array, leaving discontinuities in their detection records.

Movements were observed in response to tide stage, but some fish also showed a strong diel movement pattern superimposed on the response to tides. The effect of the day/night cycle was usually reflected in a fish’s decision to move or remain on station during periods of strong tidal current. In the usual case, if a flooding tide occurred prior to sunset, a fish would proceed with its usual up-river movement pattern. However, if the flood tide began *after* sunset, movement would not ensue and the fish remained at the location it held at sunset for the remainder of the night and through the next pre-dawn tidecycle. Tidal movements would then commence on the next flood tide (now daylight, during summer months) the following morning.

The twilight period prior to sunrise and following sunset, has important significance in the life histories and behavior of aquatic organisms, especially fishes (Hobson 1972, Helfman 1993). During this period the intensity of background light changes rapidly and may reduce the effectiveness of the camouflage properties of a counter shaded fish; what was once a protective disguise (dark object against a dark background, or light object against a light background) from predators during daylight, now becomes a dark object against a light background or vice versa, consequently increasing the organism's risk of being preyed on. This may explain why red drum did not typically initiate dispersal away from their sheltered dock habitat beyond sunset. In this scenario, both tidal and diel cycles are functioning as dual-zeitgebers, or environmental internal clock-setting mechanisms (e.g., Saunders et al. 1989, Duston & Saunders 1990, Leiner et al. 2000).

There was substantial individual variation in the duration of tracking period and pattern of movements among subadult red drum. The tracking history of individual red drum tagged in this study varied substantially in length from < 24 h to 101 d. A number of factors could account for the termination of a tracking period for an individual fish beyond the initial ~24 h recovery period, including morbidity or mortality related to surgical trauma, battery/transmitter failure, natural mortality, emigration, and angler removal.

Battery/transmitter failure could account for a short tracking duration. According to the manufacturer, the transmitters have enough battery life to last up to 120 d from the time of activation. All transmitters were activated within 48 h prior to surgical implantation and were tested to ensure that signal transmission and detection were fully

operational in each transmitter. Three of the 35 transmitters (#'s 32, 34, and 35) purchased for this study failed to transmit a signal upon activation and were not used. These failures were caused by either a faulty connection upon activation or a manufacturing defect. Emigration out of the study area is a more likely explanation to account for the sudden disappearance, or loss of a tagged fish, especially given the evidence in Appendix-E of 3 individuals released in the Upper Duplin study area moving into the Stacey Creek study area. Habitats in adjacent systems such as New Teakettle Creek, or the Mud River (Fig. 4) may have become accessible during high spring tides.

Beyond the initial 24-h post-surgical period, the most obvious, explanation for sudden and permanent signal loss from the study area was predation mortality, including bottlenose dolphin predation and angler removal. Throughout their range, bottlenose dolphins are known predators of sciaenid fishes, including red drum (Barros & Wells 1998, Young & Phillips 2002), and are often observed feeding within all portions of the Duplin River. There is also some evidence to suggest that dolphins may have been able to detect the ultrasonic “pings” associated with signal propagation from the transmitters within the tagged fish (Au et al. 2002). While the 69 kHz ultrasonic signal is within range of a dolphin’s hearing, determining whether the dolphins would have been able to effectively focus in on the signal and track the fish down is difficult to say. Whether the timeframe of the study was sufficient for dolphins to learn the association of the ultrasonic pings with potential sciaenid prey is also unclear. In any case, a tagged fish was considered dead when prolonged, continuous detections were recorded at a single site, as in the case for fish #'s 21 and 33 (see Appendix-H)

For tagged fish that did not survive the initial 24 h post-release, is post-surgical and/or hooking mortality (Jordan & Woodward 1992, Murphy et al. 1995). The high post-surgical survival of tagged fish in this study indicates that closure of small incisions with sutures, staples, and adhesives, as is commonly practiced (see Summerfelt & Smith 1990, Winter 1996), may be unnecessary and even undesirable. To my knowledge, this is the first field study to release red drum with unclosed incisions back into the environment. Not closing the incision likely reduced the overall stress on the fish because it shortened the procedure time considerably. By eliminating the need for suturing, handling time during the tagging procedure was reduced. After the initial 24 h, based on the laboratory trials, I assumed the incisions had begun to heal without complications. Survival rate through surgery to time of release (~10 min. post-recovery) into the environment was 100%. The estimated 8% mortality within the first 24-h conforms to expected post-hooking mortality for this species (Jordan & Woodward 1992, Murphy et al. 1995) and so additional mortality could not be attributed to the surgical procedure.

Association of red drum towards the floating dock structure superceded any orientation or association with particular habitat types within the estuarine system, and habitat use and movements do not seem to be associated with the abundance of potential nektonic prey. Distributions of fishes and other nekton often are associated with certain benthic habitat types and a variety of these are available to red drum and other nekton within the salt marsh-estuarine ecosystem of the southeastern U.S. Atlantic coast. Much research has focused on the relative habitat value for fishes, and red drum in particular, for vegetated (seagrass) vs. non-vegetated (mud) bottoms (Llanso et al. 1998, Rozas & Minello 1998, Stunz et al. 2002a, b), oyster reefs (Zimmerman et al. 1989, Coen et al.

1999), tributary creeks (Shenker & Dean 1979, Bozeman & Dean 1980), and marsh-edge interfaces (Baltz et al. 1993, Minello et al. 1994, Peterson & Turner 1994). Collectively, these habitat types make up the known feeding and refuge habitat for red drum in the southeastern United States Atlantic and Gulf coasts.

In this study, receivers were positioned near several distinct habitat types including mouths of subtidal and intertidal creek channels with and without associated oyster reefs to determine if these features in the landscape provided focal points for activity of subadult red drum at one or more tidal stage. Despite this effort, there was little evidence in this study of strong habitat associations of subadult red drum with any of the monitored habitat types, besides the DOCK site. The vicinity of the DOCK site dominated all other habitat sites in terms of total use by all monitored fish in the Upper Duplin study area, particularly during 2002. For the most part, use of other monitored habitats outside of the DOCK vicinity was limited to transient movements between the DOCK site and the upper reaches of the Duplin River and/or the unmonitored intertidal vegetated marsh surface, as evidenced by the time series plots of individual fish-tracks presented in Appendices B, D, F, and H. The exception to this was the SUBX site during summer 2001. Ninety-nine percent of all (over 10,000) detections at the SUBX site were attributed to a single fish (#4) (Fig. 11). This fish exhibited extremely high site fidelity and one of the most pronounced tidal relationships (Appendix-A). What characteristics of this reef-free subtidal creek mouth (SUBX) resulted in such strong associations with this particular site and/or habitat type are not clear. The IMF1 site during autumn also exhibited a disproportionate number of detections from a single fish (#13) (Fig. 11). In this case, however, the site fidelity and tidal relationships were not as pronounced as that

of fish #4, as shown in Appendix-D. Clearly, there are individual behaviors and environmental cues that determine the habits and habitat use by red drum in the Upper Duplin River system.

Red drum are known to use the vegetated marsh surface at high tide, yet there has been little empirical evidence to suggest that they feed within this habitat. Collins et al. (2002) noted that anglers often pursue subadult red drum in these shallow water “flats” during high tide. Presumably, if some fish are actively taking a hook in these flats, others must also be feeding independently in these same areas. Fiddler crabs *Uca sp.* comprise a large component (16% to 53% by numbers) of the diet for 18-53 cm subadult red drum (Music et al. 1984, Wenner 1992). The primary habitat of these crabs is the vegetated intertidal marsh surface and mud-flat areas, accessible to red drum only during high tide. In this study, 13 of the 22 fish (59%) with > 10 d at large, exhibited strong tidal patterns (located within subtidal areas during low tide, not detected during high tide) (Table 3, Appendices A, C, E, G). These fish probably moved away from their subtidal low-tide staging areas onto the marsh surface during the flooding tide to feed primarily on fiddler crabs – an important food resource with limited accessibility. The potential food resources sampled in this study were not collected from any intertidal vegetated marsh surface sites, only intertidal/subtidal creek and edge sites, so consequently fiddler crabs were not present in any of the catch (Table 5). Some portion, in this case up to 59%, of the subadult red drum population may actively pursue fiddler crabs and other available food resources, undetected within the intertidal vegetated marsh surface during high tide. Indirect evidence of this habitat use exists in the form of “site-skipping” described earlier, where a fish bypassed a monitored site by utilizing an alternative creek or marsh surface

route. However, the relationship between the remaining 41% of red drum that apparently did not frequent the marsh surface to feed is unclear. Presumably, these individuals rely more on the available prey items within the subtidal/intertidal creek habitats, shown in Fig. 18.

During the period of September to November, 3 of 22 (14%) of the > 10 d at large tagged subadult red drum dispersed into other habitats 2 – 8 km downriver in the Duplin River/Doboy Sound estuarine system. This larger-scale dispersal consequently carried out another phase of the trophic-relay production transfer. Such movements, closer to the open ocean and its complex of predators, have important implications to the trophic support of larger offshore ecosystems (Deegan 1993). Dispersal away from the areas surrounding their natal habitat and into different areas of the estuary is common for age 12-14 mo subadults (Wenner 1992).

Summary of Findings

The findings in this study support the following: (1) The subadult population of red drum in the Upper Duplin River exhibited a high degree of individual variation in habitat use and movement patterns, as measured by ultrasonic telemetry; (2) Red drum exhibit strong site fidelity within the study area; (3) Subadult red drum aggregated in the vicinity of the DOCK site during low-tide, then dispersed at high-tide to known (upriver) and unknown (downriver, on-marsh) sites; (4) high-tide dispersal was often inhibited by the onset of twilight; (5) During high tide, some red drum are swimming onto or across the marsh surface, either to forage or in route to other channel habitats.

Management Implications and comments

The pre-reproductive subadult class of red drum investigated here falls within the 14 – 27 inch (36 – 69 cm) slot limit for the coastal waters of Georgia and is subject to significant pressure from recreational anglers (Pafford & Nicholson 1989, Vaughan 1996, <http://www.state.ga.us/dnr/coastal/2000data.html>). The impact of recreational anglers on fisheries research within the SINERR is currently unmonitored, yet potential impacts were demonstrated by the permanent removal of up to 42% of tagged fish from this study. During 2002, three transmitters (#24, #28, and one unknown) were recovered from angler-caught tagged fishes. Two more tagged fish (#'s 21 and 33) were suspected to have been removed from the study area by recreational fishing activity within and adjacent to the 2002 Upper Duplin study area. Evidence for angler recoveries during 2001 is lacking, but recreational anglers were unaware of the study. If we can assume that losses due to angling were similar in both years, at least 15 transmitters may have been lost to this source of mortality. The monetary cost in equipment alone would have been \$4500, making the live weight value of the lost fish about \$1.67 g-1 (\$759 lb-1). However, the real cost was in the loss of scientific information that would have contributed to understanding the role of this species in the estuarine ecosystem and the sustainable management of the resource.

The SINERR, as currently managed by the Georgia Department of Natural Resources (GA-DNR), is not closed to recreational fishing and is therefore subject to fishing pressure comparable to or greater than adjacent estuarine locations in coastal Georgia. Fishing pressure within the boundaries of the SINERR, where the study areas are located, may be more intense than in adjacent estuarine habitats within the Doboy

Sound system as a result of promotion designed to increase public use and access to Sapelo Island (Kneib, Hurley – personal communication.). Given the apparent fishing pressure within the boundaries of the SINERR and the potential impacts future research projects, it may be timely to consider an adjustment in management plans. Removal of large predatory species as a result of overexploitation of resources by human populations has been linked to a variety of disruptions in the functioning of estuarine ecosystems (e.g., Jackson et al. 2001).

Future studies of this nature would benefit from one or more of the following measures to protect the investment in telemetered fish: 1) restrict access to recreational fishing within the study area for the duration of the project. 2) Incorporate an external tag, such as T-bar, anchor, or similar, combined with a reward-for-information-only incentive, on tagged fish so that anglers will be more likely to release the fish. 3) Invest more time in informing and educating the fishing community about the project, its goals, and how anglers can help the research effort.

To date, none of the 26 National Estuarine Research Reserves restrict recreational fishing. Indeed, there are no fully protected “no-take” marine reserves dedicated to conducting research in the absence of direct human uses of resources in any estuary along the U.S. east coast (Palumbi 2002). Collins et al. (2002) suggested that a network of small ($< 6 \text{ km}^2$) no-take reserves may be sufficient to minimize the impacts of recreational anglers on recruitment of red drum into the spawning stock biomass. The scale at which such a reserve network would be effective however, remains unclear. Alternatively a single large reserve, such as the $\sim 40 \text{ km}^2$ portion of the Merritt Island National Wildlife Refuge adjacent to the Kennedy Space Center in Florida has been

effective in producing more recreationally important species including red drum than nearby non-protected waters (Johnson et al. 1999). Whether no-take marine reserves are “single large” or “several small”, they probably would help to enhance populations of red drum and other organisms that use salt marsh or estuarine habitats, both within and adjacent to such reserves.

This study had several limitations that rendered the extent to which subadult red drum used different habitat types difficult to fully characterize and quantify. First, only 10 stationary receivers were available to track tagged fish. This limited the number of replicates of each habitat type that could be monitored simultaneously. Second, the use of free-ranging fish in an open estuarine environment meant that the selection of a site to monitor added a certain haphazard element to the sampling program because there was no certainty that one or more of the tagged fish would spend any time within the detection range of any given receiver (200 – 400 m). There was partial compensation by ‘fine-tuning’ the placement of receivers in the array based on incoming telemetry data. The effect was evident in the increased number of detections recorded in 2002 compared to 2001. Third, the strong tendency for fish to move only during a portion of the tidal cycle limited their exposure to different habitat types outside the area around the DOCK site, which was the low-tide staging area for most of the tagged fish in this study. With this new knowledge of subadult red drum movement and behavior, perhaps further characterization of their high-tide dispersals and movement between sites would be possible by incorporating a greater number of tracking stations outside the “zone of influence” of this dock, particularly downriver from the dock. Given the very strong site fidelity demonstrated in the study, it seems imperative that we identify other sites and

habitats within the estuarine landscape that function as low tide staging areas for subadult red drum. From a management perspective, it should be clear that characterizing, monitoring and protecting such sites is crucial for maintaining a viable fishery for red drum in estuaries of the southeastern U.S.

TABLE 1: Published stomach contents (percent occurrence) for red drum from the southeastern U.S. Atlantic and Gulf Coasts. GRSH (grass shrimp); PESH (Penaeid shrimp); UNID. SHRIMP (unidentified shrimp-like organism); BLCR (blue crab); FISH (fishes); MOLL (mollusk); POLY (polychaete); BRYZ (bryozoan); SQUI (squid); AMPH (amphipod); ECHI (echinoderm).

CITATION	SIZE (cm)	GRSH	PESH	SHMP	BLCR	CRAB	FISH	MOLL	POLY	BRYZ	SQUI	AMPH	ECHI
Wenner 1992	18 - 53	19.0	0.0	0.0	7.0	63.0	7.0	0.0	0.0	0.0	0.0	0.0	0.0
Overstreet 1978	19 - 35	18.6	44.2	0.0	48.8	37.2	30.2	0.0	18.6	3.3	2.3	7.0	0.0
Music et al. 1984	20 - 40	4.1	20.3	0.0	2.7	16.2	15.2	0.0	0.0	0.0	0.7	0.0	0.0
Boothby et al. 1971	25 - 93	10.0	0.0	0.0	41.9	21.5	74.1	0.0	0.0	0.0	1.8	2.1	0.0
Scharf et al. 2000	29 - 76	1.8	24.4	39.3	29.8	7.8	41.7	0.0	0.0	0.0	0.0	0.0	0.0
Overstreet 1978	43 - 102	0.0	0.0	0.0	43.8	37.6	62.9	6.3	0.0	0.0	0.0	0.0	56.3

TABLE 2: Summary of surgical procedures for fish implanted and released with ultrasonic transmitters during 2001 and 2002.

VARIABLE	RECOMMENDED	MEAN	MIN	MAX	STDEV
LENGTH (cm)	< 35.6 ¹	30.8	24.0	38.5	4.336
WEIGHT (g)	> 120.7 ²	330.2	145.0	615.0	135.814
TAG % BODY WEIGHT	< 2.90% ²	1.26%	0.57%	2.41%	0.530
INDUCTION TIME (min.)	< 10 ²	3.2	2.0	5.0	0.920
SURGERY TIME (min.)	-- --	4.1	2.0	8.0	1.340
RECOVERY TIME (min.)	< 5	1.6	1.0	4.0	0.709
TOTAL EXPOSURE TIME (min.)	3x induction time ³	9.4	6.0	15.0	1.992
DAYS AT LARGE	-- --	43.2	5.0	101.0	33.719

¹ Minimum legal size in Georgia is 35.6 cm.

² Winter 1996, % of weight in water

³ Manufacturer recommendation

TABLE 3: Summary of 31 subadult red drum (24.0 – 38.5 cm TL, 145 – 615 g.) tagged and released with ultrasonic transmitters within the Upper Duplin (UD) and Stacey Creek (SC) study areas during 2001 and 2002

ID	L	W	DATE TAGGED	RELEASE SITE	DAYS AT LARGE	TIDE CYCLE REPLICATES	SUSPECTED LOSS
1	26.3	219	26-Jun-01	UD	26	46	--
2	24.0	145	24-Jun-01	UD	66	121	BATT/EMIGRATION
3	25.5	201	27-Jun-01	UD	32	61	EMIGRATION
4	26.9	221	03-Jul-01	UD	25	45	--
5	29.0	280	03-Jul-01	UD	26	47	--
6	26.0	165	04-Jul-01	UD	35	61	EMIGRATION
8	25.5	180	10-Jul-01	UD	22	35	EMIGRATION
9	26.0	185	10-Jul-01	UD	29	49	EMIGRATION
10	27.5	295	10-Jul-01	UD	19	17	--
11	31.3	345	01-Sep-01	UD ^{SC}	27	43	EMIGRATION
12	30.6	310	01-Sep-01	UD	101	111	BATT/EMIGRATION
13	30.8	350	01-Sep-01	UD ^{SC}	59	110	BATT/EMIGRATION
14	32.1	365	01-Sep-01	UD ^{SC}	24	42	EMIGRATION
15	35.7	490	23-Sep-01	SC	99	72	BATT/EMIGRATION
16	35.2	485	23-Sep-01	SC	5	6	--
17	35.1	490	23-Sep-01	UD	5	6	--
18	37.5	545	23-Sep-01	UD	6	6	--
19	36.2	520	23-Sep-01	SC	6	7	--
20	33.9	430	28-Sep-01	SC	< 1	0	POST-SURG. MORT.
21	27.1	210	29-Jun-02	UD	86	164	ANGLER
22	29.4	230	30-Jun-02	UD	< 1	0	POST-SURG. MORT.
23	26.8	180	30-Jun-02	UD	6	9	--
24	27.4	185	30-Jun-02	UD	97	185	¹ ANGLER/EMIGRATION
25	26.1	180	30-Jun-02	UD	97	185	BATT
26	31.4	315	14-Aug-02	UD	54	101	EMIGRATION
27	34.2	380	14-Aug-02	UD	65	119	BATT
28	34.4	410	14-Aug-02	UD	99	119	² ANGLER
29	35.1	410	15-Aug-02	UD	< 1	0	POST-SURG. MORT.
30	33.2	355	15-Aug-02	UD	64	118	BATT
31	38.5	615	14-Sep-02	UD	21	38	--
33	37.5	545	14-Sep-02	UD	9	15	ANGLER

^{SC}Fish released in Upper Duplin, detected in Stacey Creek

¹confirmed angler recovery in Doboy Sound, 02 NOV 02

²confirmed angler recovery in Upper Duplin study area, 21 NOV 02

Table 4: Occurrence of common habitat use and movement patterns observed for the Upper Duplin study area, 2002. Percent occurrences below were calculated based on the number of tide-cycle replicates observed for each pattern behavior patterns for tagged fish within the Upper Duplin study area. Fish #'s 22 and 29 did not survive beyond the initial 24-h post-tagging period.

FISH I.D.	TIDE REPS.	LOW-TIDE DOCK AGGREGATION	HIGH-TIDE DISPERSAL UPRIVER	LOW-TIDE DISPERSAL DOWNRIVER OR UNKNOWN	DIURNAL PATTERN	SITE SKIPPING
21	164	✓	✓		✓	✓
22	0	--	--	--	--	--
23	9	✓	✓			✓
24	185	✓		✓	✓	
25	185	✓		✓		
26	101	✓		✓		
27	119	✓		✓	✓	
28	119	✓	✓		✓	✓
29	0	--	--	--	--	--
30	118	✓		✓	✓	
31	38	✓		✓	✓	
33	15	✓	✓			✓
N=12	1053	100%	29.2%	70.8%	70.6%	29.2%

NOTE: Percent occurrences are scaled to the number of tide replicates represented for each pattern

Table 5: Total nekton catch from the Upper Duplin study area, sampling with cast net, minnow trap, and hook-line methods during the May - July 2002 sampling period. Length measurements are in cm.

SPECIES/TAXA	COMMON NAME	CODE	TOTAL CATCH	% TOTAL CATCH		¹ MEAN LENGTH ± S.D.	
<i>Litopenaeus setiferus</i>	white shrimp	WESH	1413	32.11%	5.2	3.90	
<i>Palaemonetes pugio</i>	daggerblade grass shrimp	PAPU	1192	27.08%	2.0	0.40	
<i>Mugil curema</i>	white mullet	WHMU	518	11.77%	9.4	1.58	
<i>Brevoortia tyrannus</i>	Atlantic menhaden	ATME	425	9.66%	14.7	2.00	
<i>Mugil cephalus</i>	striped mullet	STMU	209	4.75%	19.9	2.63	
<i>Palaemonetes vulgaris</i>	marsh grass shrimp	PAVU	187	4.25%	1.3	0.28	
<i>Bairdiella chrysoura</i>	silver perch	SIPE	90	2.04%	8.3	1.71	
<i>Leiostomus xanthurus</i>	spot	SPOT	90	2.04%	7.2	1.27	
<i>Anchoa mitchilli</i>	bay anchovy	BAAN	62	1.41%	3.5	0.40	
<i>Rhizoprionodon terraenovae</i>	Atlantic Sharpnose Shark	ATSH	62	1.41%	39.3	6.40	
<i>Fundulus heteroclitus</i>	mummichog	MUMM	45	1.02%	6.7	2.02	
<i>Callinectes sapidus</i>	blue crab	BLCR	18	0.41%	5.6	3.40	
<i>Lolliguncula brevis</i>	Atlantic brief squid	SQUI	15	0.34%	3.5	0.64	
<i>Dasyatis sabina</i>	Atlantic stingray	STIN	14	0.32%	--	--	
<i>Dasyatis americana</i>	Southern stingray	SOST	7	0.16%	--	--	
<i>Eucinostomus argenteus</i>	spotfin mojarra	SPMO	7	0.16%	6.0	0.63	
<i>Chilomycterus schoepfi</i>	striped burrfish	STBU	6	0.14%	2.5	0.63	
<i>Pomatomus saltatrix</i>	bluefish	BLUE	6	0.14%	20.2	2.00	
<i>Syngnathus sp.</i>	pipefish	PIPE	5	0.11%	11.8	3.98	
<i>Gobiosoma bosci</i>	naked goby	NAGO	4	0.09%	3.4	0.22	
<i>Paralichthys lethostigma</i>	Southern flounder	SOFL	4	0.09%	23.1	18.31	
<i>Cynoscion nebulosus</i>	spotted seatrout	SPSE	3	0.07%	26.9	18.67	
<i>Etropus crossotus</i>	fringed flounder	FRFL	3	0.07%	6.2	1.48	
<i>Orthopristis chrysoptera</i>	pigfish	PIGF	3	0.07%	13.8	10.82	
<i>Menticirrhus americanus</i>	Southern kingfish	SOKI	2	0.05%	30.2	0.42	
<i>Archosargus probatocephalus</i>	sheepshead	SHEE	1	0.02%	37.2	--	
<i>Caranx sp.</i>	jack	JACK	1	0.02%	5.1	--	
<i>Elops saurus</i>	ladyfish	LADY	1	0.02%	25.4	--	
<i>Etropus microstomus</i>	smallmouth flounder	SMFL	1	0.02%	4.1	--	
<i>Lagodon rhomboides</i>	pinfish	PINF	1	0.02%	29.6	--	
<i>Lobotes surinamensis</i>	triple tail	TRIP	1	0.02%	3.8	--	
<i>Micropogon undulatus</i>	Atlantic croaker	ATCR	1	0.02%	15.9	--	
<i>Oligoplites saurus</i>	leatherjacket	LEJA	1	0.02%	7.2	--	
<i>Opsanus tau</i>	oyster toadfish	OYTO	1	0.02%	11.1	--	
<i>Sphoeroides maculatus</i>	northern puffer	NOPU	1	0.02%	10.1	--	
<i>Squilla empusa</i>	mantis shrimp	MASH	1	0.02%	--	--	

¹All length measurements are total length (TL), except for blue crab where length = carapace width.

Table 6: Fish abundance data (mean \pm S.D.) from nekton sampling. ATME = Atlantic menhaden *Brevoortia tyrannus*; MUMM = mummichog *Fundulus heteroclitus*; SPOT = spot *Leiostomus xanthurus*; WHMU = white mullet *Mugil curema*. Below the abundance data are the summary results of a 2-way Kruskal-Wallis ANOVA using the Scheirer-Ray-Hare extension, testing for effects of site type and tidestage on ranked abundance data. H substitutes for the F-ratio ($F = SS_{\text{factor}}/MS_{\text{total}}$) of the standard 2-way ANOVA and is distributed as a chi-square variable.

SITE	TIDE	ATME	MUMM	SPOT	WHMU
DER1	LOW	0	0	0.5 \pm 0.84	2.8 \pm 6.46
	MID	0	0	0	0
	HIGH	0	0	0	0
SUBR1	LOW	0	0	0	0.5 \pm 1.23
	MID	8.5 \pm 20.82	0	0	6.2 \pm 11.64
	HIGH	0	0	0	0
IMFR2	LOW	0	0	1.0 \pm 2.00	16.7 \pm 33.93
	MID	0	0	2.0 \pm 4.90	2.3 \pm 5.72
	HIGH	0	0	0	2.0 \pm 4.90
DE2	LOW	0	0	0	6.0 \pm 12.78
	MID	0	0	0	0
	HIGH	0	0	0	0
SUB3	LOW	0	0	0	9.0 \pm 21.56
	MID	0	0.2 \pm 0.41	0	0
	HIGH	0	0	0	0
SUB2	LOW	2.8 \pm 6.94	0	0.7 \pm 1.63	8.8 \pm 9.35
	MID	15.5 \pm 37.97	0	0	10.7 \pm 26.13
	HIGH	8.8 \pm 21.64	0	0	0
SUB1	LOW	0	0	0.3 \pm 0.82	0.5 \pm 0.84
	MID	13.2 \pm 32.25	0	0	0.5 \pm 1.23
	HIGH	0	0	0	0
DE1	LOW	20.5 \pm 50.22	0.7 \pm 0.82	0.7 \pm 1.21	9.7 \pm 16.31
	MID	0	0	0.7 \pm 1.21	0
	HIGH	0	0	0	0
IMFR1	LOW	1.5 \pm 3.67	0.7 \pm 13.91	4.0 \pm 9.32	4.7 \pm 11.43
	MID	0	0	0.3 \pm 0.52	2.8 \pm 6.94
	HIGH	0	0	0	0
IMF1	LOW	0	0	4.5 \pm 7.06	3.2 \pm 5.53
	MID	0	0	0	0
	HIGH	0	0	0	0

FISHES	d.f.	M.S.	H (F-ratio)	p-value	
<i>TIDE</i> .	2	284175.000	29.681	< 0.001	*
<i>SITE</i>	9	17749.641	1.854	0.056	n/s
<i>TIDE</i> \times <i>SITE</i>	18	13556.404	1.416	0.117	n/s

Table 7: Crustacean abundance data (mean ± S.D.) from nekton sampling. BLCR = blue crab *Callinectes sapidus*; PAPU = daggerblade grass shrimp *Palaemonetes pugio*; PAVU = spot *Palaemonetes vulgaris*; WSHH = white shrimp *Litopenaeus setiferus*. Below the abundance data are the summary results of a 2-way Kruskal-Wallis ANOVA using the Scheirer-Ray-Hare extension, testing for effects of site type and tidestage on ranked abundance data.

SITE	TIDE	BLCR	PAPU	PAVU	WSHH
DER1	LOW	0	3.3 ± 5.20	18.5 ± 44.83	7.2 ± 8.89
	MID	0	0	0	0
	HIGH	0	0.3 ± 0.82	0	0.2 ± 0.41
SUBR1	LOW	0.8 ± 1.33	11.5 ± 22.52	0	38.7 ± 44.36
	MID	0	0	0	1.3 ± 3.27
	HIGH	0	0	0	0
IMFR2	LOW	0.3 ± 0.82	30 ± 72.99	0	5.3 ± 7.74
	MID	0	0.2 ± 0.41	0.5 ± 1.23	12.5 ± 28.70
	HIGH	0	0	0	0.3 ± 0.82
DE2	LOW	0	0.7 ± 1.63	0	4.0 ± 7.01
	MID	0.2 ± 0.41	0	0	0.8 ± 2.04
	HIGH	0	0	0	0
SUB3	LOW	0	23.0 ± 56.34	0	6.0 ± 7.40
	MID	0.2 ± 0.41	3.3 ± 6.06	0	3.7 ± 7.06
	HIGH	0	0	0	0
SUB2	LOW	0.3 ± 0.82	0	0	6.0 ± 12.79
	MID	0	0	0	0
	HIGH	0	0	0	0.2 ± 0.41
SUB1	LOW	0.3 ± 0.52	18.7 ± 28.50	0	13.3 ± 19.50
	MID	0	0.3 ± 0.82	0	2.5 ± 5.21
	HIGH	0	0	0	0.2 ± 0.41
DE1	LOW	0	25.7 ± 43.27	3.0 ± 6.38	16.3 ± 28.86
	MID	0	0	0	0
	HIGH	0.3 ± 0.82	0	0	2.7 ± 4.84
IMFR1	LOW	0	51.7 ± 79.99	6.8 ± 13.89	68.0 ± 46.24
	MID	0	0	0	3.3 ± 8.17
	HIGH	0	0	0	0
IMF1	LOW	0.3 ± 0.52	30 ± 67.78	2.2 ± 5.31	44.8 ± 67.05
	MID	0	0	0	0
	HIGH	0	0	0	0

CRUSTACEANS	d.f.	M.S.	H (F-ratio)	p-value	
TIDE	2	789416.000	58.594	0.000	*
SITE	9	13802.005	1.025	0.419	n/s
TIDE x SITE	18	29455.716	2.186	0.003	*

Table 8: Summary statistics (mean \pm S.D., min, max) and tables for two-way ANOVA testing for effects of site type and tidestage on temperature, oxygen, and salinity data - 2002 (N = 180, $\alpha = 0.01$)

	TEMP.	OXYGEN	SALINITY
<i>MEAN</i> \pm <i>S.D.</i>	28.78 \pm 1.689	3.44 \pm 1.27	26.27 \pm 1.503
<i>MIN</i>	25.00	1.49	15.70
<i>MAX</i>	32.30	7.78	28.60

TEMPERATURE	d.f.	M.S.	F-ratio	p-value	
<i>TIDE.</i>	2	24.902	8.696	0.000	*
<i>SITE</i>	9	0.426	0.149	0.998	n/s
<i>TIDE</i> \times <i>SITE</i>	18	1.507	0.526	0.942	n/s

OXYGEN	d.f.	M.S.	F-ratio	p-value	
<i>TIDE.</i>	2	4.407	2.568	0.080	n/s
<i>SITE</i>	9	0.914	0.533	0.849	n/s
<i>TIDE</i> \times <i>SITE</i>	18	0.895	0.522	0.944	n/s

SALINITY	d.f.	M.S.	F-ratio	p-value	
<i>TIDE.</i>	2	0.157	0.066	0.936	n/s
<i>SITE</i>	9	1.272	0.534	0.848	n/s
<i>TIDE</i> \times <i>SITE</i>	18	1.934	0.812	0.684	n/s

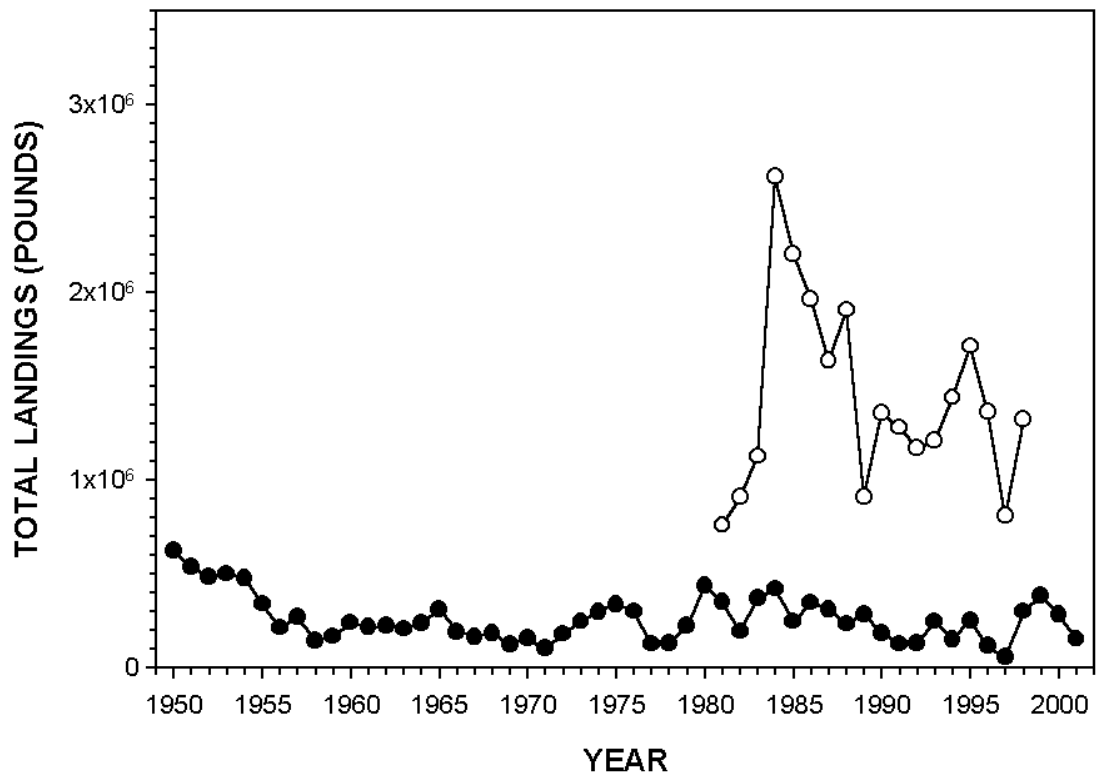


Figure 1: Total commercial (●) and recreational (○) landings of red drum for Atlantic coastal U.S. during 1950-2001 and 1981-1998, respectively (source: Atlantic states fishery management commission 1999 review of the fishery management plan for red drum)

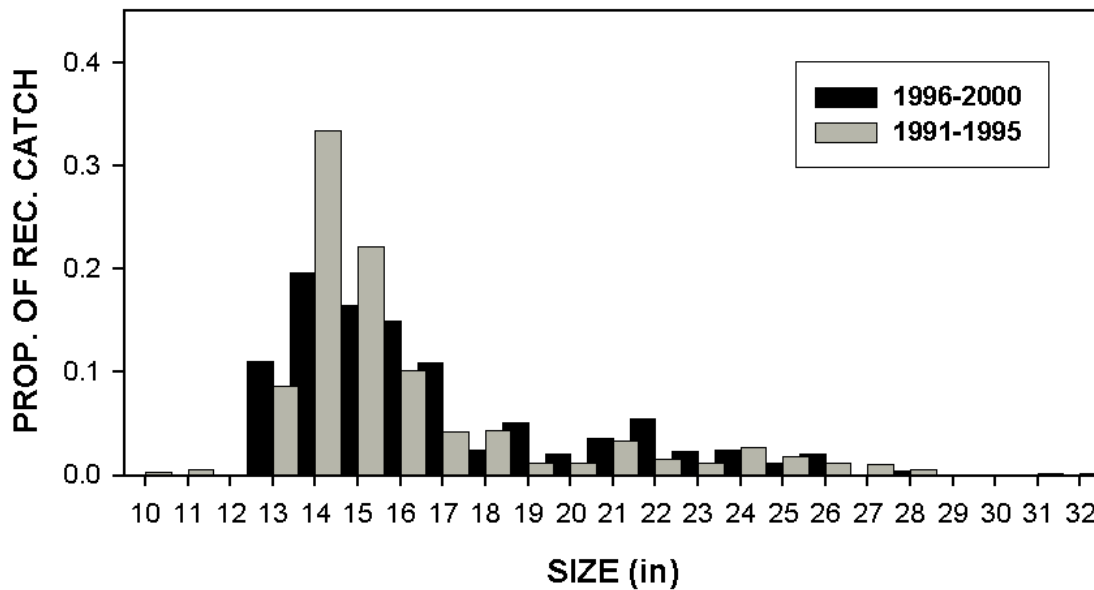


Figure 2: Length-frequency distribution for size of recreational catch for red drum prior to (1991-1995) and after (1996-2000) implementing the 14-27" slot limit. Distributions were not significantly different (Kolmogorov-Smirnov two-sample test, $p = 0.376$). Data are from the Marine Recreational Fisheries Statistics Survey (MRFSS) administered through the National Marine Fisheries Service (NMFS). (Source: database query of NMFS-MRFSS recreational fisheries statistics at - http://www.st.nmfs.gov/st1/recreational/queries/catch/length_distribution.html)

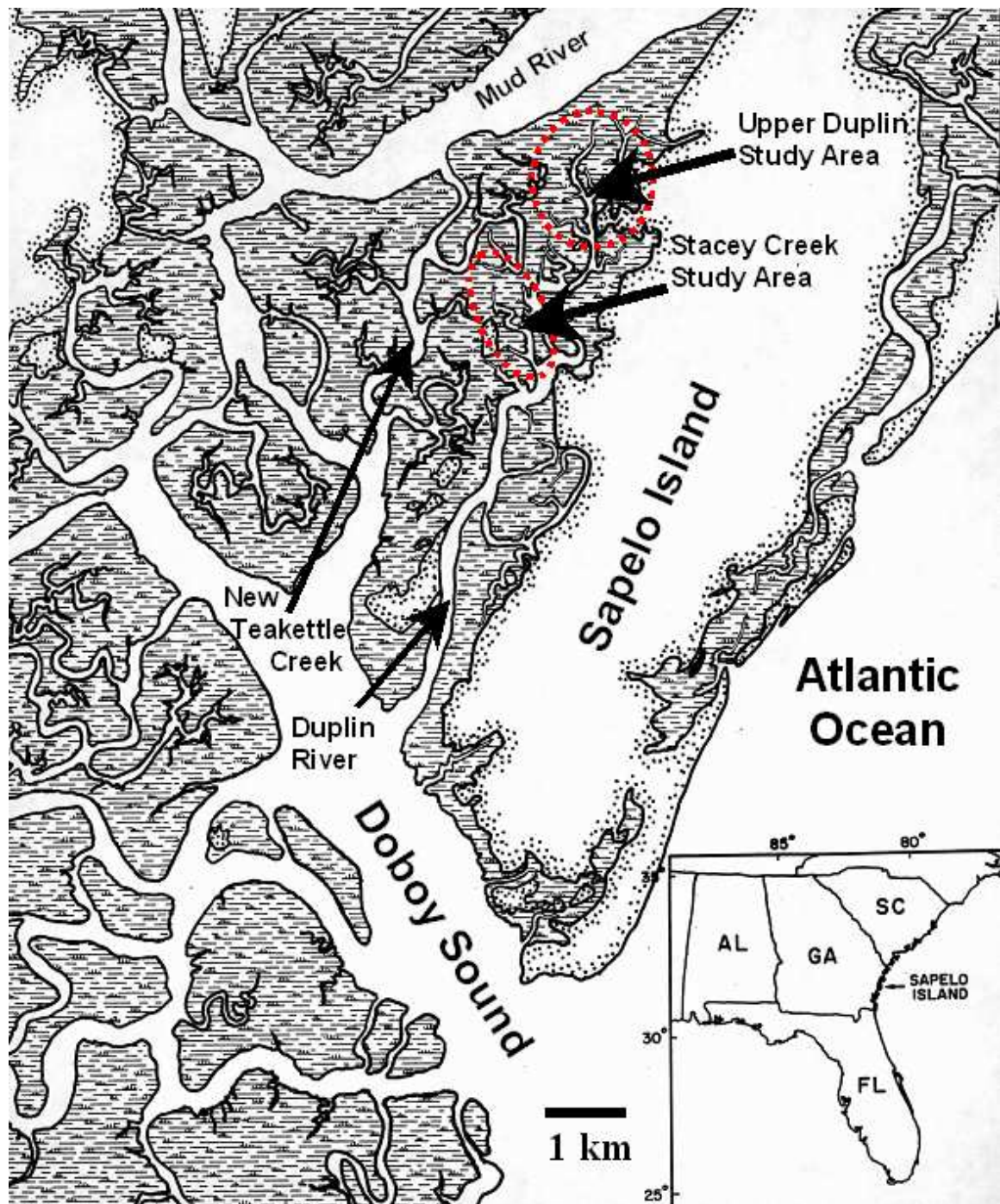


Figure 3: Map of Sapelo Island, Doboy Sound, and the Duplin River. Upper Duplin and Stacey Creek study areas are indicated and shown in greater detail in Figure 4.

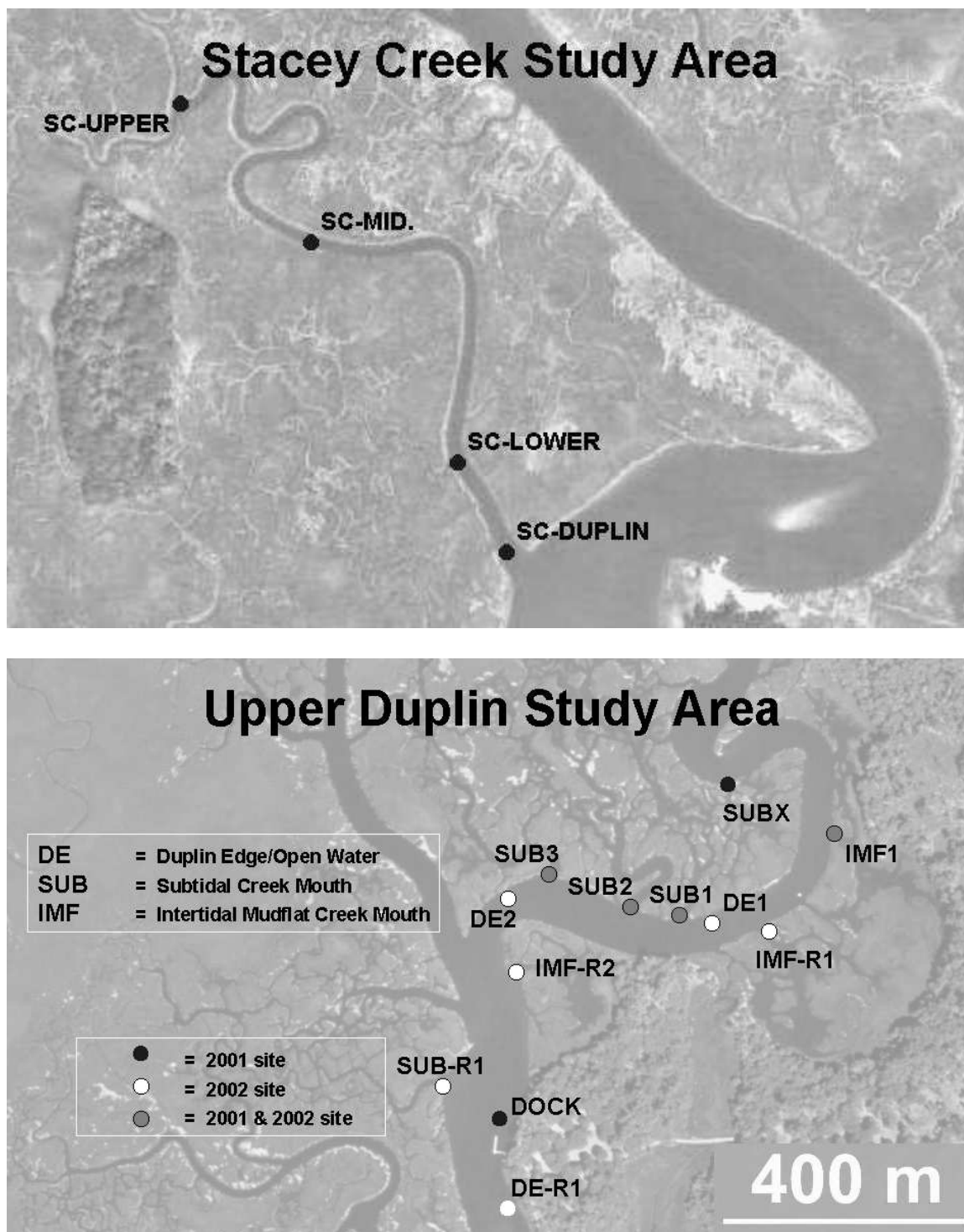


Figure 4: Upper Duplin (UD) and Stacey Creek (SC) study areas used for tracking red drum during 2001 and 2002. Nekton samples were collected at 2002 sites only within the Upper Duplin Study area.

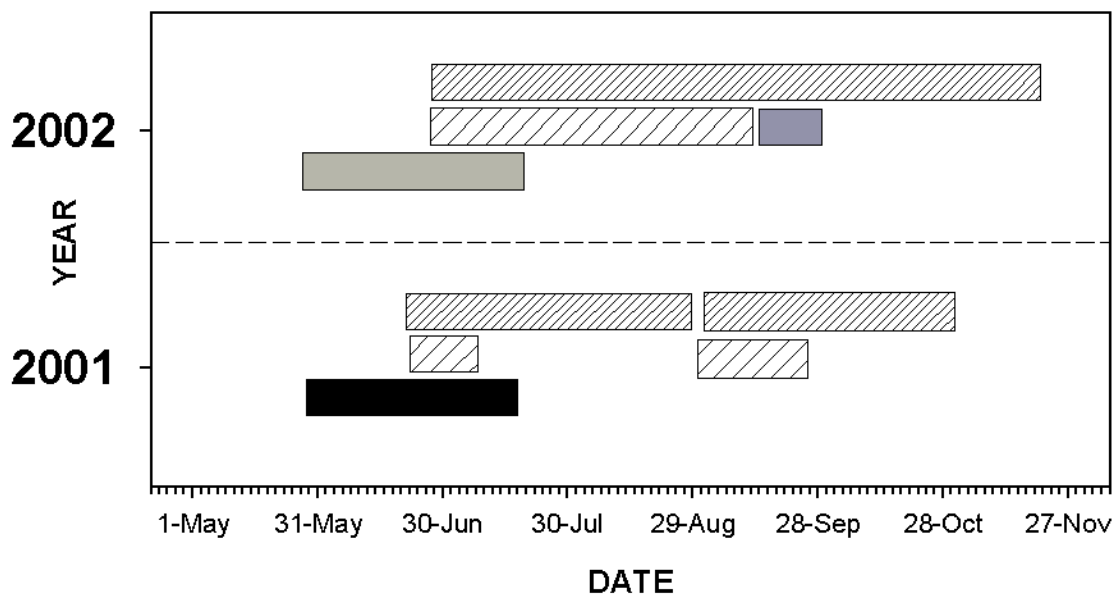


Figure 5: Timeline of fish tracking and nekton sampling efforts of this study during 2001 and 2002. Black bar=laboratory surgical trials, light gray bar=nekton sampling, dark gray bar=mobile hydrophone tracking, coarse-pattern bar=period of surgical implanting of transmitters, fine-pattern bar=period of fish tracking using stationary hydrophones within the study areas.

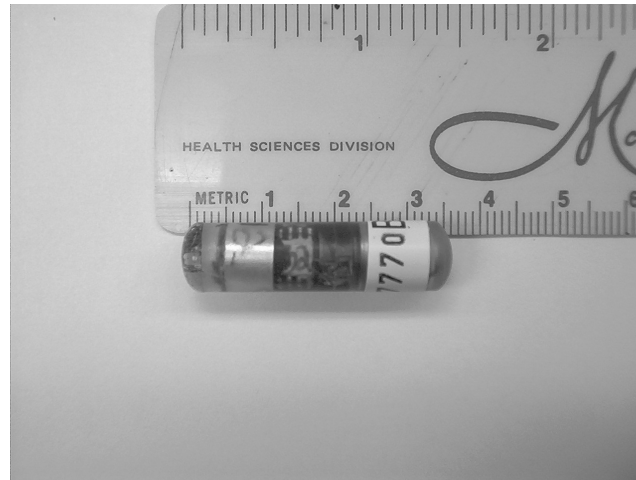


Figure 6: Photograph of the ultrasonic transmitter (pinger) used for internal implantation in this study. Transmitter is shown at approximately actual size.



Figure 7: Photograph of the surgical platform and recirculating pump apparatus. This set-up was used to perform implantations of the ultrasonic transmitters in this study.

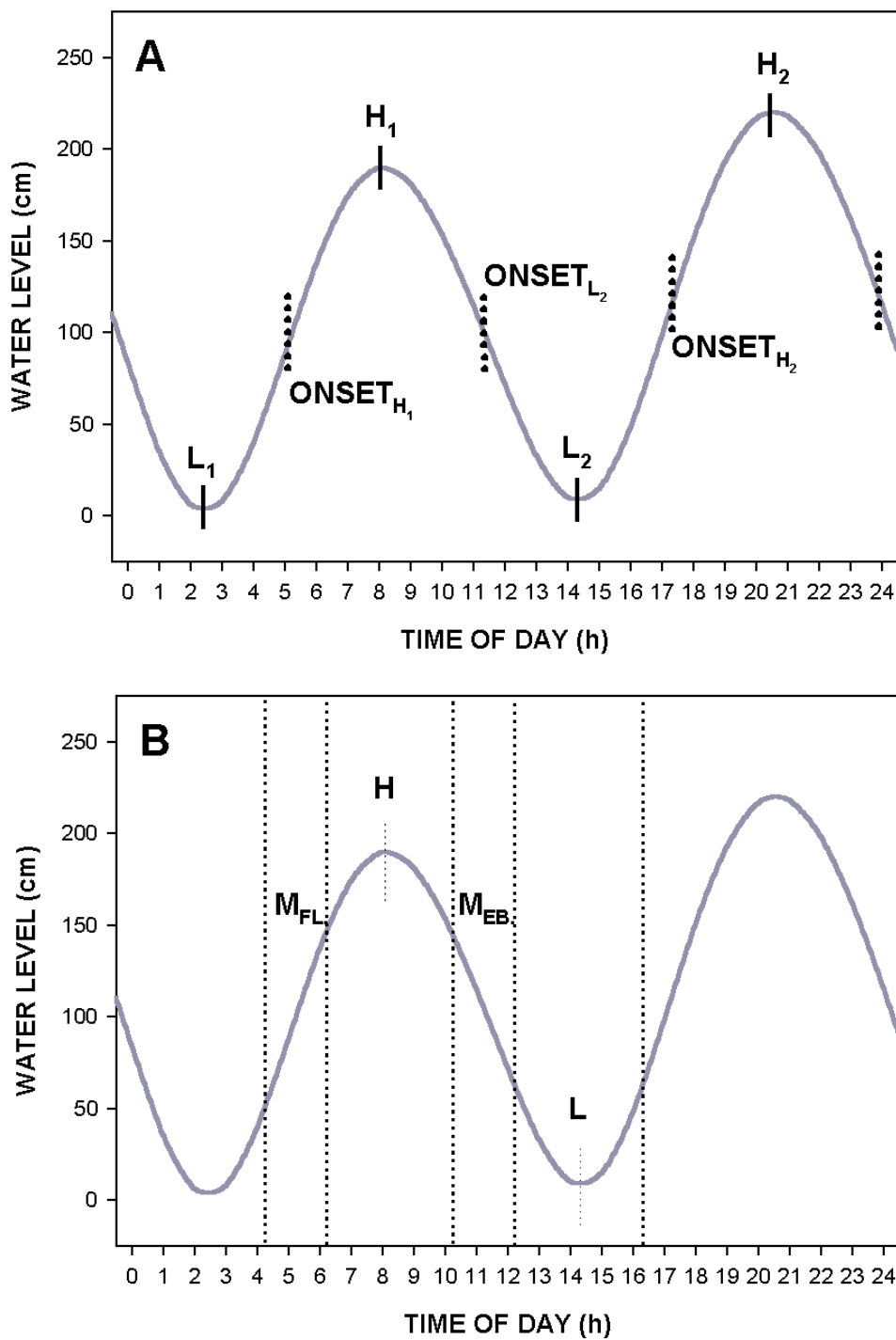


Figure 8: Schematic hydrograph showing how a given tidal cycle was broken down for this study. High tides (H) and low tides (L) include adjacent flood and ebb stages on either side of the peak & valleys of the hydrograph, respectively. Mid tides (M) include rising (flood) and falling (ebb) limbs of the hydrograph separated by a high tide period.

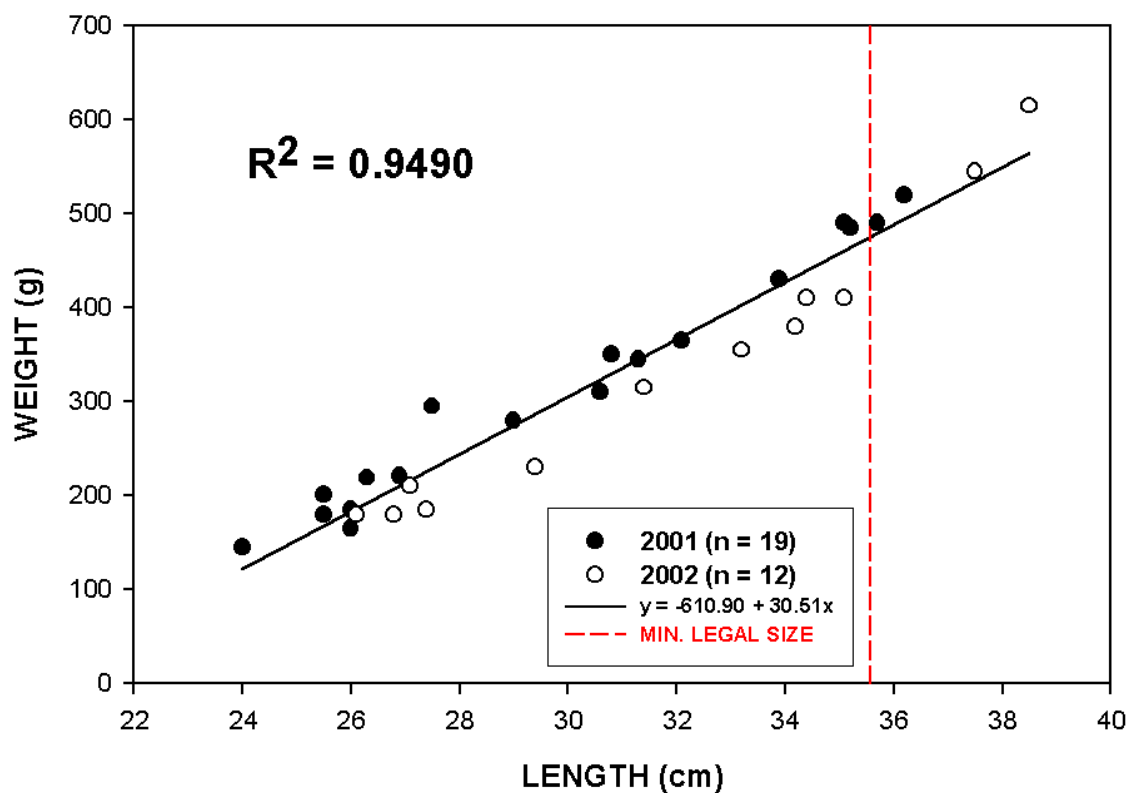


Figure 9: Length-weight relationship for sub-adult red drum used for implanting ultrasonic telemetry transmitter tags during 2001 & 2002. Closed circles represent individuals tagged during 2001; Open circles represent individuals tagged during 2002. Dashed vertical line denotes the state of Georgia minimum legal catch size for recreational anglers.

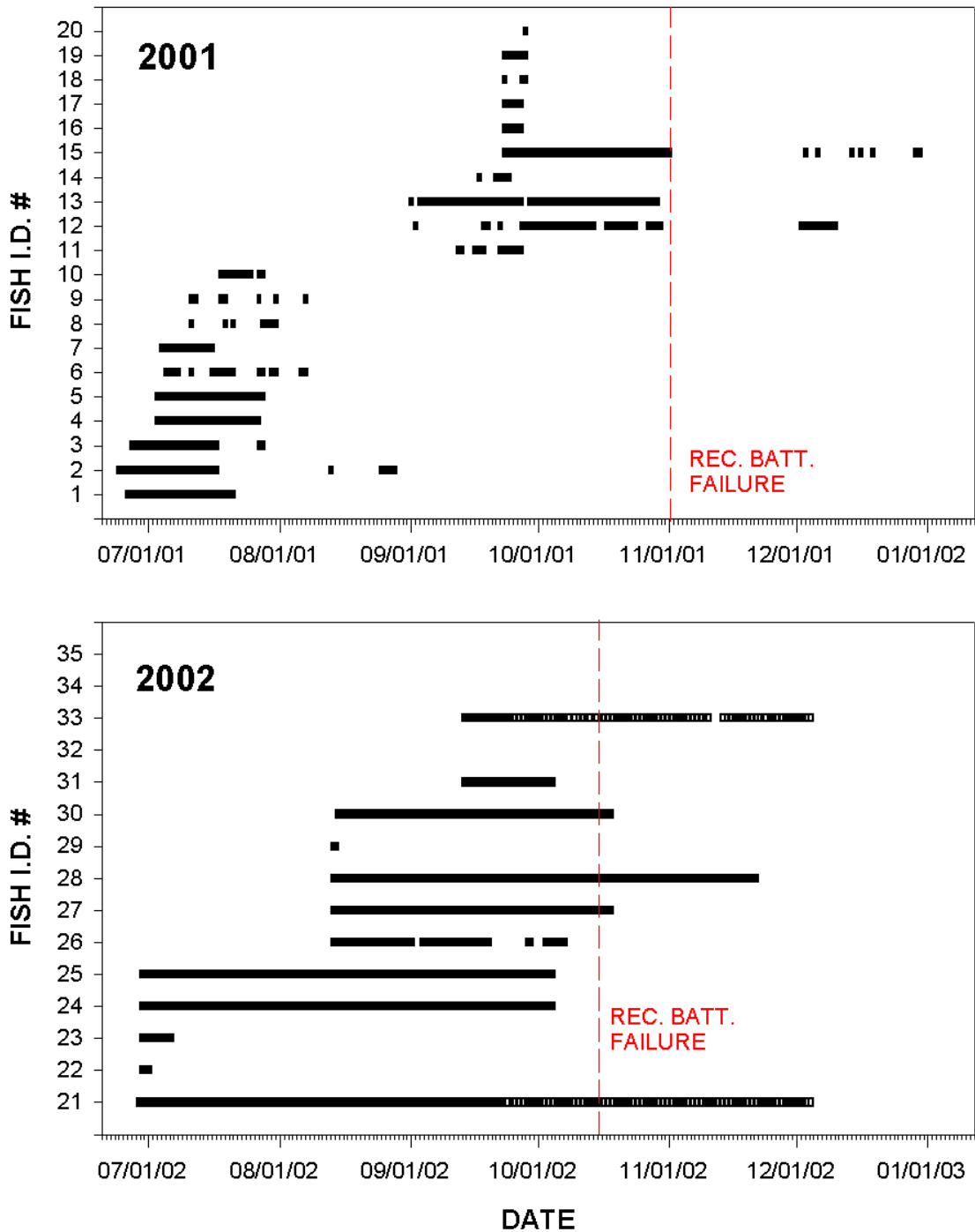


Figure 10: Daily tagged-fish detection record for 2001 & 2002 seasons. Closed square indicates fish was within range of at least one receiver, at least one time in a 24-hour period. Dashed line indicates the date when at least one receiver experienced battery failure, consequently ending the inter-site habitat utilization comparisons.

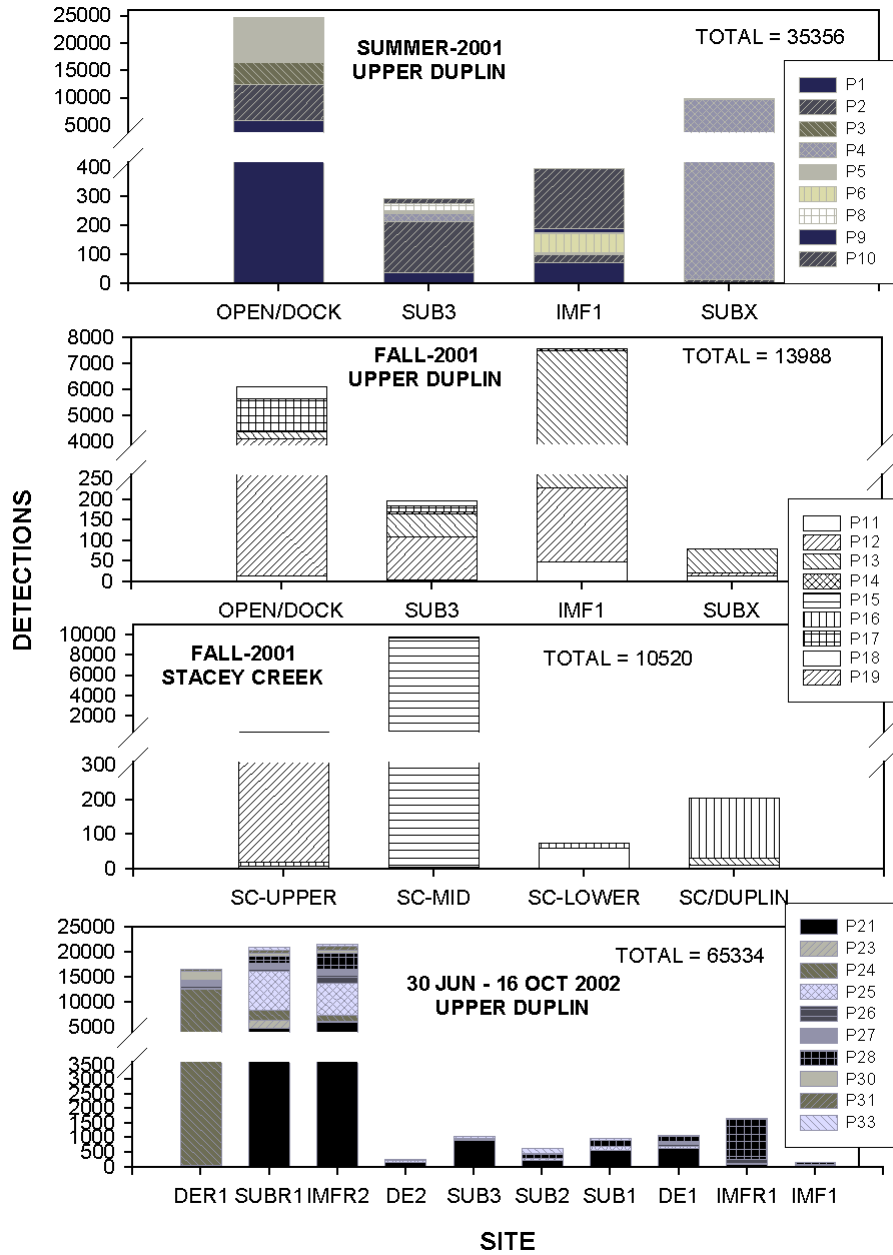


Figure 11: Total detections for all sites during 2001 & 2002. Individual fish I.D. #'s are designated by P##.

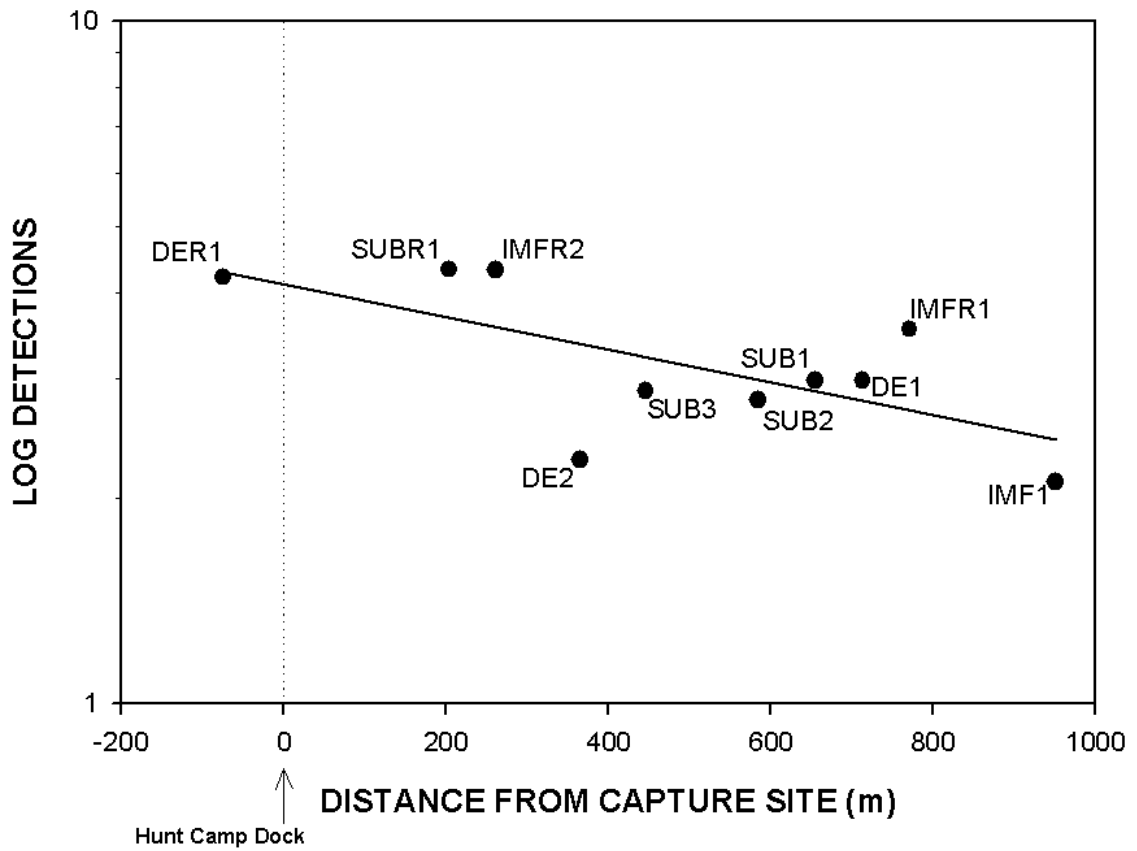


Figure 12: Total log-transformed detections of red drum at each of the 10 sites during summer/autumn 2002. Linear distances from the location of capture (Hunt Camp Dock) within the Upper Duplin study area are shown. [$r^2 = 0.470$, p -value = 0.029]

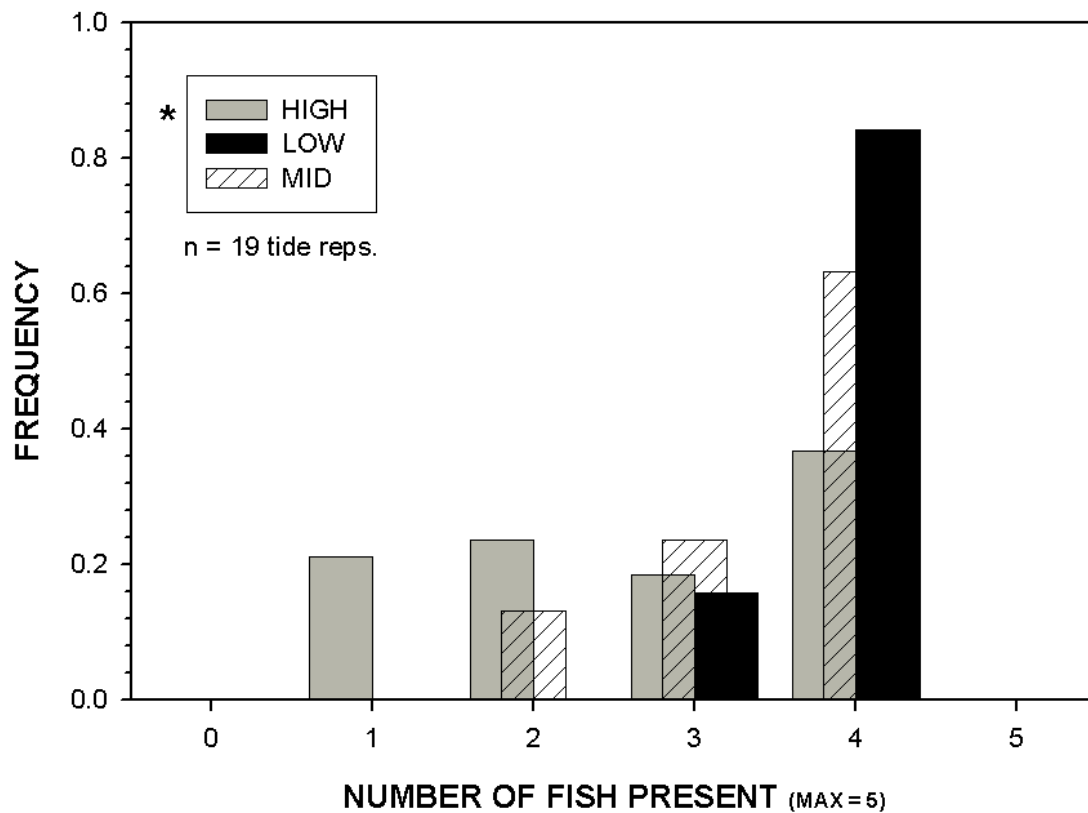


Figure 13: Frequency distributions of the observed number of fish present for three different tide-groups at the DOCK site, summer 2001. Data shown are from a continuous tracking period of 19 tide cycles (06 – 15 JUL 2001) when 5 fish were at large within the Upper Duplin study area. Distribution of fish at low tide was different than at high tide (Kolmogorov-Smirnov, $D_{MAX} = 0.474$, $p < 0.001$)

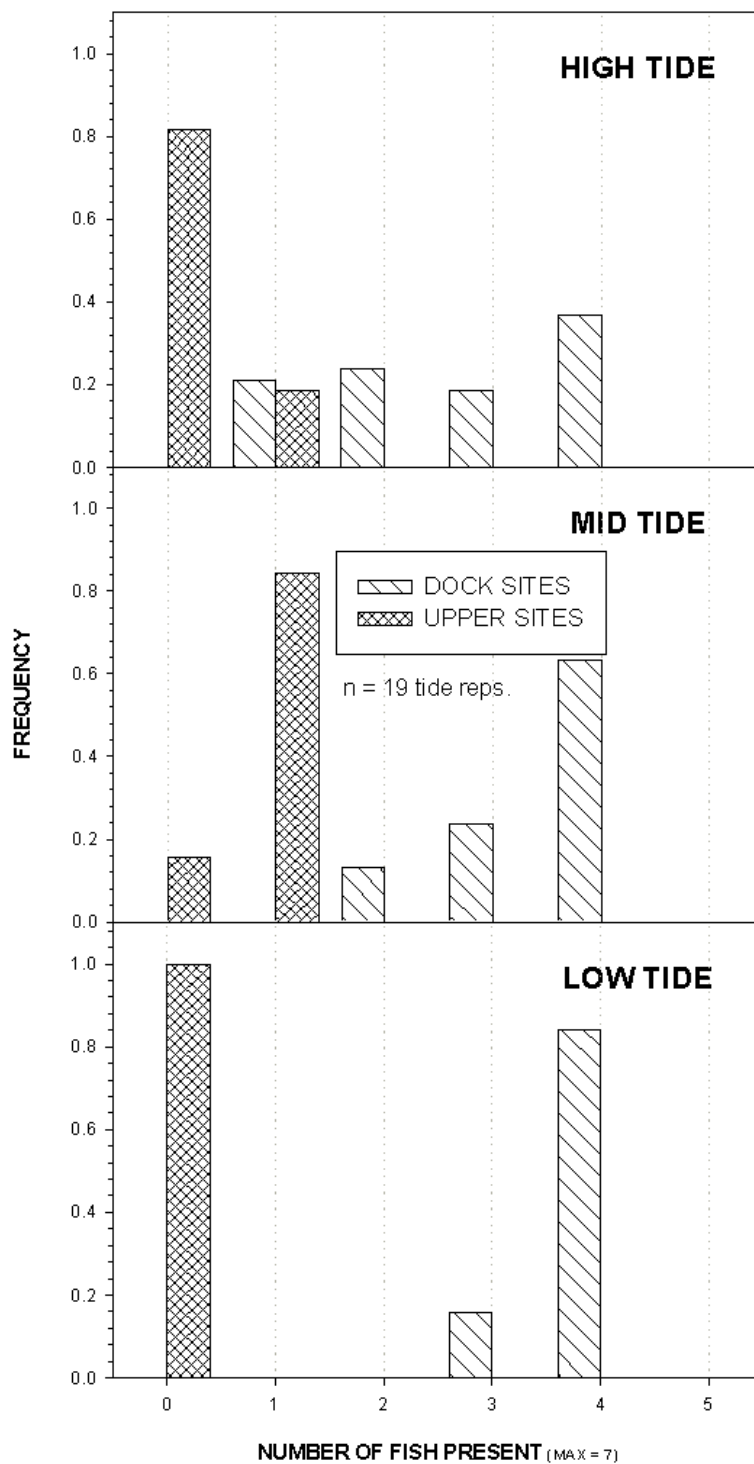


Figure 14: Frequency distributions of the observed number of fish present for three different tide-groups at the DOCK and UPPER (SUBX) sites, summer 2001. Data shown are from a continuous tracking period of 19 tide cycles (06 – 15 JUL 2001) when 5 fish were at large within the Upper Duplin study area.

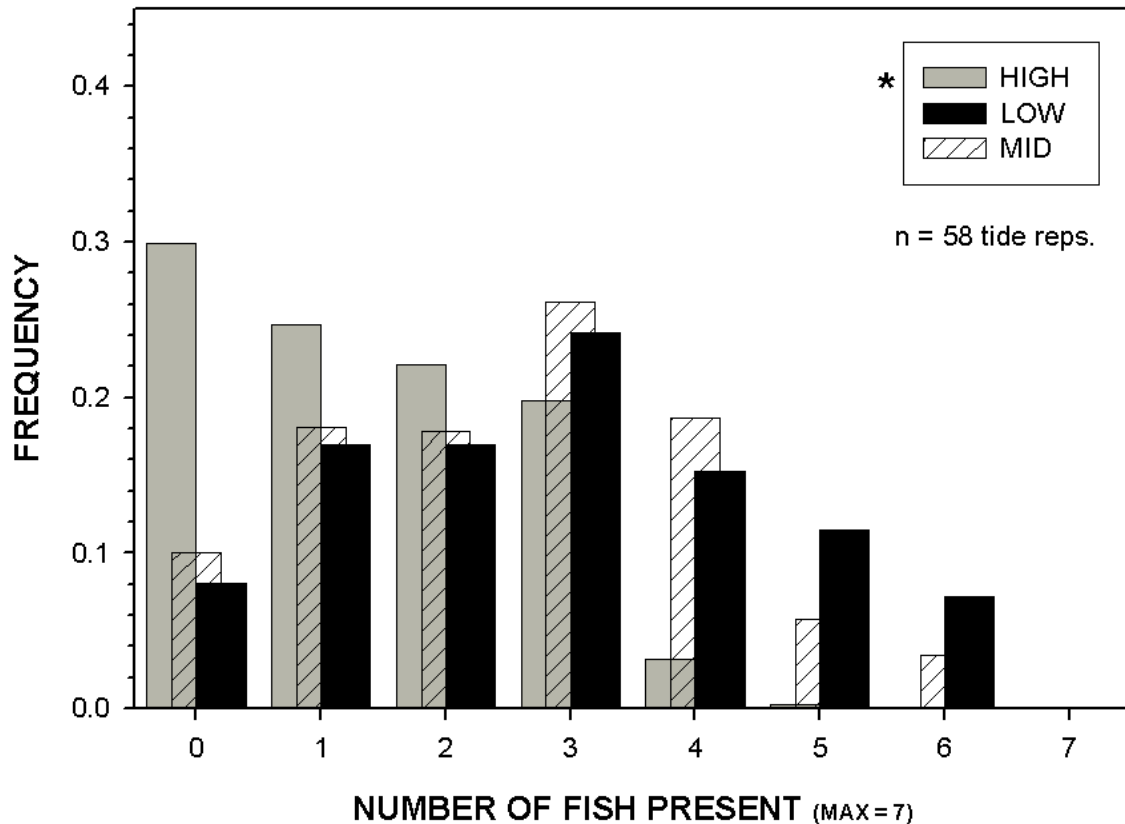


Figure 15: Frequency distributions of the observed number of fish present for three different tide-groups at the DOCK site, autumn 2002. Data (pooled data from 3 sites adjacent to the DOCK site – DER1, SUBR1, and IMFR2) shown are from a continuous tracking period of 116 tide cycles (20 AUG – 19 SEP 2002) when 7 fish were at large within the Upper Duplin study area. Distribution of fish at high tide was different than at low (Kolmogorov-Smirnov, $D_{MAX} = 0.347$, $p < 0.001$) and mid tide (Kolmogorov-Smirnov, $D_{MAX} = 0.305$, $p < 0.001$)

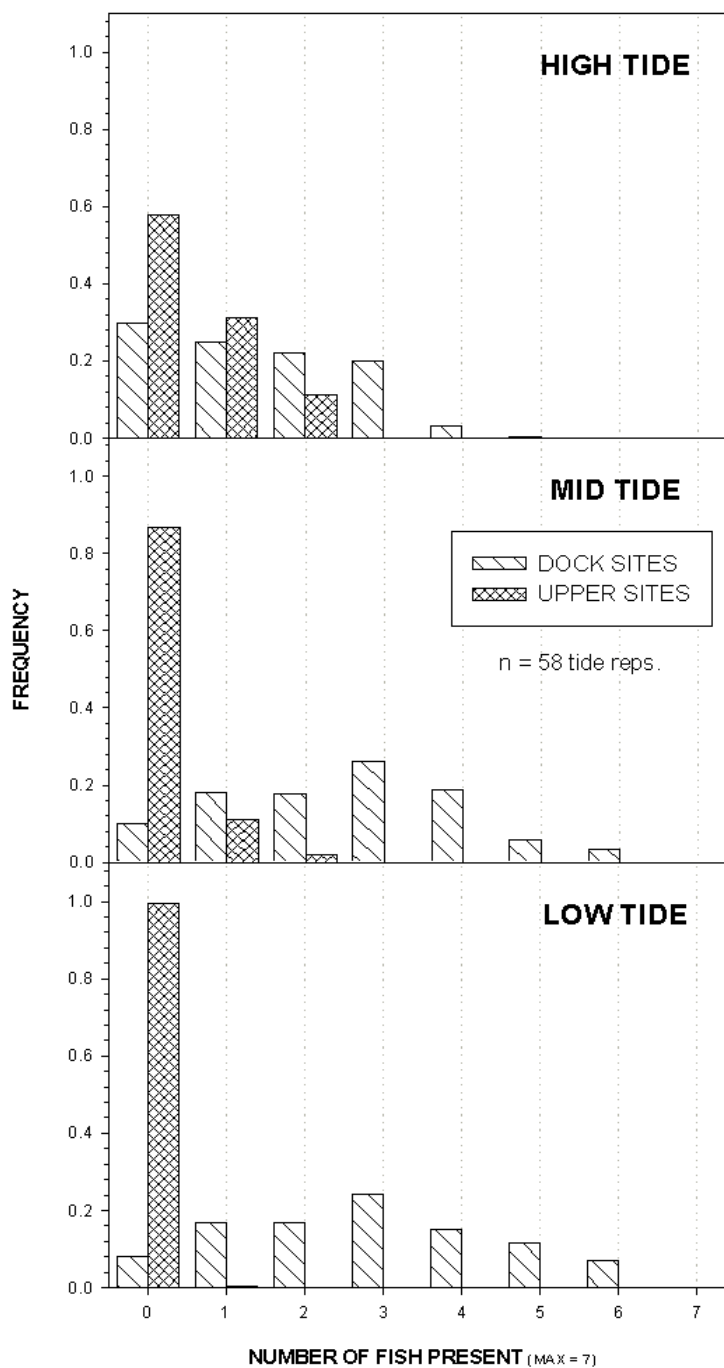


Figure 16: Frequency distributions of the observed number of fish present for three different tide-groups at the DOCK (pooled DER1, SUBR1, and IMFR1 sites) and UPPER (pooled SUB1, DE1, and IMFR1 sites), autumn 2002. Data shown are from a continuous tracking period of 58 tide cycles (20 AUG – 19 SEP 2002) when 7 fish were at large within the Upper Duplin study area.. Differences in the distribution of fish were observed (Kolmogorov-Smirnov) between sites for high tide ($D_{MAX} = 0.342$, $p < 0.001$), mid tide ($D_{MAX} = 0.797$, $p < 0.001$), and low tide ($D_{MAX} = 0.914$, $p < 0.001$).

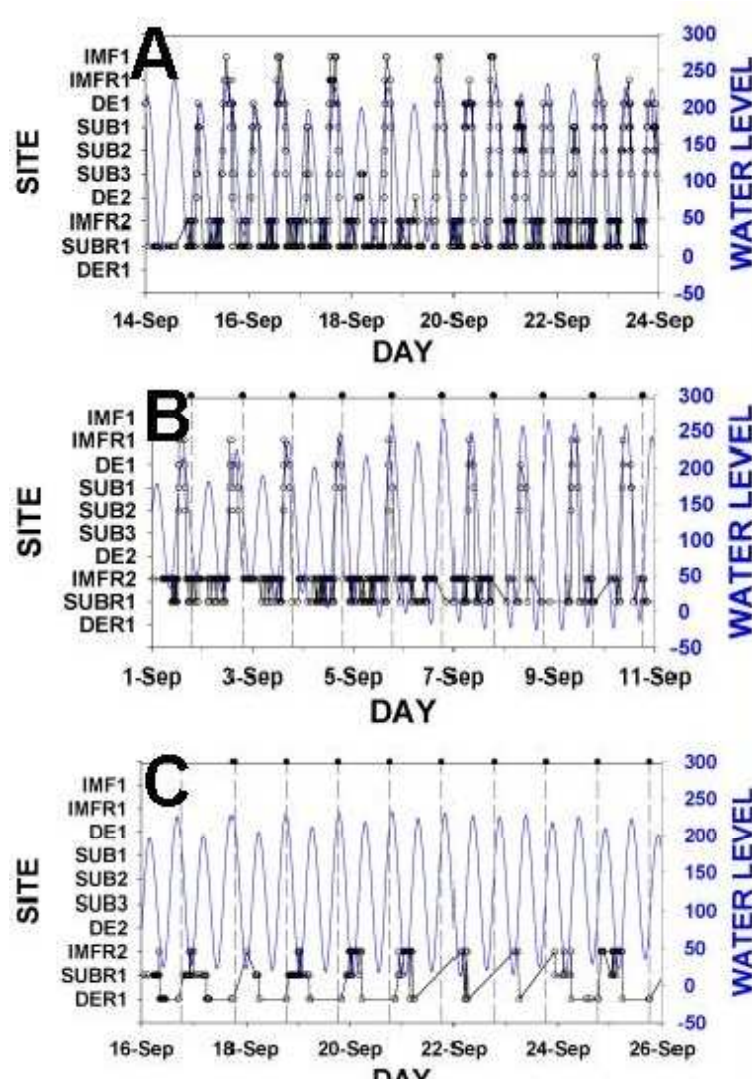


Figure 17: Examples of common dispersal patterns during high tide. (A) Upriver movement and return on every tidecycle. (B) Upriver movement and return on alternating tidecycles, as mediated by time of sunset (grey dashed vertical lines). Note also that sites SUB3 and DE2 are skipped consistently. (C) Unmonitored movement beyond the detection limits of the study area (downriver, on-marsh, etc.)

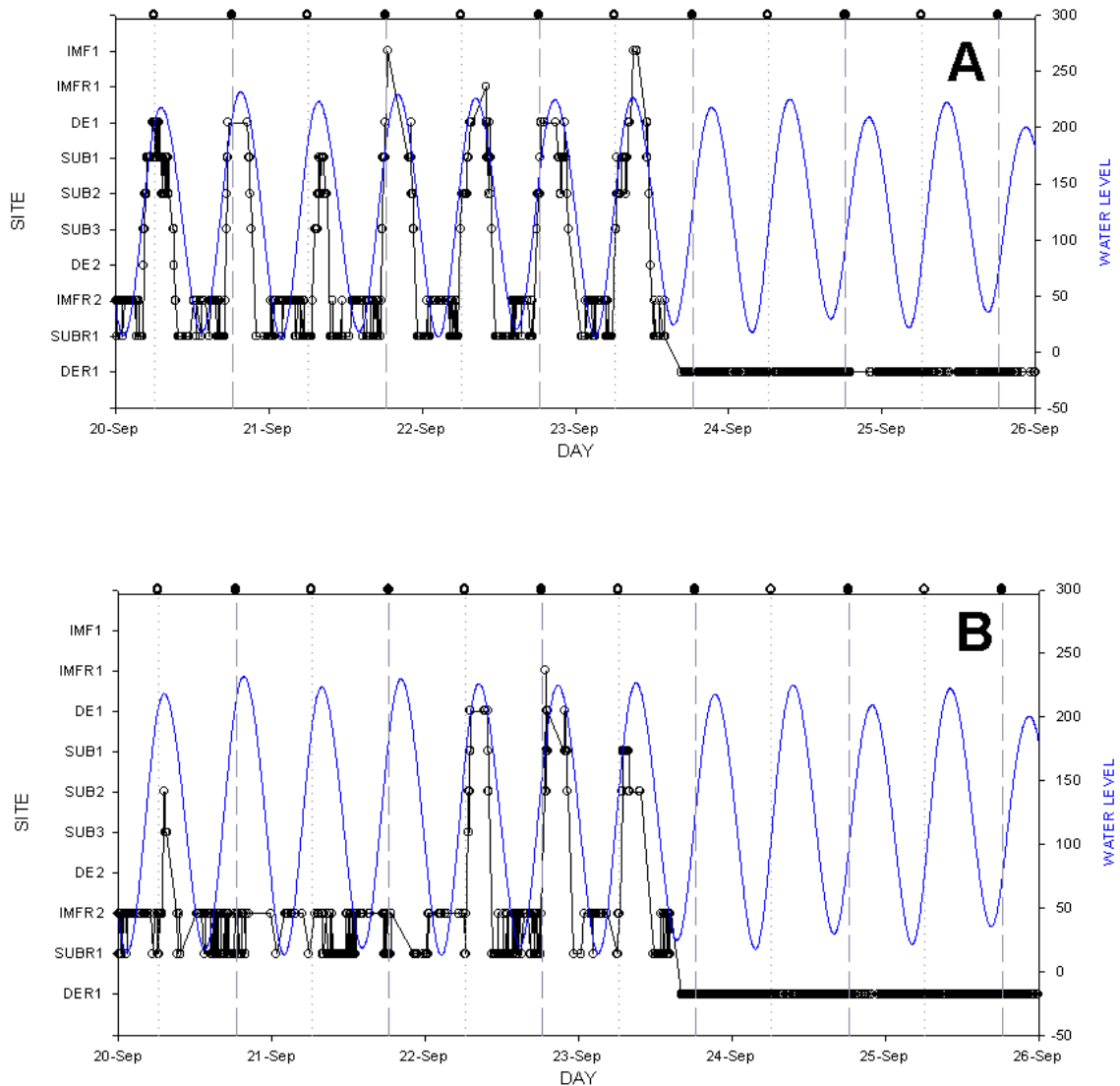


Figure 18: Diurnal and tidal movement patterns of tagged fish #21 and #33 followed by sudden cessation of movement pattern presented as evidence for angler removal of fish from the study area. Refer to Appendix C for complete graphs and description. Note that both fish exhibit "flatline" detection patterns at precisely the same date/time, suggesting angler interference (e.g., fish was cleaned on-site, then carcass discarded back into the river where its transmitter was continuously detected).

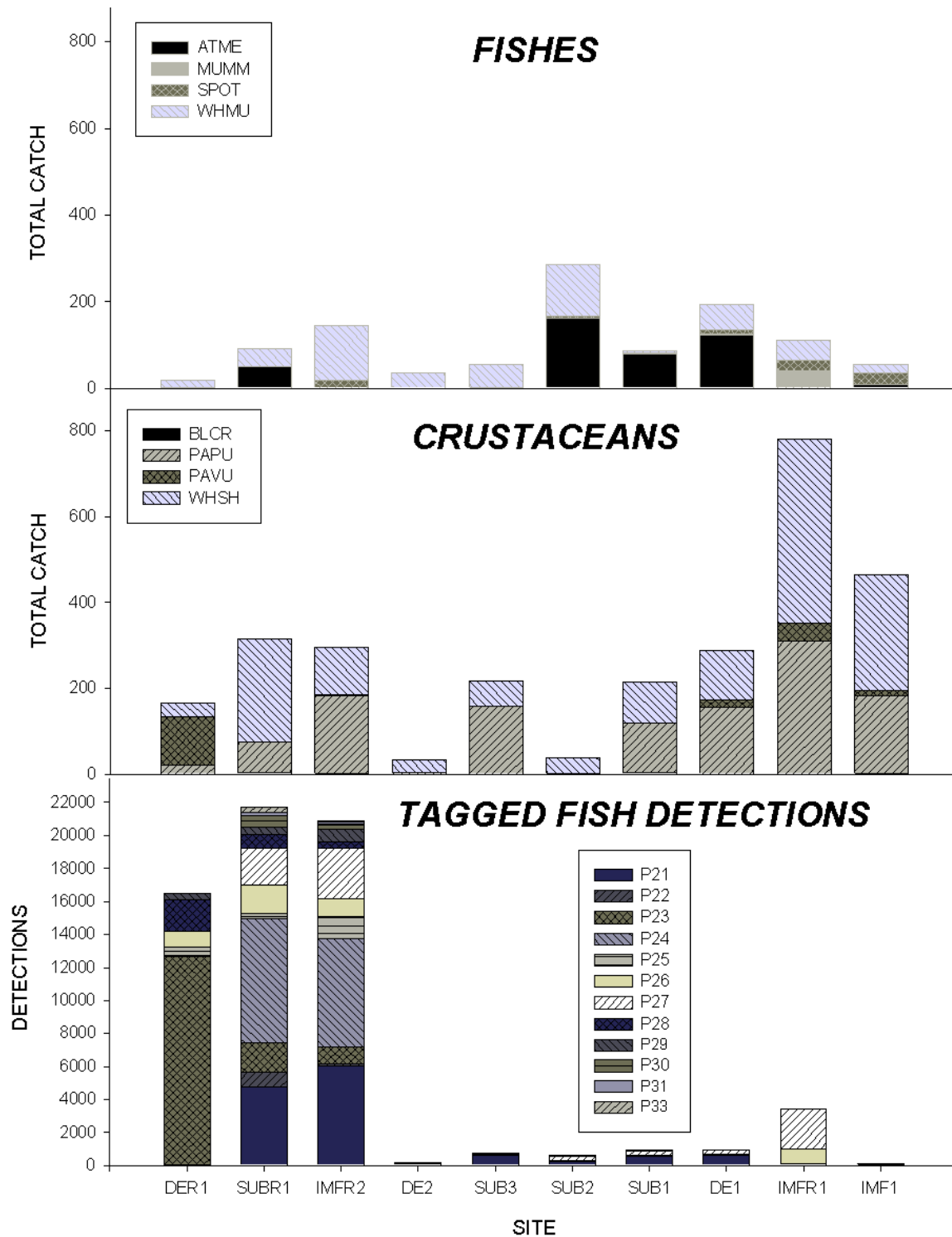


Figure 19: Composition of total catch (fishes & crustaceans only) 29 MAY through 22 JUL 2002 and total (n = 12) tagged fish detections, 29 JUN through 07 NOV 2002. [ATME (Atlantic Menhaden), MUMM (Mummichog), SPOT (Spot), BLCR (Blue Crab), PAPU (Daggerblade Grass Shrimp), PAVU (Marsh Grass Shrimp), WSHH (White Shrimp)].

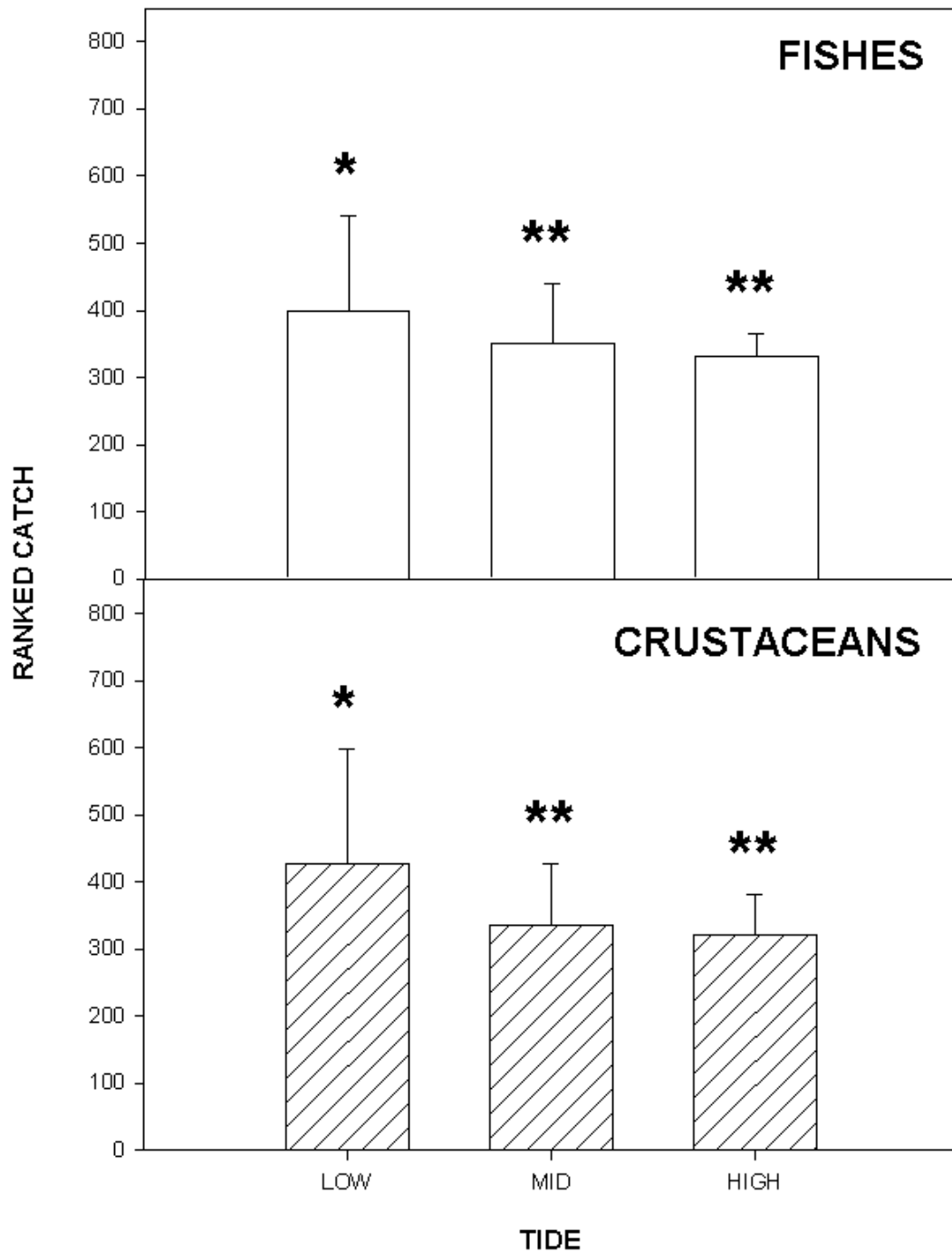


Figure 20: Ranked catch of fishes and crustaceans collected during nekton sampling from three tide stages within the Upper Duplin study area, 29 MAY - 22 JUL 2002. Tide stages without common symbols (* or **) were significantly different. 2-way ANOVA performed on the ranked data using the Scheirer-Ray-Hare extension of the Kruskal-Wallis test. ($p < 0.0001$)

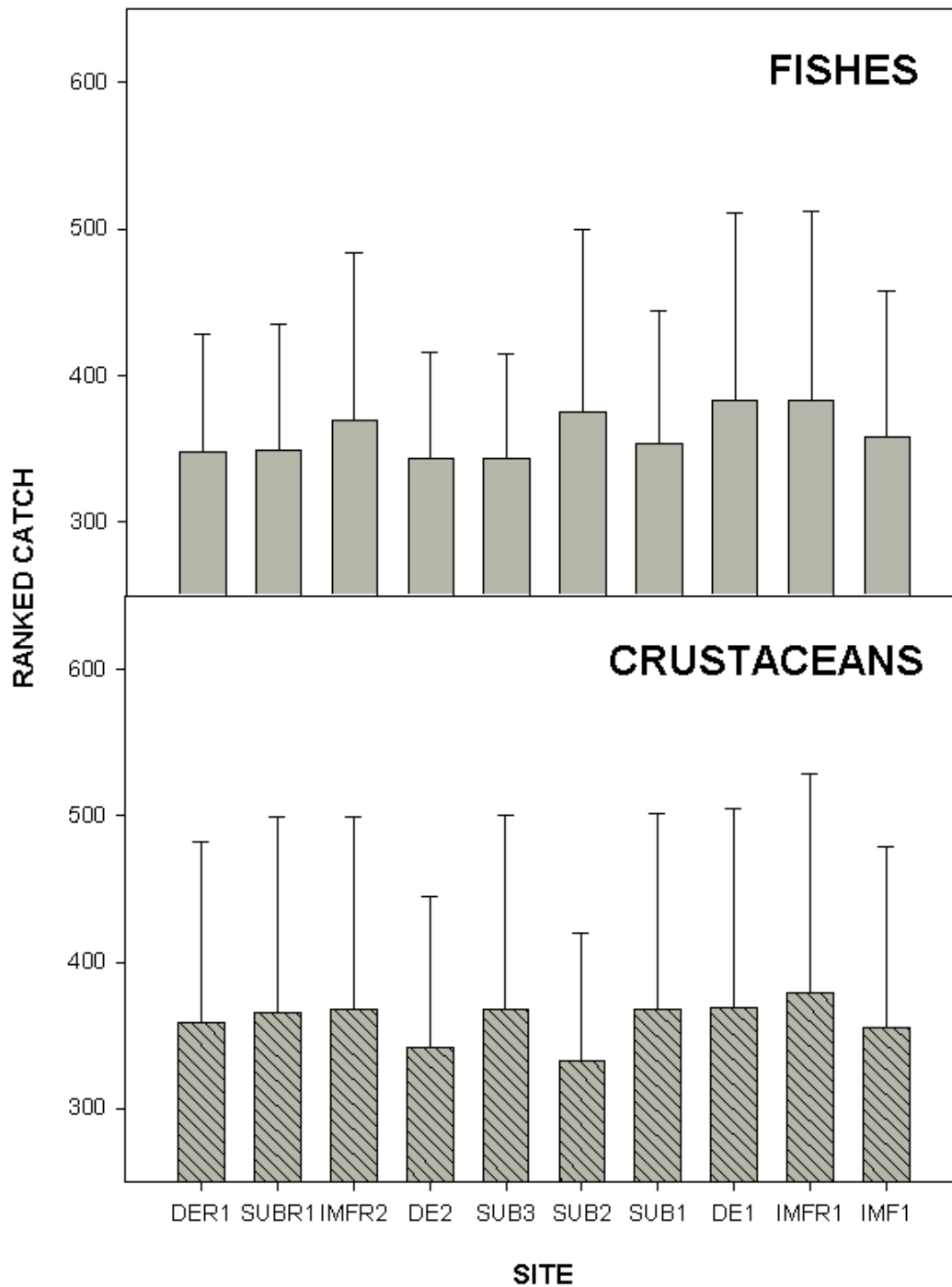


Figure 21: Ranked catch of fishes and crustaceans collected during nekton sampling from all sites within the Upper Duplin study area, 29 MAY - 22 JUL 2002. No significant differences between sites were observed. 2-way ANOVA performed on the ranked data using the Scheirer-Ray-Hare extension of the Kruskal-Wallis test. ($\alpha = 0.01$)

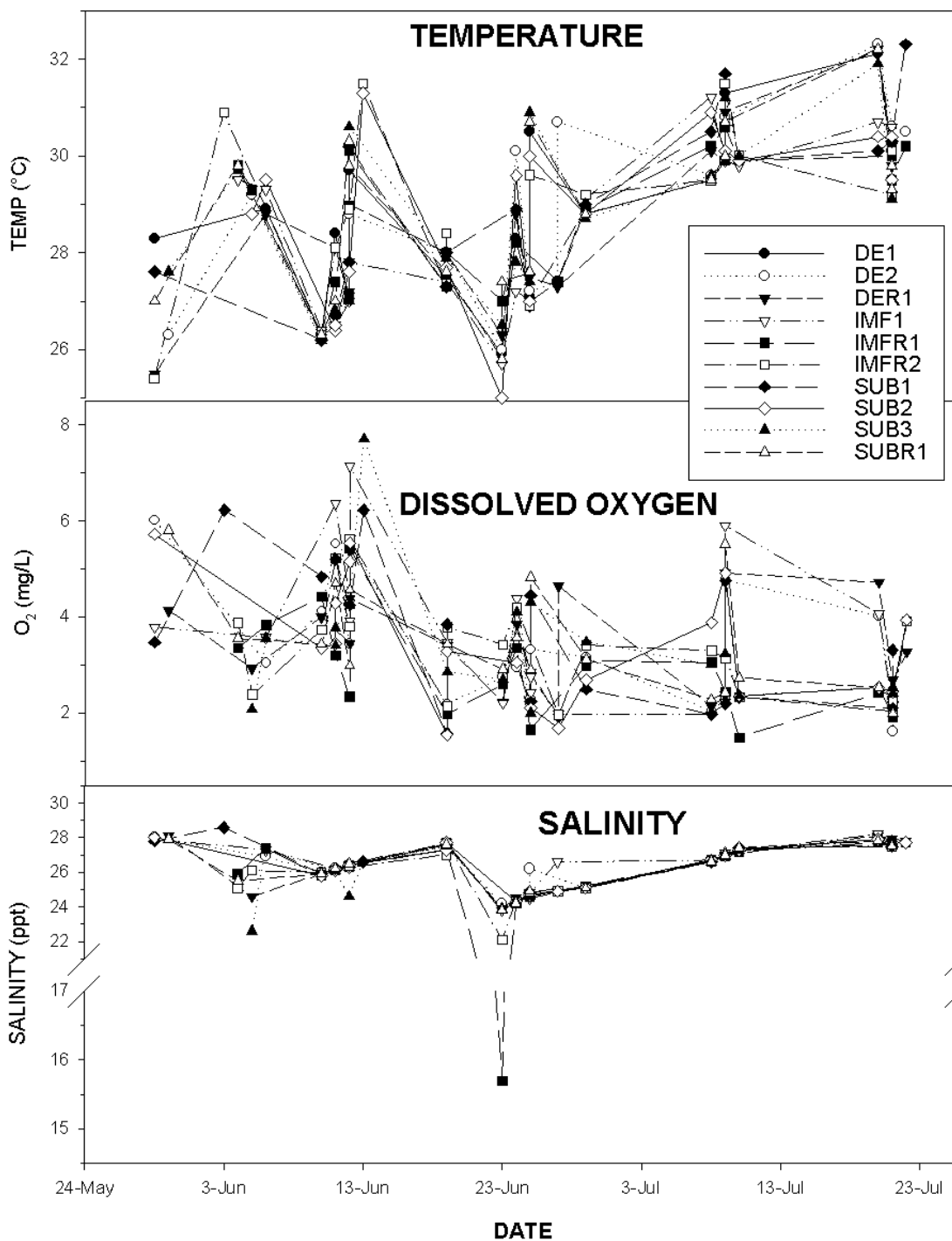


Figure 22: Time series of physical/chemical parameters at Upper Duplin Study Area sites during 29 MAY - 22 JUL 2002.

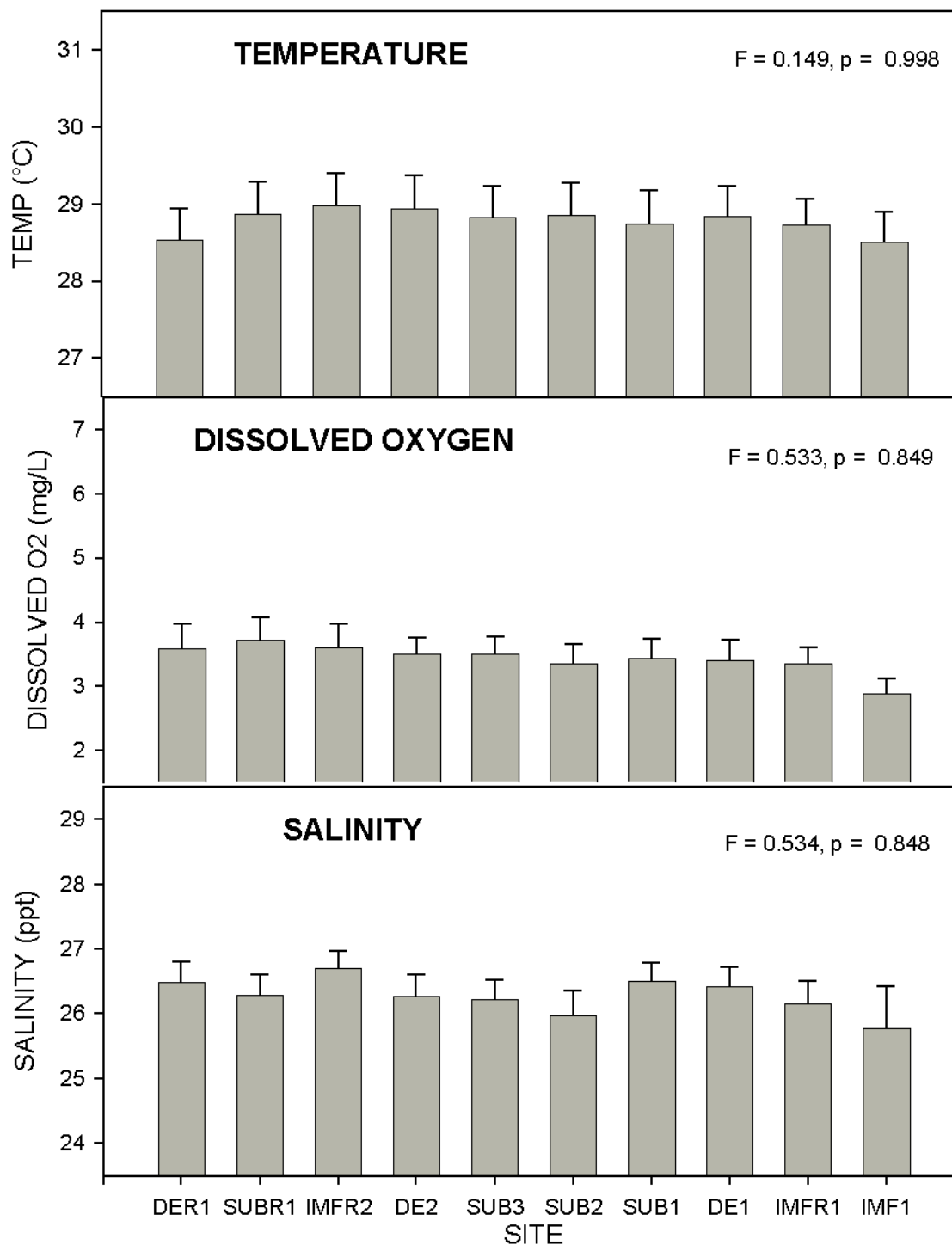


Figure 23: Mean \pm S.E. water temperature ($^{\circ}$ C), dissolved oxygen (mg L^{-1}), and salinity (ppt) by site [DER1, SUBR1, IMFR2, DE2, SUB3, SUB2, SUB1, DE1, IMFR1, IMF1] within the Upper Duplin Study Area sites. Significant differences are denoted with an (*) $\alpha = 0.010$

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APPENDIX – A: SCATTER-PLOTS, UPPER DUPLIN, SUMMER 2001.

This section contains a series of time-series scatter plots, which display movement and habitat use patterns for individual tagged fish used in the study. Onset times of high and low tides (exact midpoint between high and low tide overlay the plot to visually approximate the tide stage in which detections were observed. The following is the caption that is applicable to all figures within this section, where “X”s replaced by the fish I.D.-#:

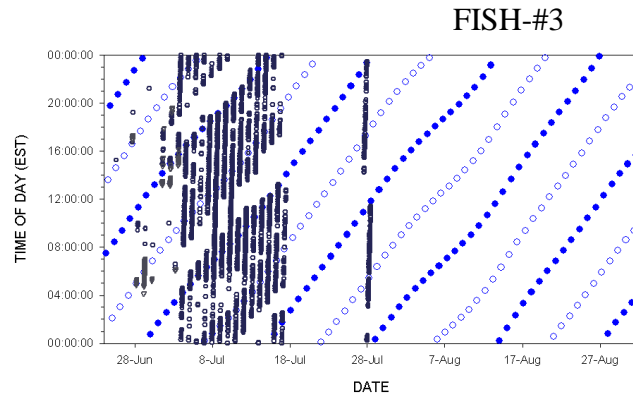
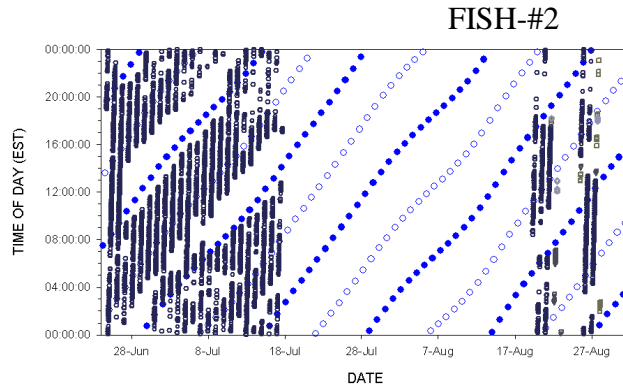
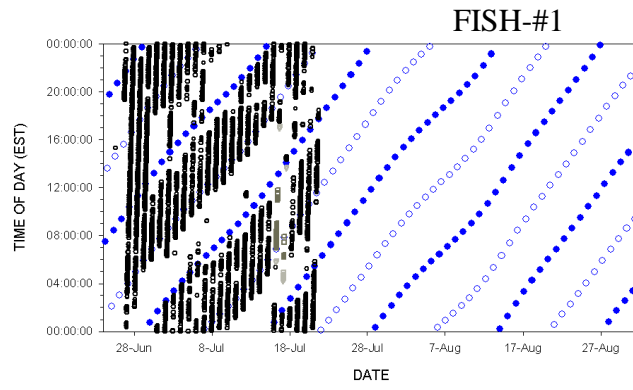
FISH-X: The individual scatter-plots show the overall tidal and pattern(s) of individual fish detections at each of the four sites plotted in a time series. Symbols (see below) are as follows: open circle=DOCK, open triangle=SUB3, open square=IMF1, open diamond=SUBX. Onset times for high tide (large, closed circles), and low tide (large, open circles).

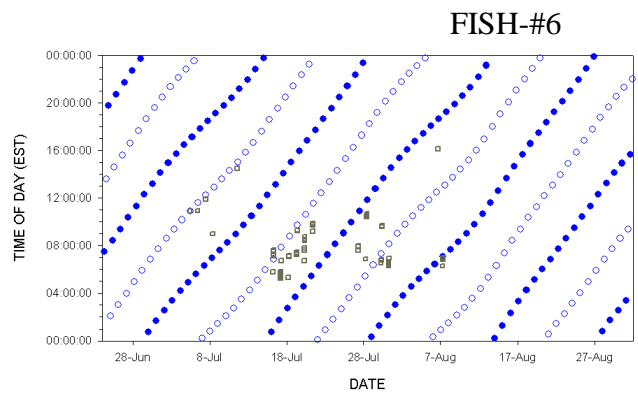
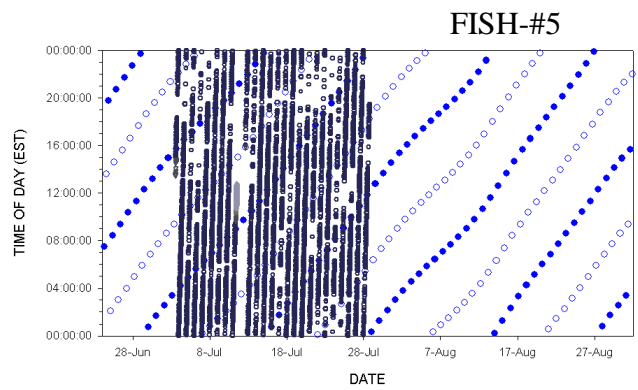
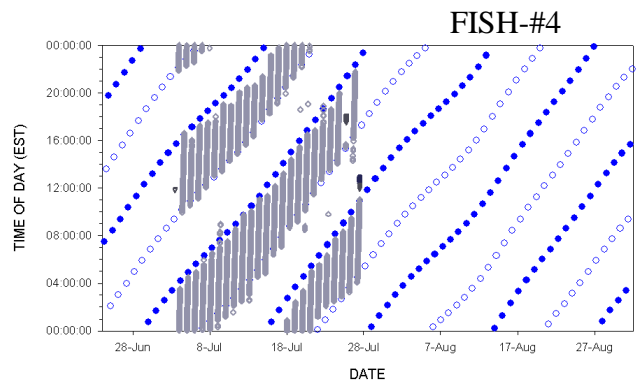
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○	ONSET - LOW TIDE
○	OPEN/DOCK
▽	SUB3
□	IMF1
◇	SUBX

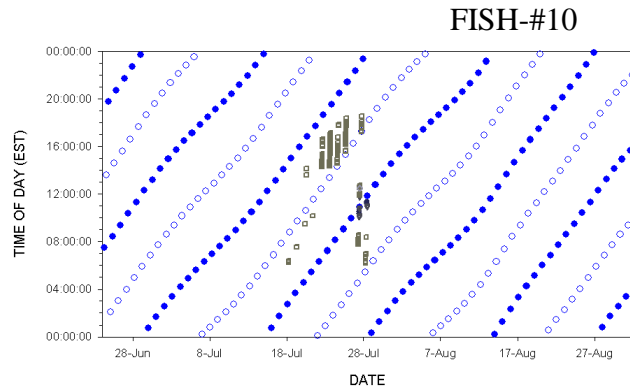
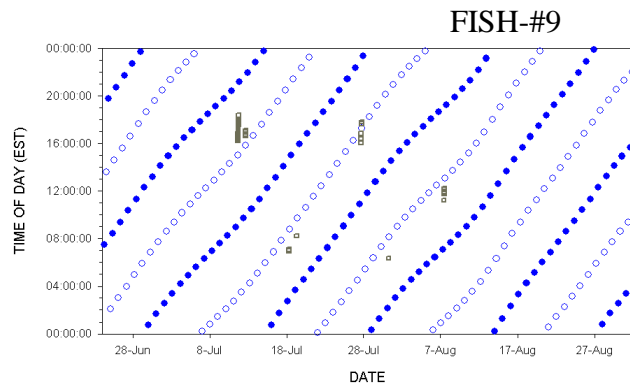
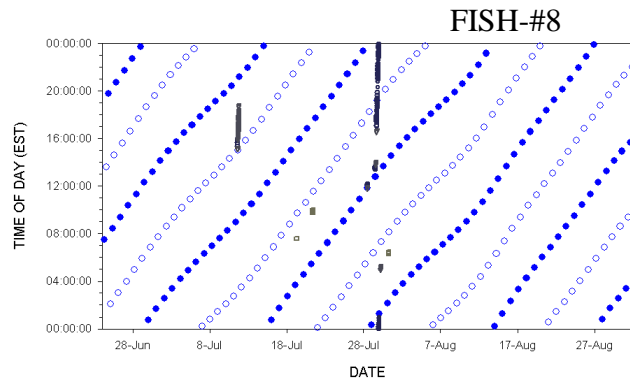
Legend of symbols used in “scatter”graphs for this section:

GRAPHS INCLUDED IN THIS SECTION, 3-PER PAGE (3 total pages)

- *FISH-1, SCATTER, UPPER DUPLIN*
- *FISH-2, SCATTER, UPPER DUPLIN*
- *FISH-3, SCATTER, UPPER DUPLIN*
- *FISH-4, SCATTER, UPPER DUPLIN*
- *FISH-5, SCATTER, UPPER DUPLIN*
- *FISH-6, SCATTER, UPPER DUPLIN*
- *FISH-8, SCATTER, UPPER DUPLIN*
- *FISH-9, SCATTER, UPPER DUPLIN*
- *FISH-10, SCATTER, UPPER DUPLIN*







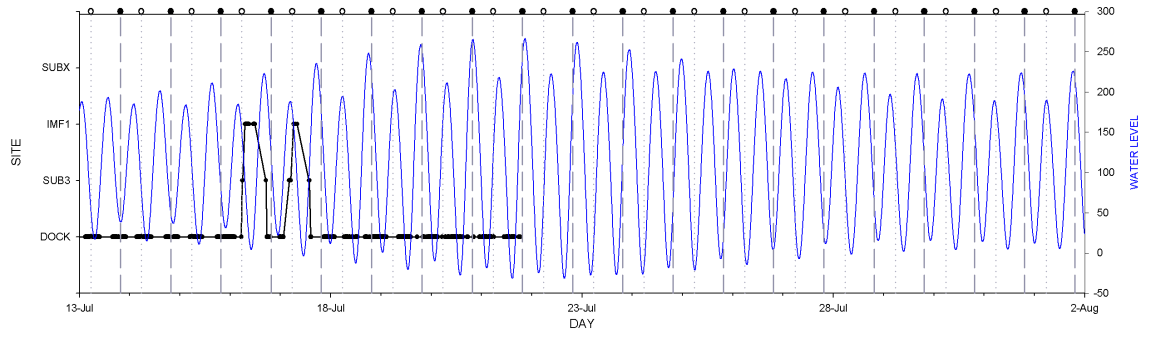
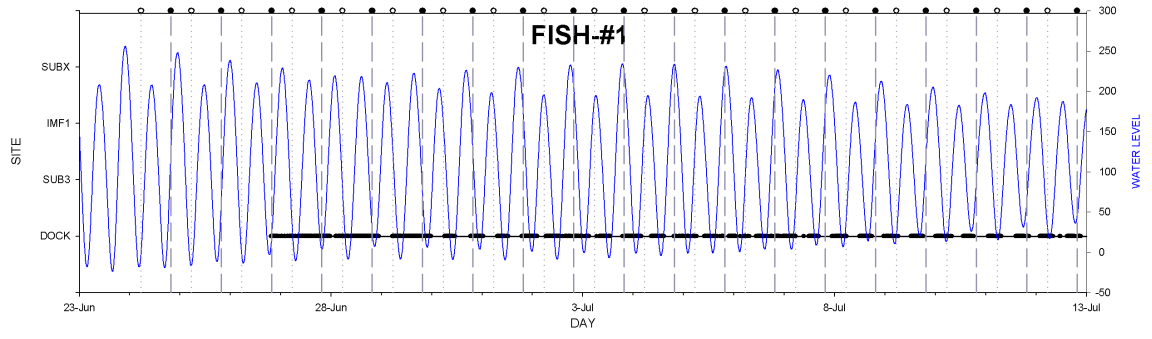
APPENDIX – B: FISH-TRACKER PLOTS, UPPER DUPLIN, SUMMER 2001.

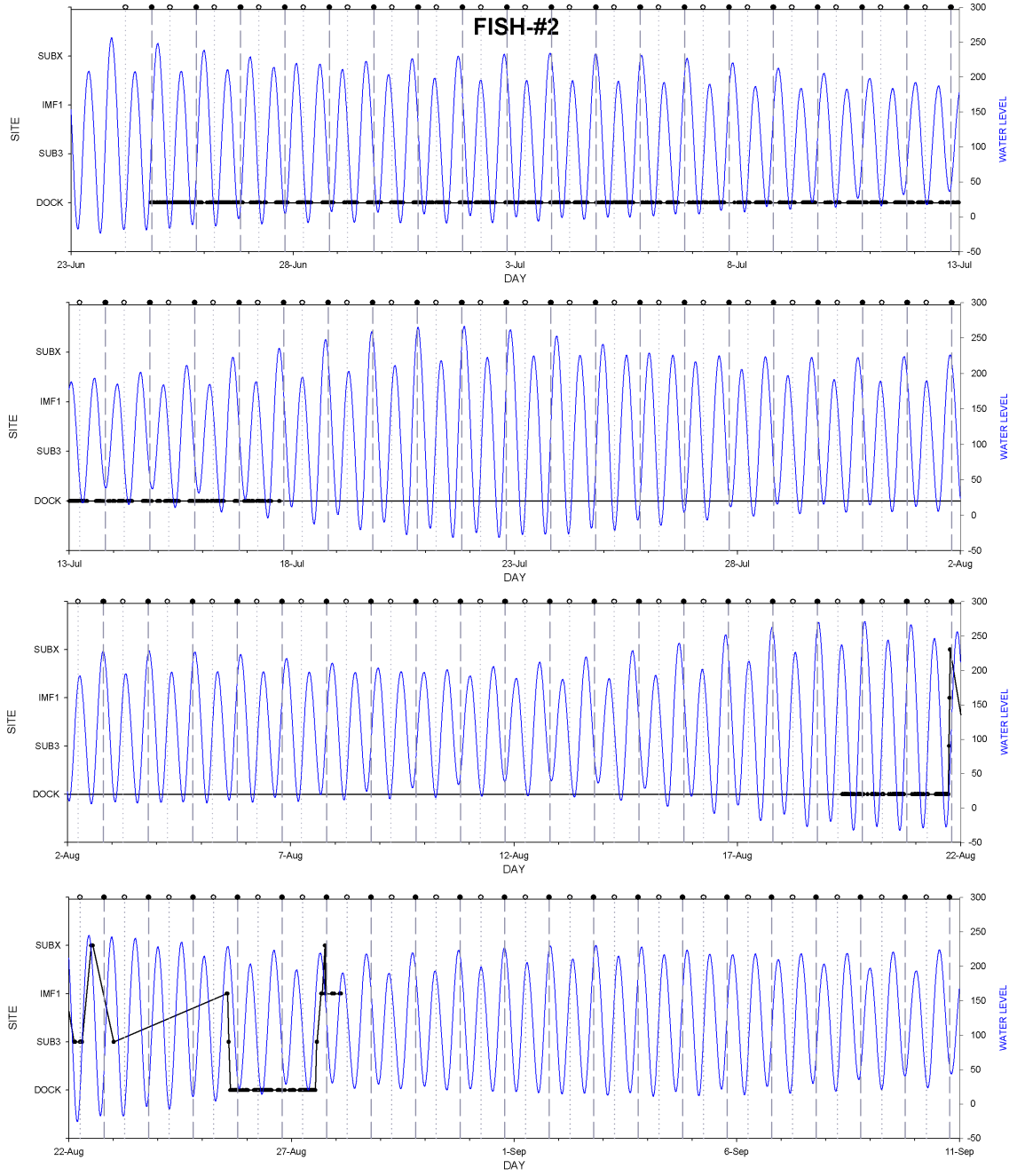
This section contains a set of time-series “fish-tracker” plots, which display movement patterns related to tidal and diel cycles. Tidestage and sunrise/sunset are overlaid onto each plot. The following is the caption that is applicable to all figures within this section, where “X” is replaced by the fish I.D.-#:

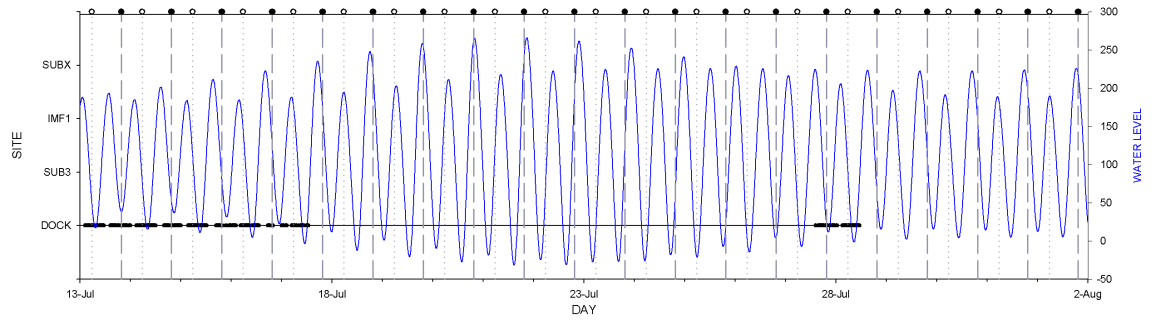
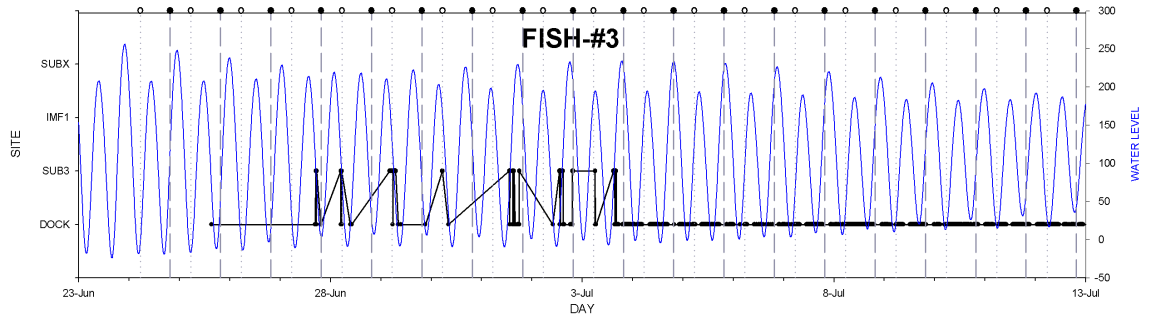
FISH-X: Individual fish detections (open circles) are plotted in a time series to indicate the location of a fish at any given point throughout the study period. Connecting lines between detections are drawn to show continuity between detections and should not be viewed as a direct pathway by the fish in its movements between any two sites. Sunrise (dotted vertical line), and sunset (dashed vertical line) times are indicated. Tidestage is represented by the sinusoidal line.

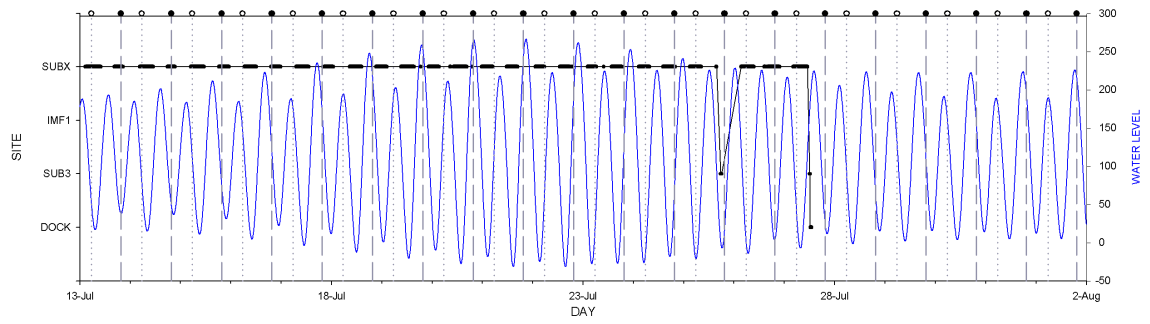
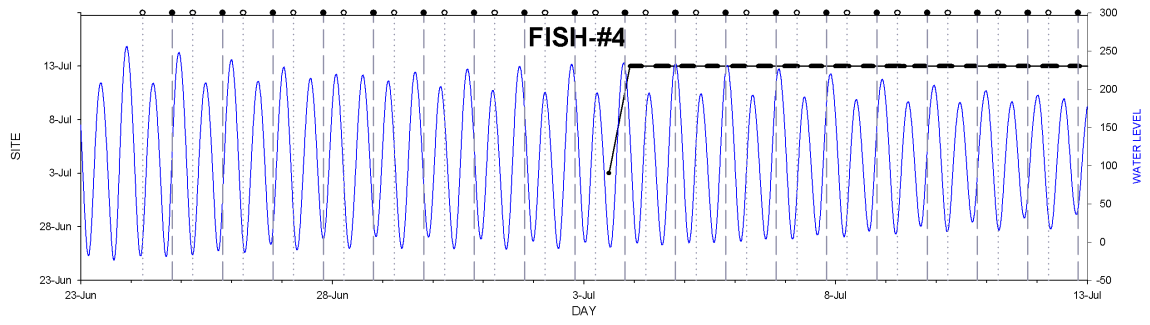
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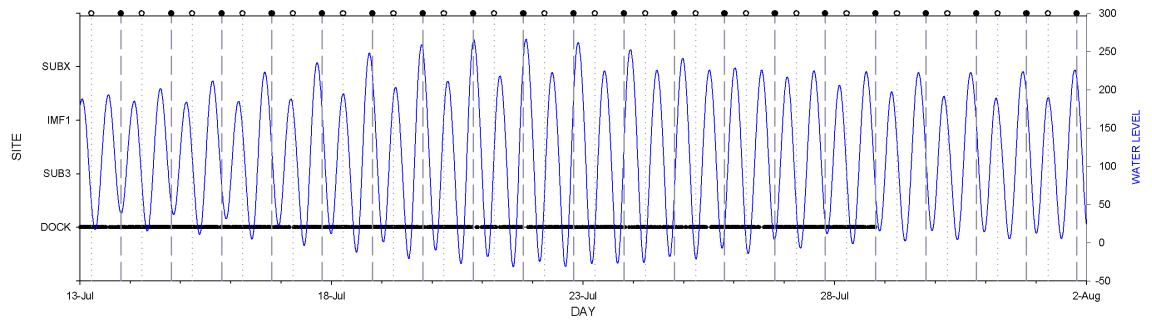
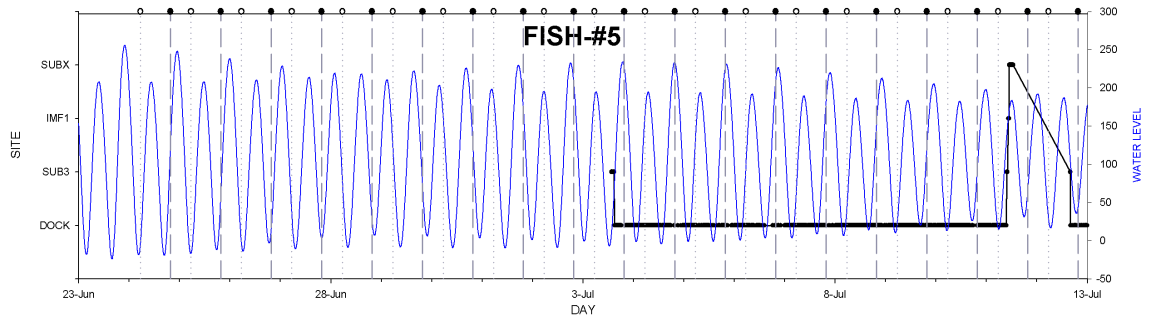
- *FISH-1, FISH-TRACKER, UPPER DUPLIN*
- *FISH-2, FISH-TRACKER, UPPER DUPLIN*
- *FISH-3, FISH-TRACKER, UPPER DUPLIN*
- *FISH-4, FISH-TRACKER, UPPER DUPLIN*
- *FISH-5, FISH-TRACKER, UPPER DUPLIN*
- *FISH-6, FISH-TRACKER, UPPER DUPLIN*
- *FISH-8, FISH-TRACKER, UPPER DUPLIN*
- *FISH-9, FISH-TRACKER, UPPER DUPLIN*
- *FISH-10, FISH-TRACKER, UPPER DUPLIN*

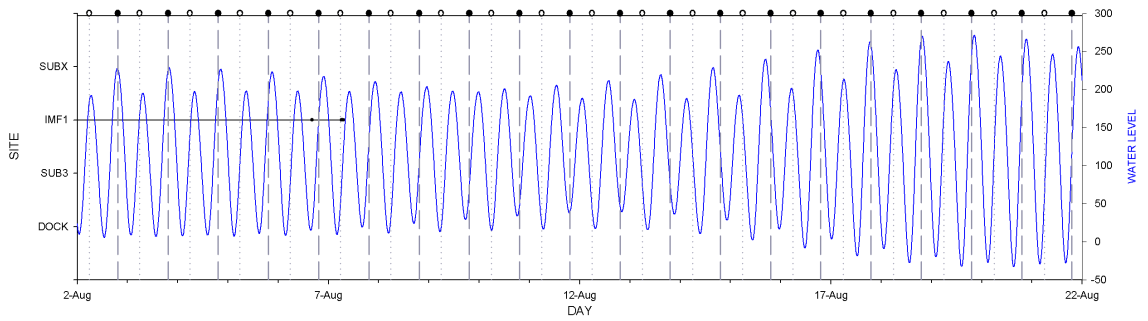
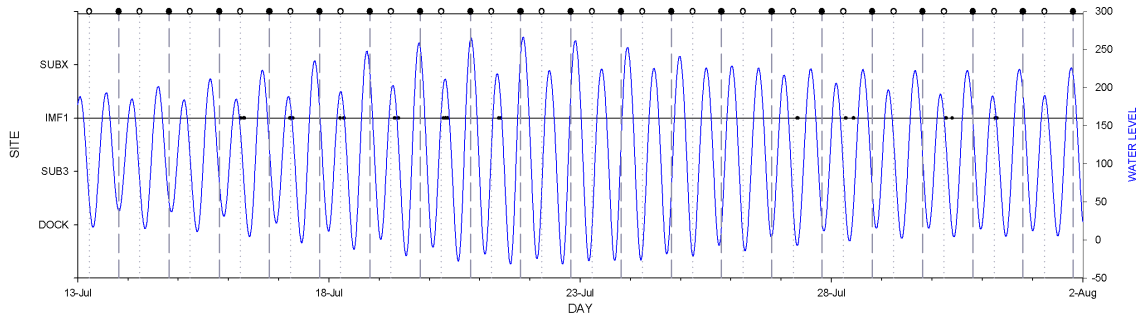
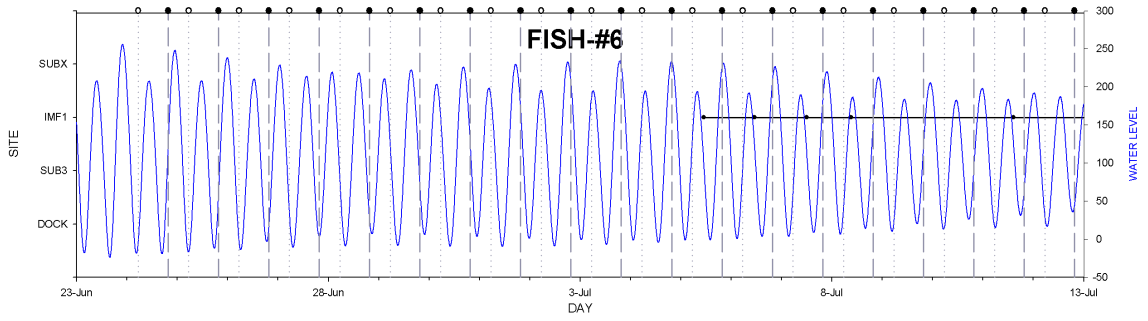


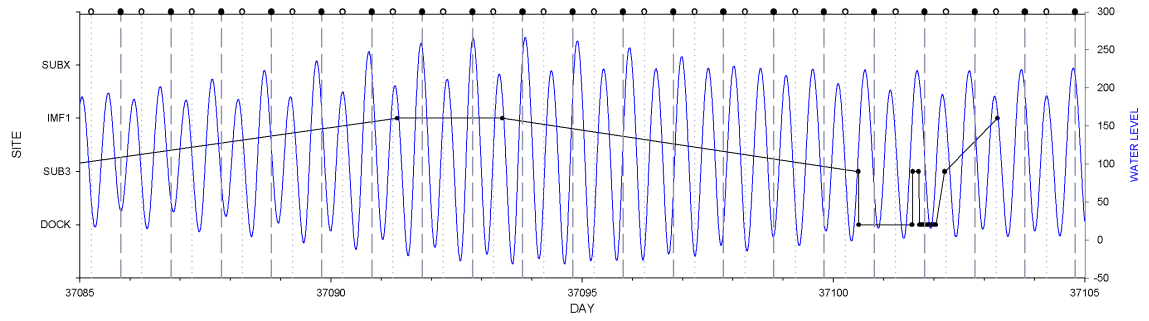
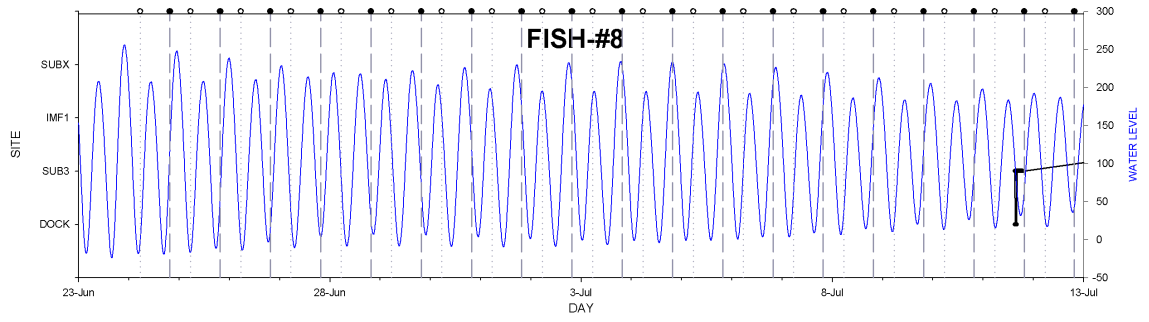


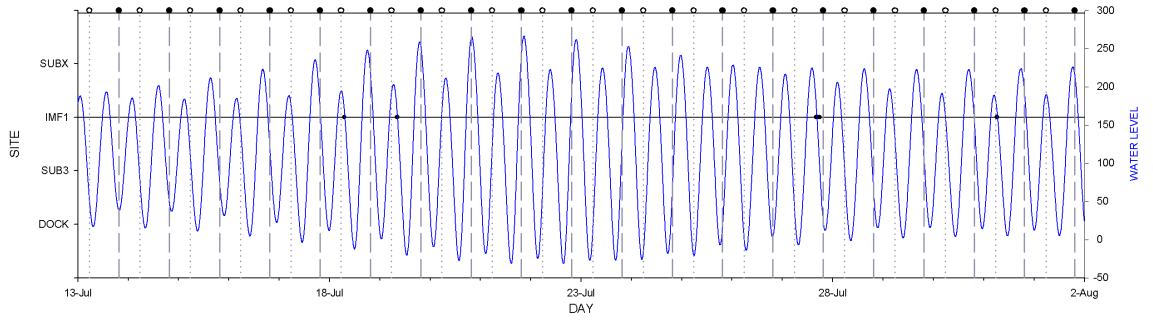
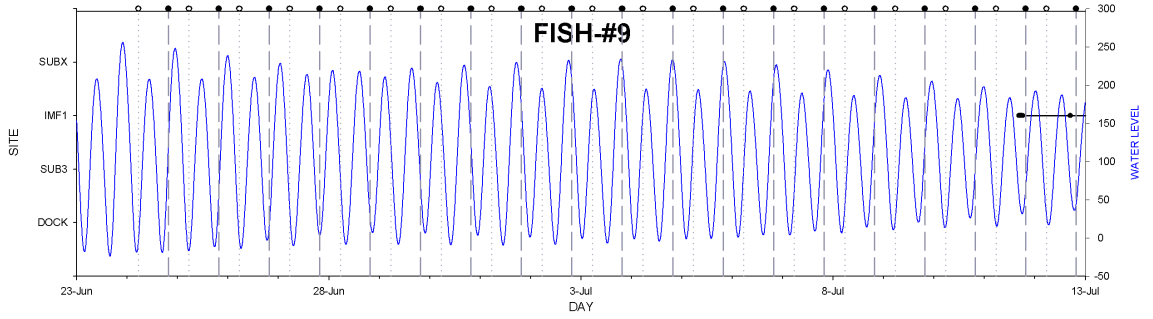


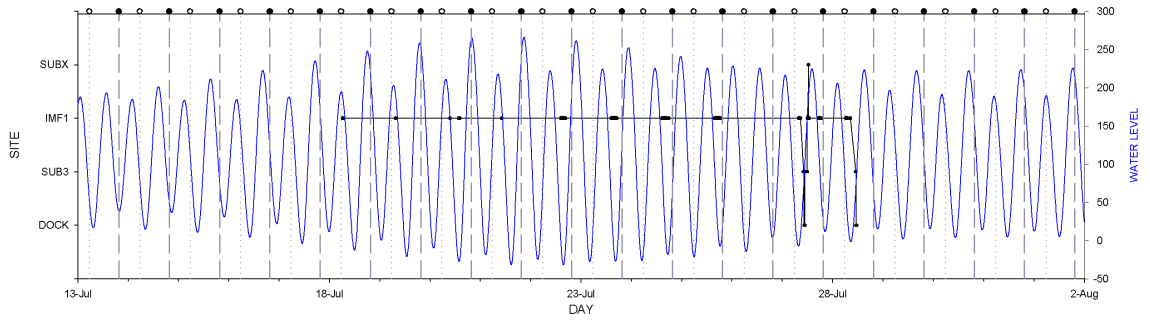
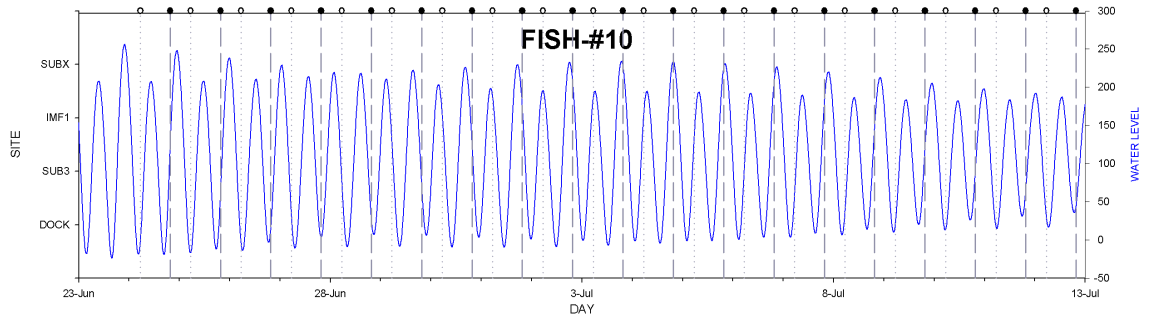












APPENDIX – C: SCATTER-PLOTS, UPPER DUPLIN, AUTUMN 2001.

This section contains a series of time-series scatter plots, which display movement and habitat use patterns for individual tagged fish used in the study. Onset times of high and low tides (exact midpoint between high and low tide overlay the plot to visually approximate the tide stage in which detections were observed. The following is the caption that is applicable to all figures within this section, where “X”s replaced by the fish I.D.-#:

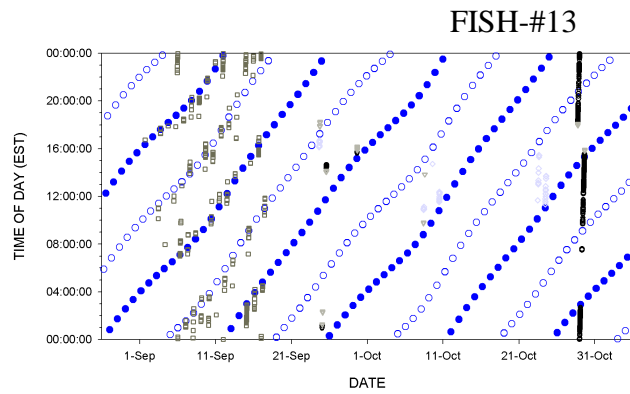
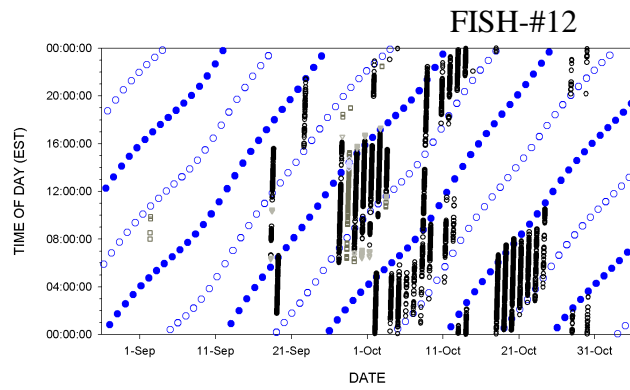
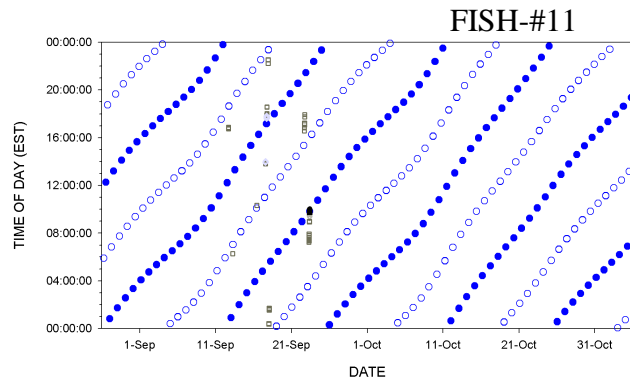
FISH-X: The individual scatter-plots show the overall tidal and pattern(s) of individual fish detections at each of the four sites plotted in a time series. Symbols (see below) are as follows: open circle=DOCK, open triangle=SUB3, open square=IMF1, open diamond=SUBX. Onset times for high tide (large, closed circles), and low tide (large, open circles).

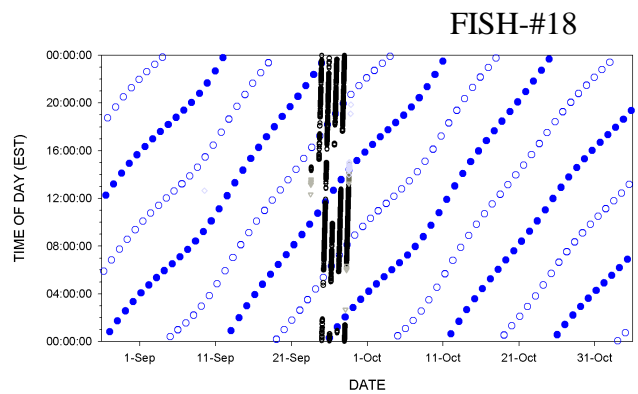
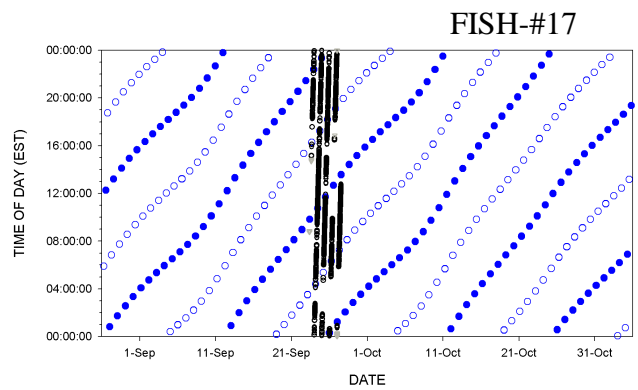
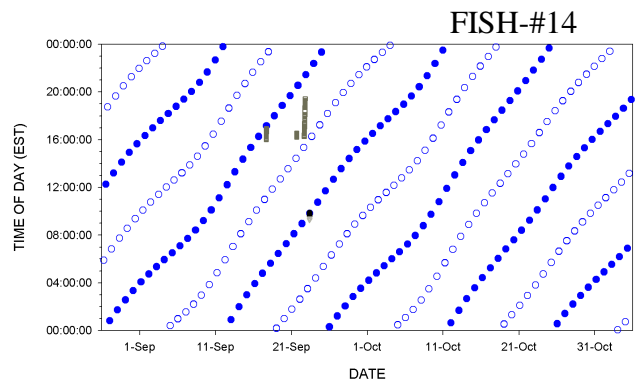
●	ONSET - HIGH TIDE
○	ONSET - LOW TIDE
○	OPEN/DOCK
▽	SUB3
□	IMF1
◇	SUBX

Legend of symbols used in “scatter”graphs for this section:

GRAPHS INCLUDED IN THIS SECTION, 3-PER PAGE (2 total pages)

- *FISH-11, SCATTER, UPPER DUPLIN*
- *FISH-12, SCATTER, UPPER DUPLIN*
- *FISH-13, SCATTER, UPPER DUPLIN*
- *FISH-14, SCATTER, UPPER DUPLIN*
- *FISH-17, SCATTER, UPPER DUPLIN*
- *FISH-18, SCATTER, UPPER DUPLIN*





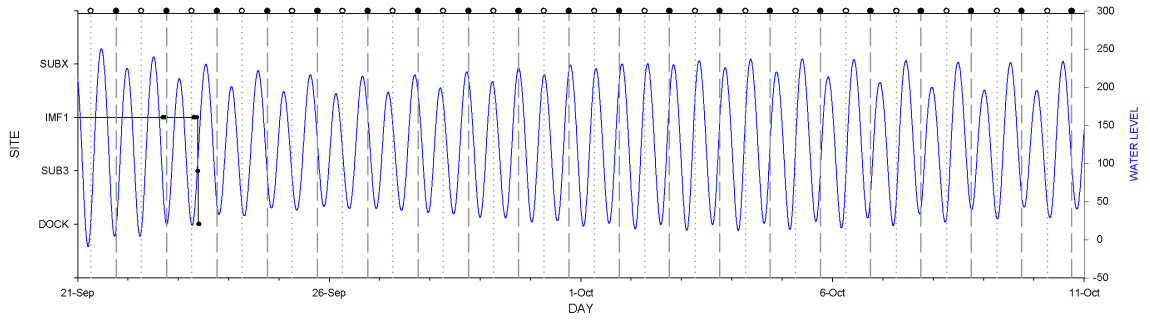
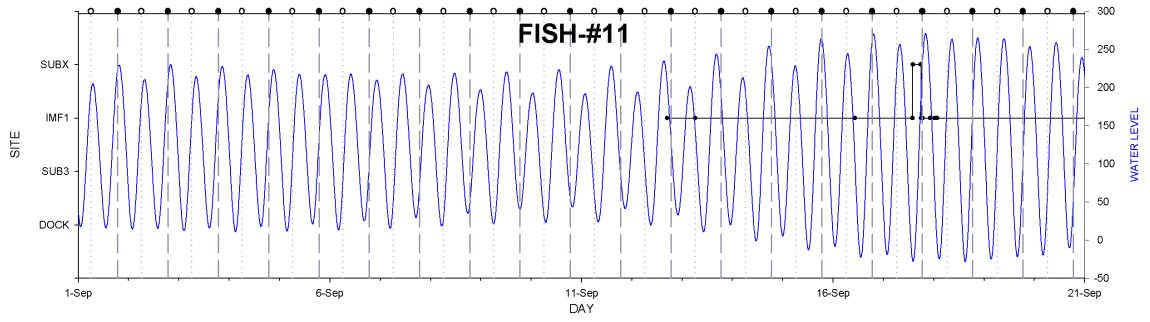
APPENDIX – D: FISH-TRACKER PLOTS, UPPER DUPLIN, AUTUMN 2001.

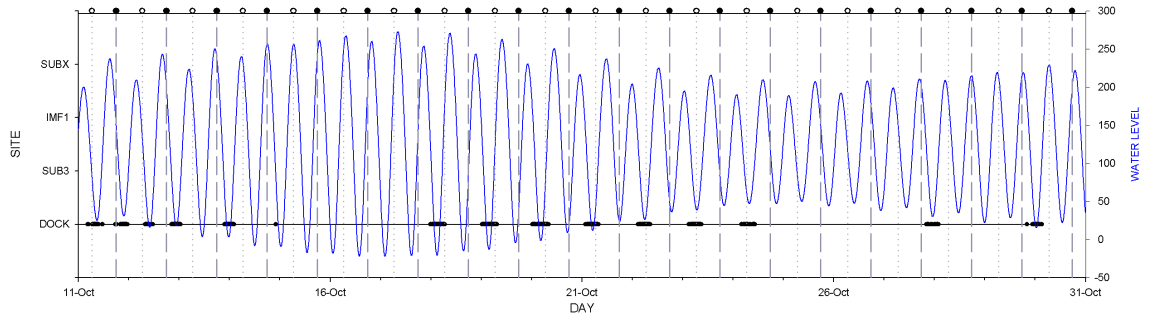
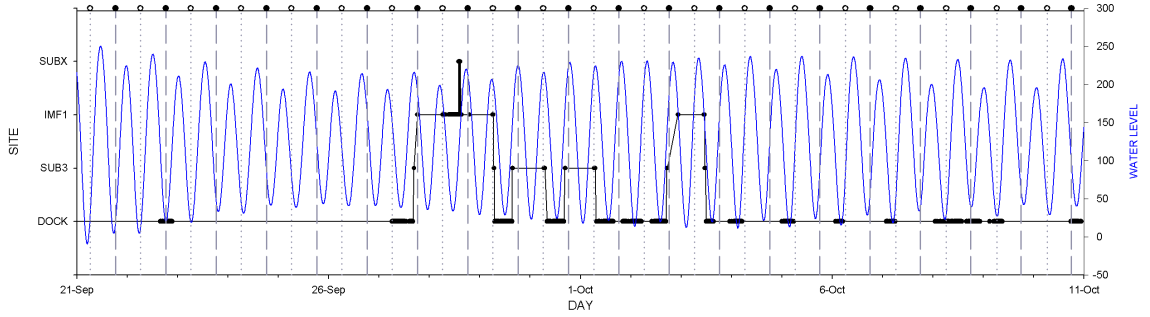
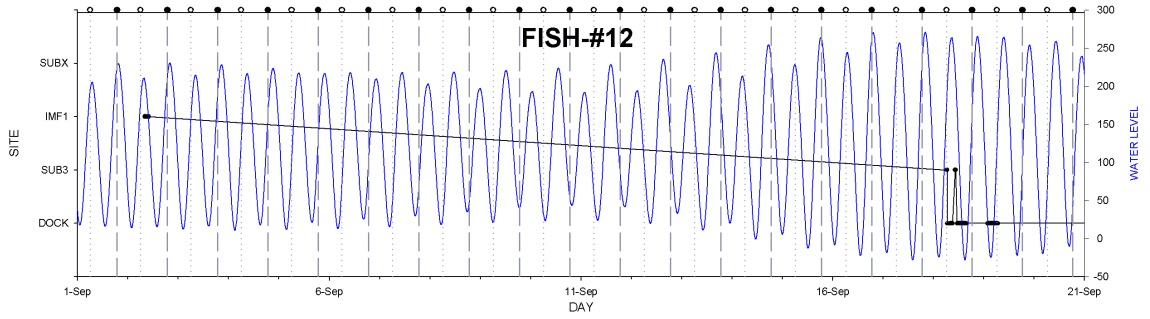
This section contains a set of time-series “fish-tracker” plots which display movement patterns related to tidal and diel cycles. Tidestage and sunrise/sunset are overlaid onto each plot. The following is the caption that is applicable to all figures within this section, where “X” is replaced by the fish I.D.-#:

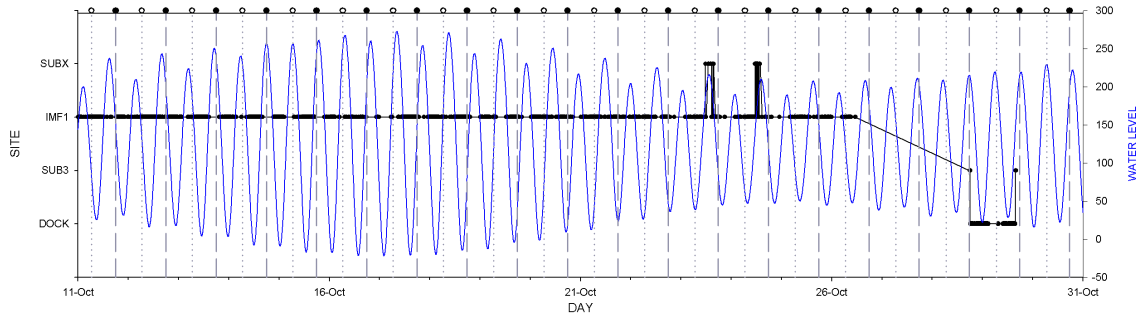
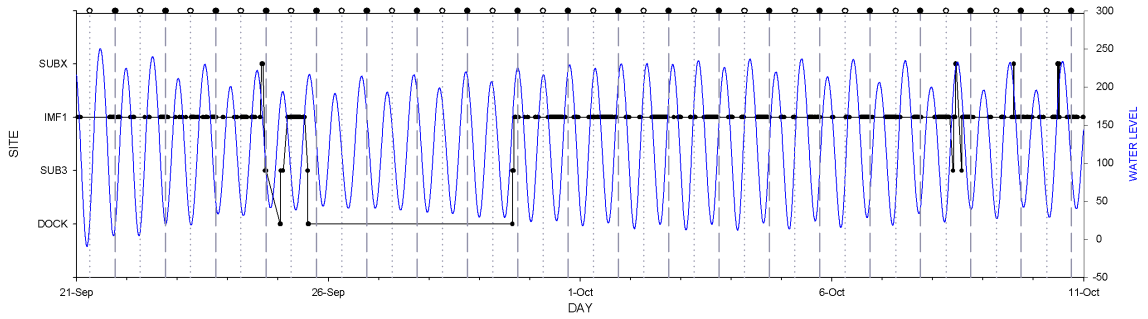
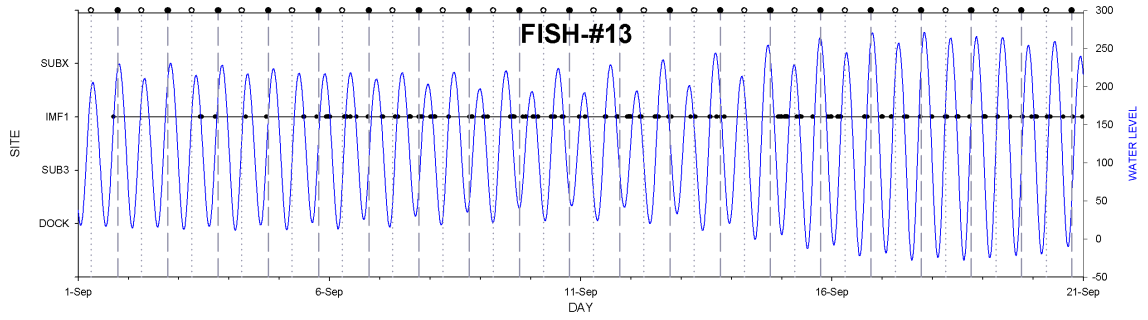
FISH-X: Individual fish detections (open circles) are plotted in a time series to indicate the location of a fish at any given point throughout the study period. Connecting lines between detections are drawn to show continuity between detections and should not be viewed as a direct pathway by the fish in its movements between any two sites. Sunrise (dotted vertical line), and sunset (dashed vertical line) times are indicated. Tidestage is represented by the sinusoidal line.

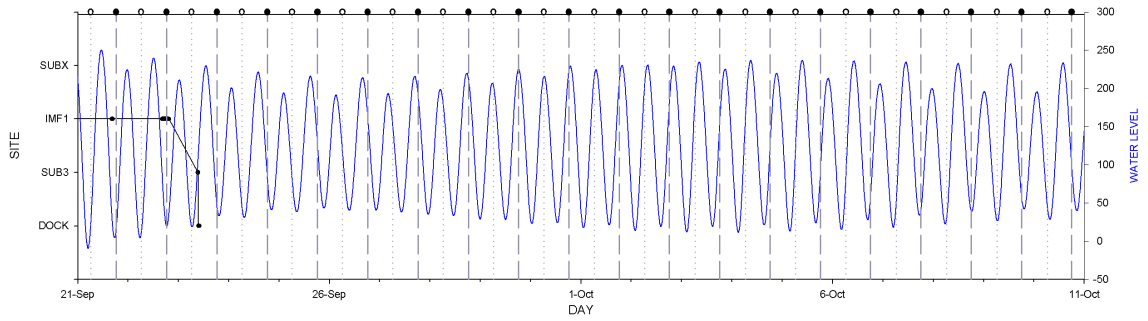
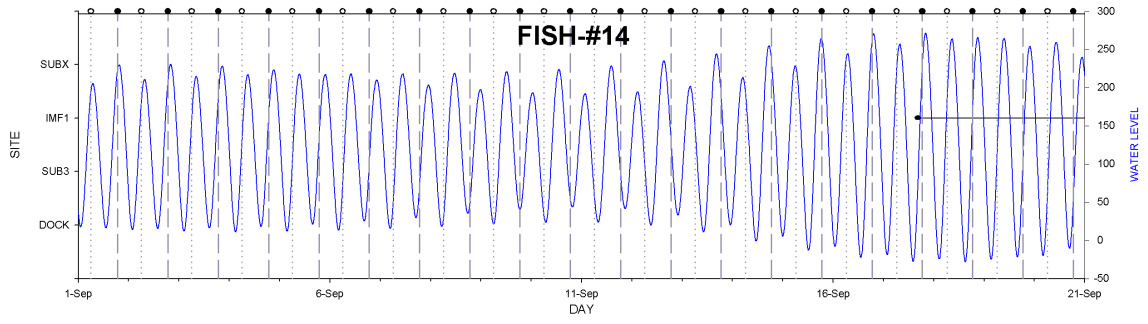
GRAPHS INCLUDED IN THIS SECTION, 1-PER PAGE (6 total pages)

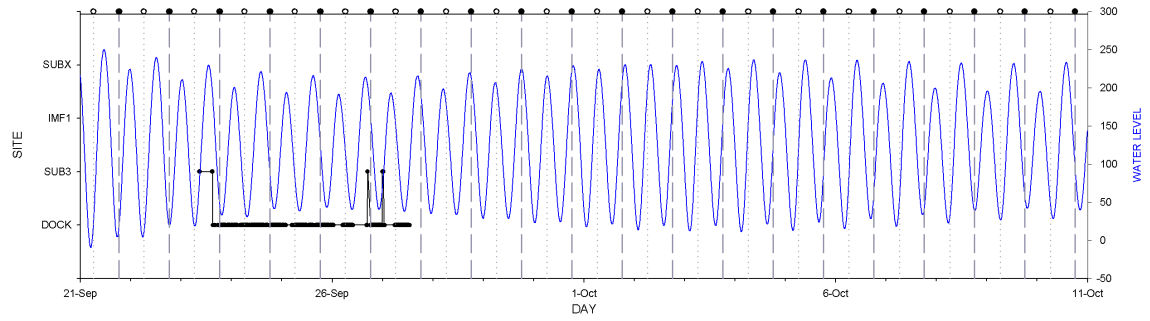
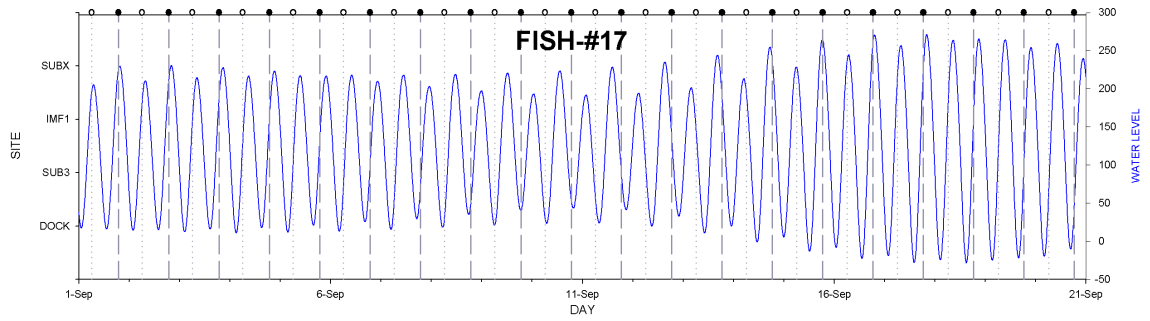
- *FISH-11, FISH-TRACKER, UPPER DUPLIN*
- *FISH-12, FISH-TRACKER, UPPER DUPLIN*
- *FISH-13, FISH-TRACKER, UPPER DUPLIN*
- *FISH-14, FISH-TRACKER, UPPER DUPLIN*
- *FISH-17, FISH-TRACKER, UPPER DUPLIN*
- *FISH-18, FISH-TRACKER, UPPER DUPLIN*

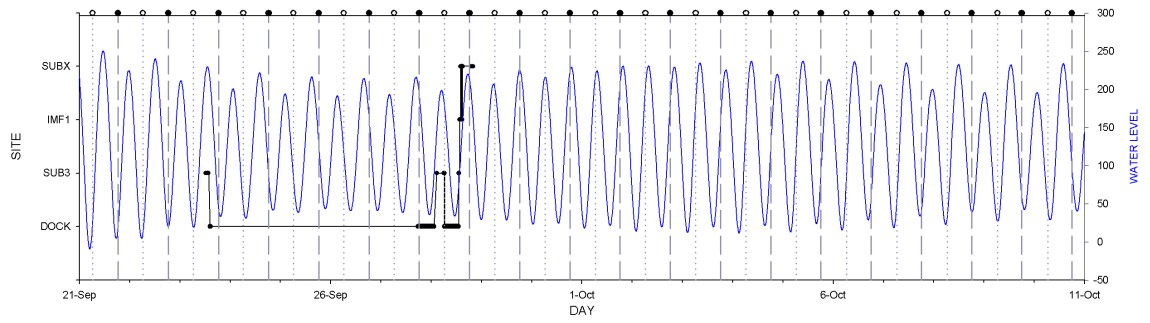
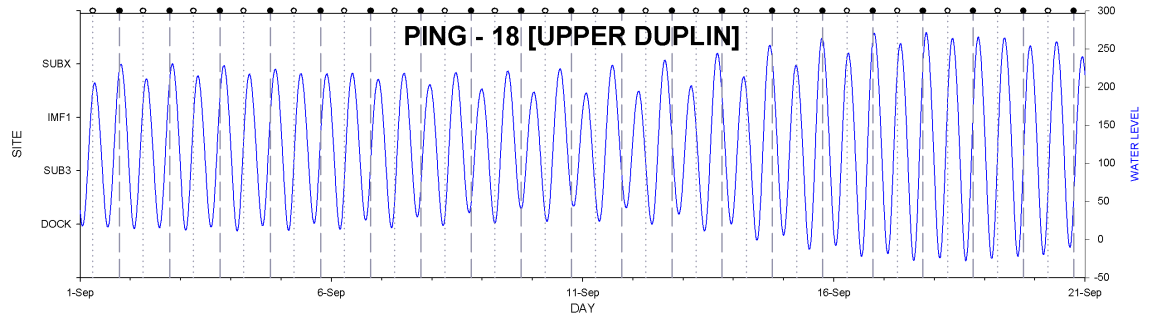












APPENDIX – E: SCATTER-PLOTS, STACEY CREEK, AUTUMN 2001.

This section contains a series of time-series scatter plots, which display movement and habitat use patterns for individual tagged fish used in the study. Onset times of high and low tides (exact midpoint between high and low tide overlay the plot to visually approximate the tide stage in which detections were observed. The following is the caption that is applicable to all figures within this section, where “X”s replaced by the fish I.D.-#:

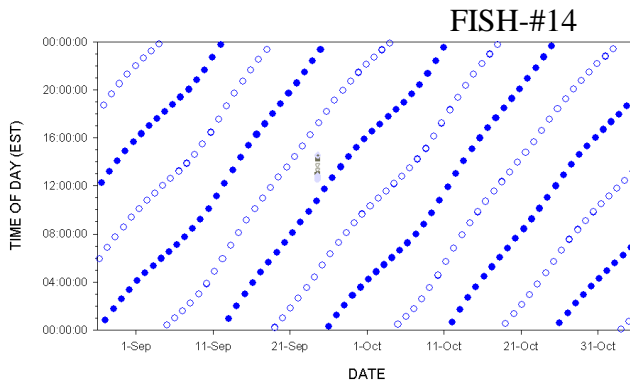
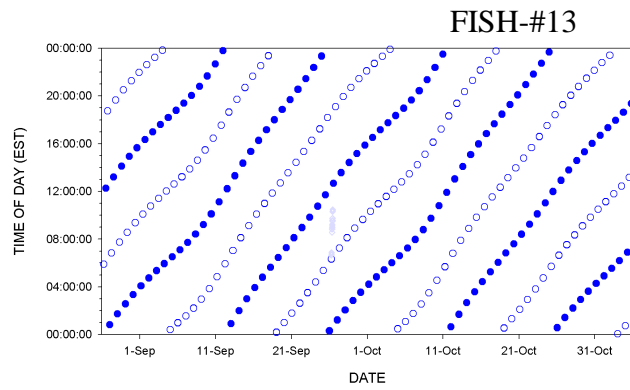
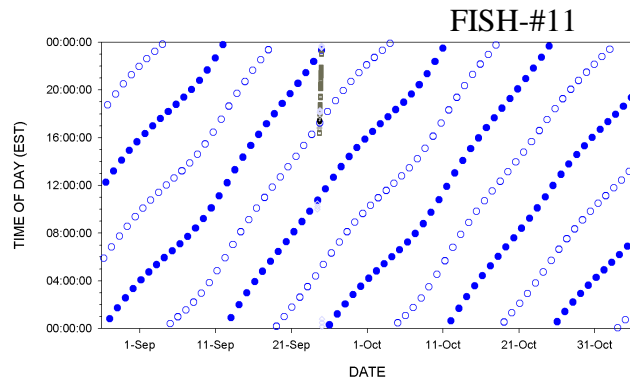
FISH-X: The individual scatter-plots show the overall tidal and pattern(s) of individual fish detections at each of the four sites plotted in a time series. Symbols (see below) are as follows: open circle=SC-UPPER, open triangle=SC-MID, open square=SC-LOWER, open diamond=SC-DUPLIN. Onset times for high tide (large, closed circles), and low tide (large, open circles).

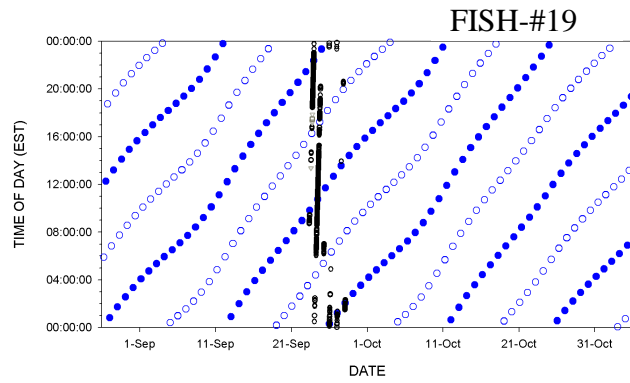
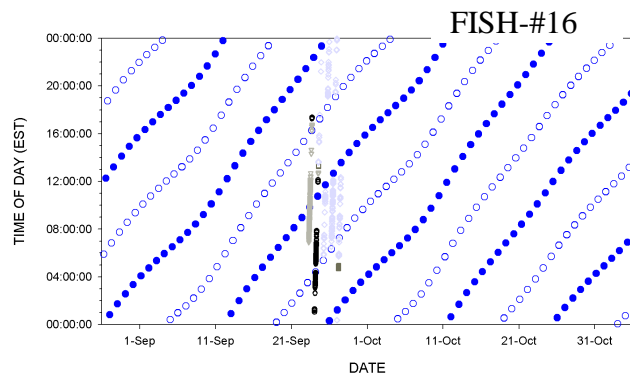
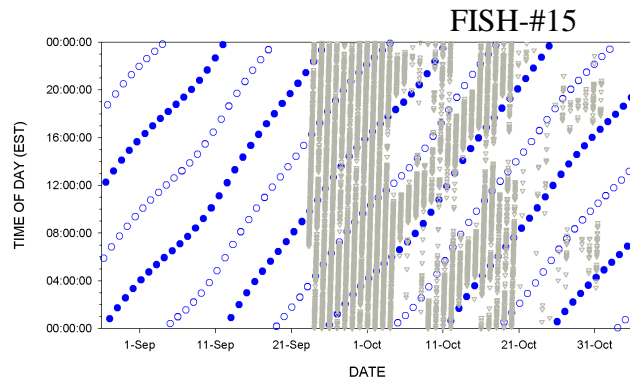
●	ONSET - HIGH TIDE
○	ONSET - LOW TIDE
○	SC-UPPER
▽	SC-MID
□	SC-LOWER
◇	SC/DUPLIN

Legend of symbols used in “scatter”graphs for this section:

GRAPHS INCLUDED IN THIS SECTION, 3-PER PAGE (2 total pages)

- *FISH-11, SCATTER, STACEY CREEK*
- *FISH-13, SCATTER, STACEY CREEK*
- *FISH-14, SCATTER SCACEY CREEK*
- *FISH-15, SCATTER, STACEY CREEK*
- *FISH-16, SCATTER, STACEY CREEK*
- *FISH-19, SCATTER, STACEY CREEK*





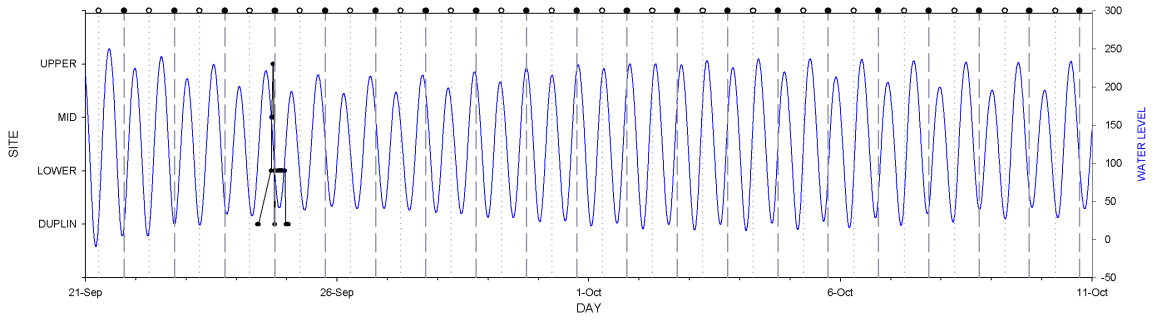
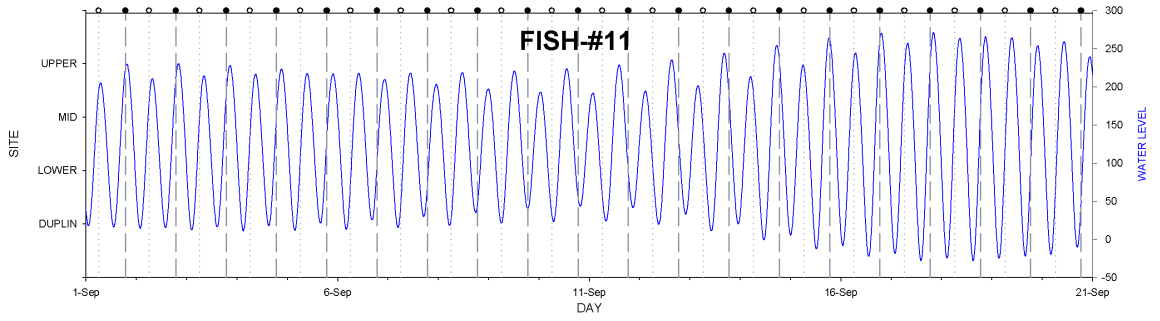
APPENDIX – F: FISH-TRACKER PLOTS, STACEY CREEK, AUTUMN 2001.

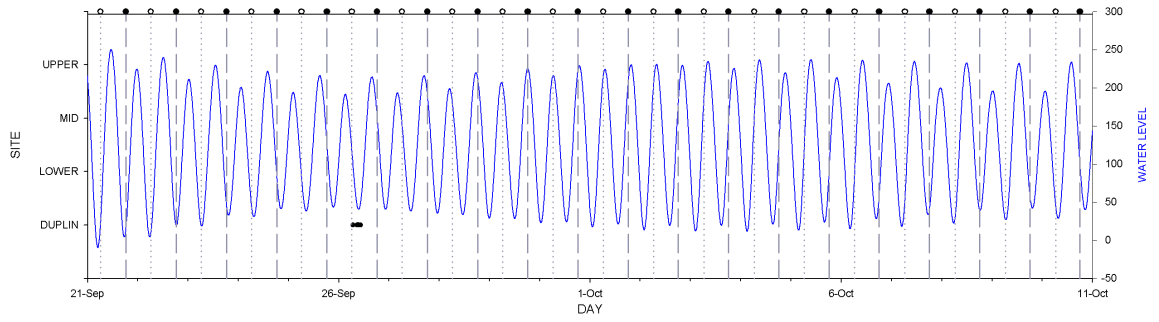
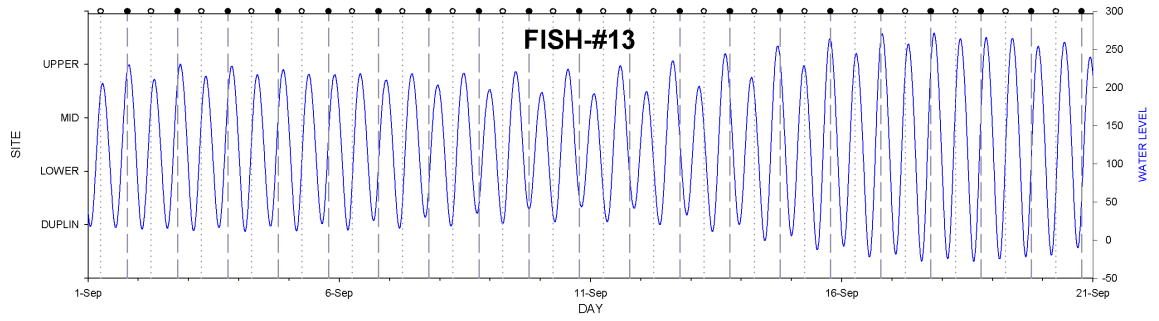
This section contains a set of time-series “fish-tracker” plots which display movement patterns related to tidal and diel cycles. Tidestage and sunrise/sunset are overlaid onto each plot. The following is the caption that is applicable to all figures within this section, where “X” is replaced by the fish I.D.-#:

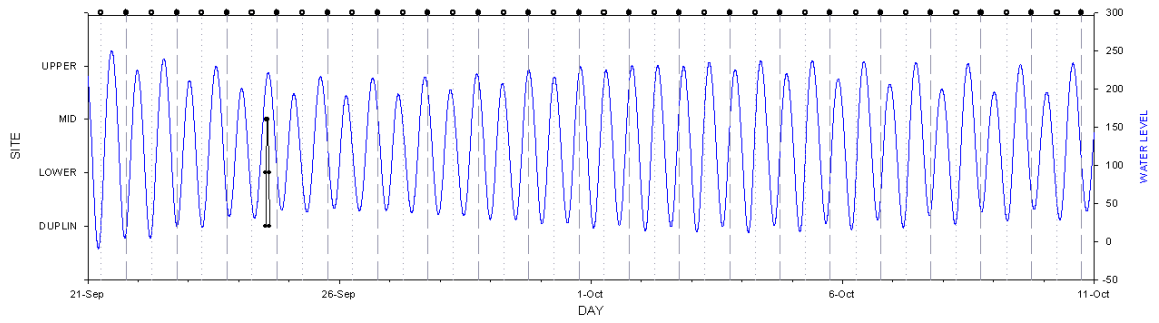
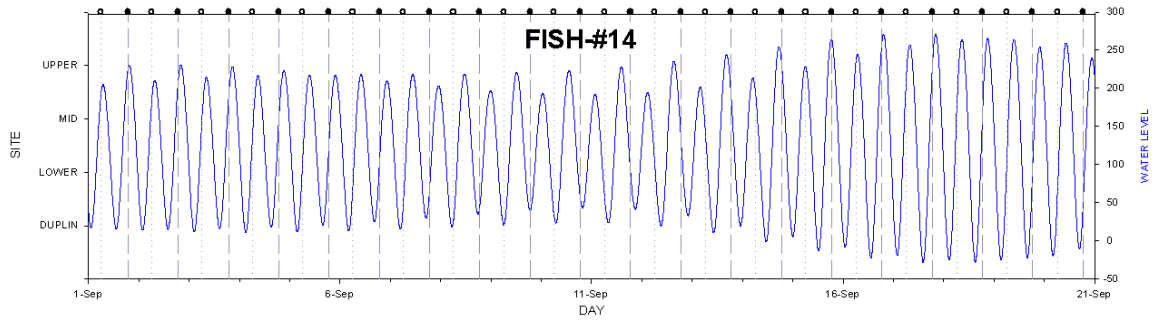
FISH-X: Individual fish detections (open circles) are plotted in a time series to indicate the location of a fish at any given point throughout the study period. Connecting lines between detections are drawn to show continuity between detections and should not be viewed as a direct pathway by the fish in its movements between any two sites. Sunrise (dotted vertical line), and sunset (dashed vertical line) times are indicated. Tidestage is represented by the sinusoidal line.

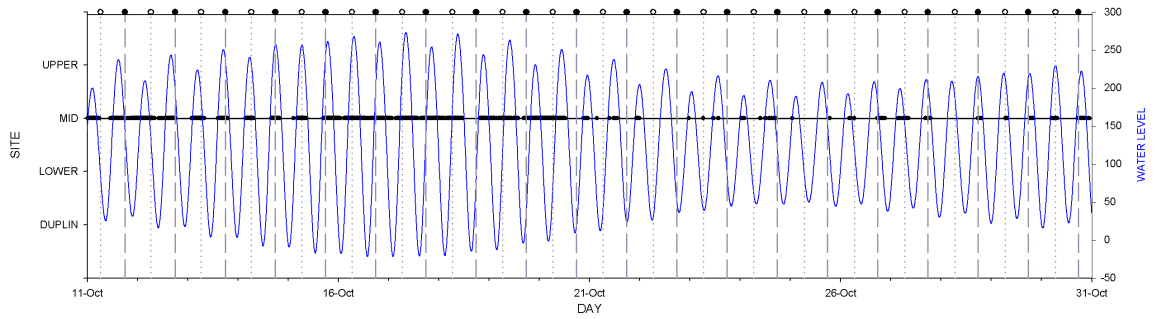
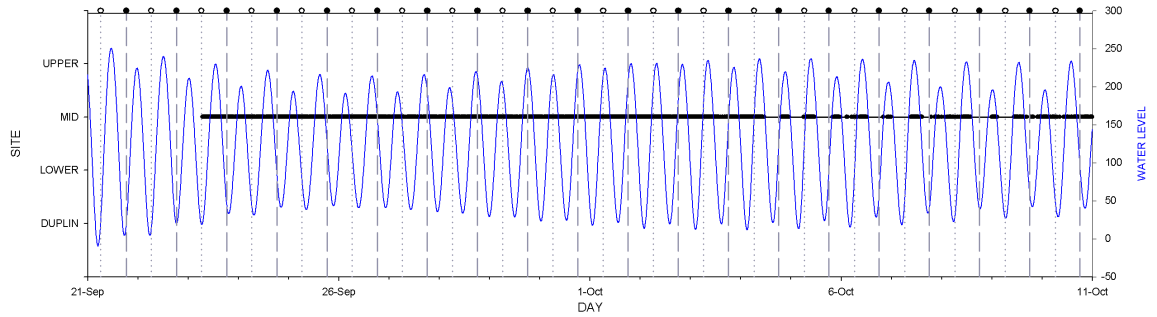
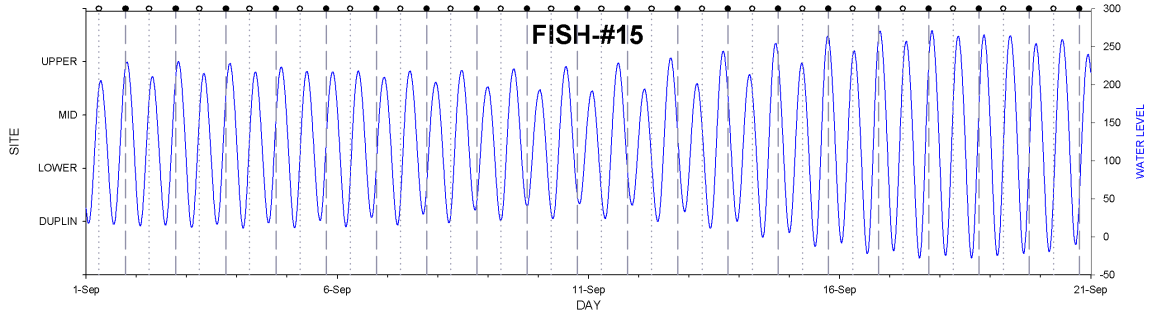
GRAPHS INCLUDED IN THIS SECTION, 1-PER PAGE (6 total pages)

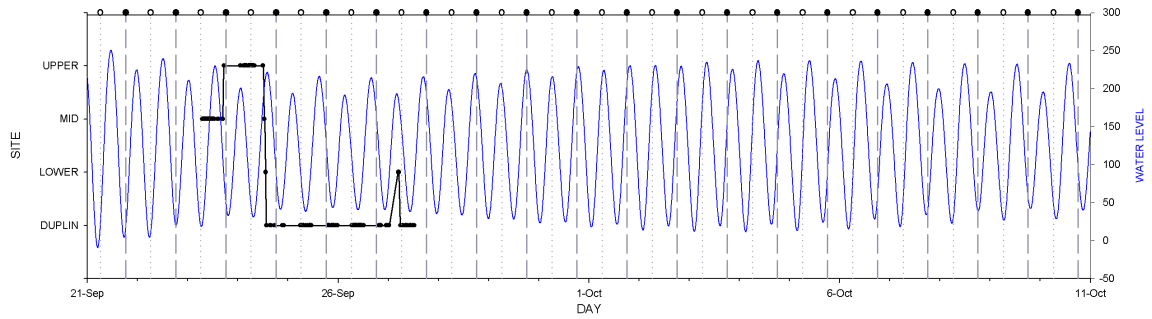
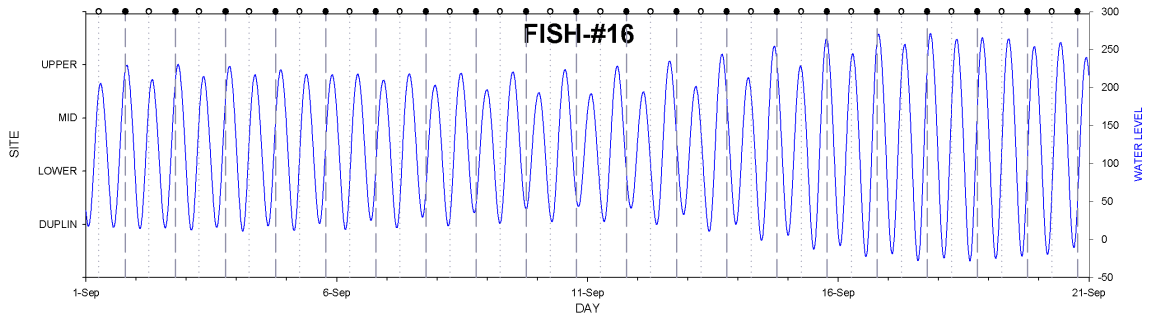
- *FISH-11, FISH-TRACKER, STACEY CREEK*
- *FISH-13, FISH-TRACKER, STACEY CREEK*
- *FISH-14, FISH-TRACKER, STACEY CREEK*
- *FISH-15, FISH-TRACKER, STACEY CREEK*
- *FISH-16, FISH-TRACKER, STACEY CREEK*
- *FISH-19, FISH-TRACKER, STACEY CREEK*

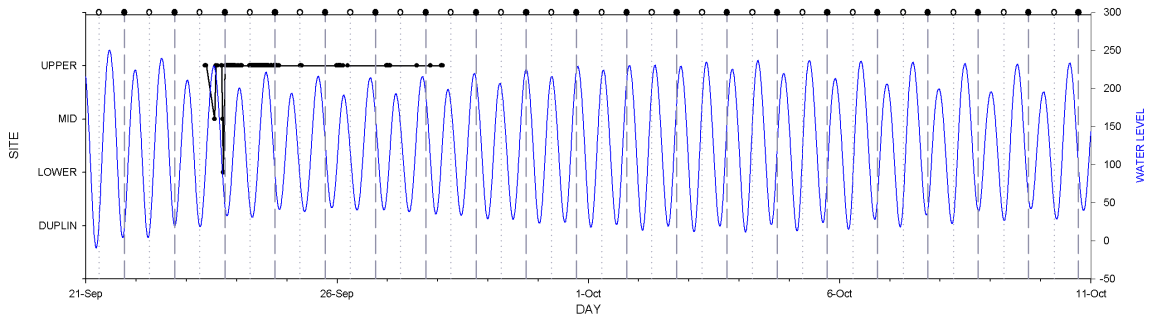
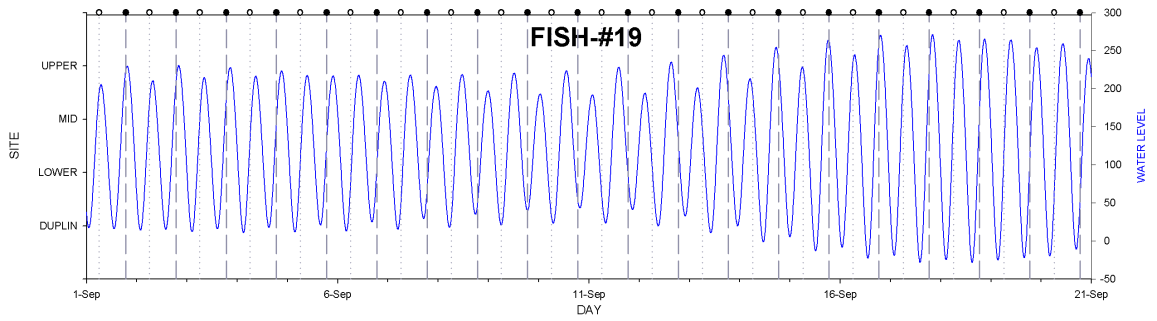












APPENDIX – G: SCATTER-PLOTS, UPPER DUPLIN, SUMMER-AUTUMN 2002.

This section contains a series of time-series scatter plots, which display movement and habitat use patterns for individual tagged fish used in the study. Onset times of high and low tides (exact midpoint between high and low tide overlay the plot to visually approximate the tide stage in which detections were observed. The following is the caption that is applicable to all figures within this section, where “X” is replaced by the fish I.D.-#:

FISH-X: The individual scatter-plots show the overall tidal and pattern(s) of individual fish detections at each of the four sites plotted in a time series. Symbols (see below) are as follows: open circle=DOCK, open triangle=SUB3, open square=IMF1, open diamond=SUBX. Onset times for high tide (large, closed circles), and low tide (large, open circles).

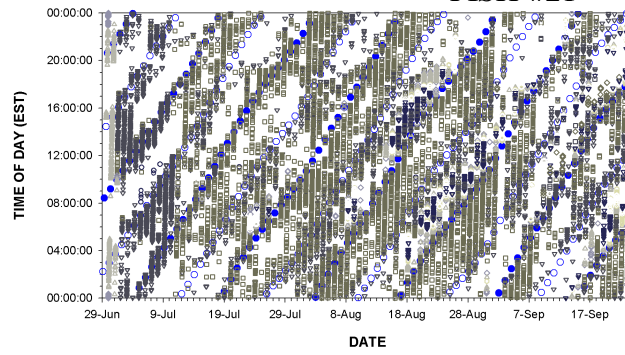
●	ONSET - HIGH TIDE
○	ONSET - LOW TIDE
○	DER1
▽	SUBR1
□	IMFR2
◇	DE2
△	SUB3
○	SUB2
○	SUB1
▽	DE1
□	IMFR1
◇	IMF1

Legend of symbols used in “scatter”graphs for this section:

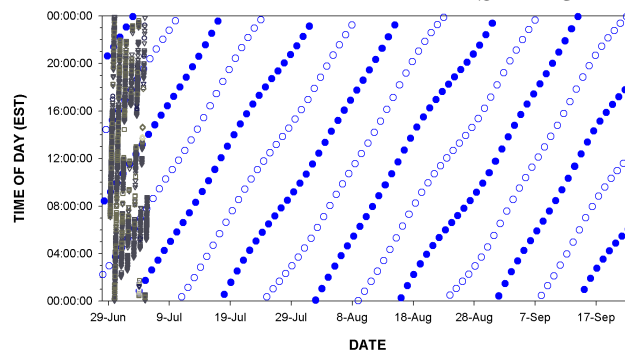
GRAPHS INCLUDED IN THIS SECTION, 3-PER PAGE (4 total pages)

- *FISH-21, SCATTER, UPPER DUPLIN*
- *FISH-23, SCATTER, UPPER DUPLIN*
- *FISH-24, SCATTER, UPPER DUPLIN*
- *FISH-25, SCATTER, UPPER DUPLIN*
- *FISH-26, SCATTER, UPPER DUPLIN*
- *FISH-27, SCATTER, UPPER DUPLIN*
- *FISH-28, SCATTER, UPPER DUPLIN*
- *FISH-30, SCATTER, UPPER DUPLIN*
- *FISH-31, SCATTER, UPPER DUPLIN*
- *FISH-33, SCATTER, UPPER DUPLIN*

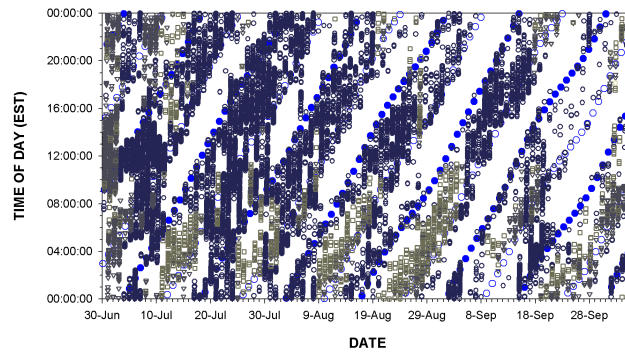
FISH-#21



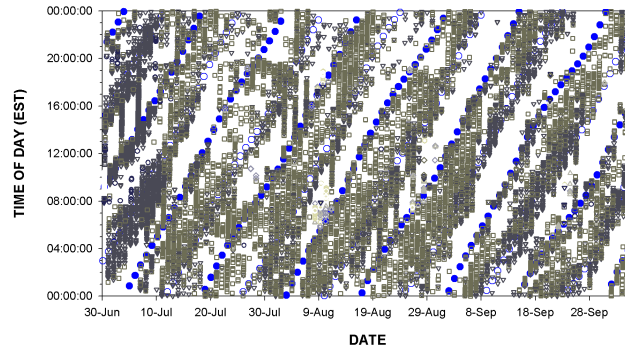
FISH-#23



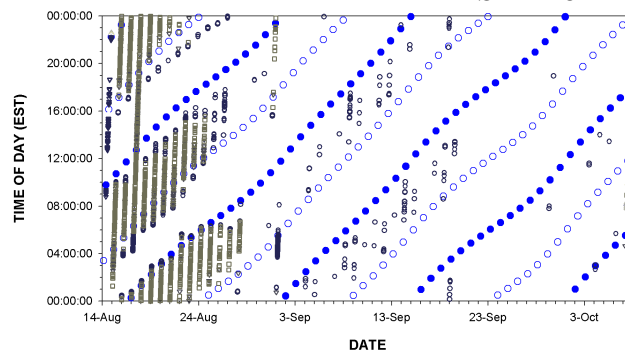
FISH-#24



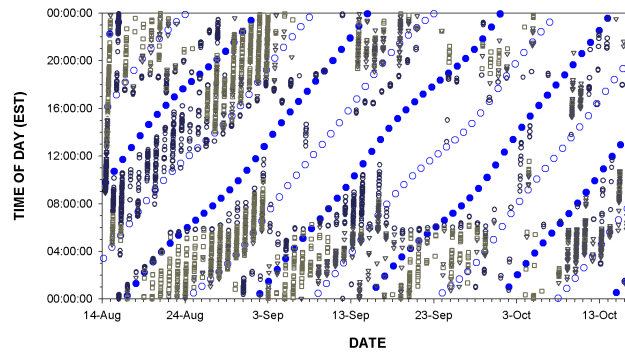
FISH-#25



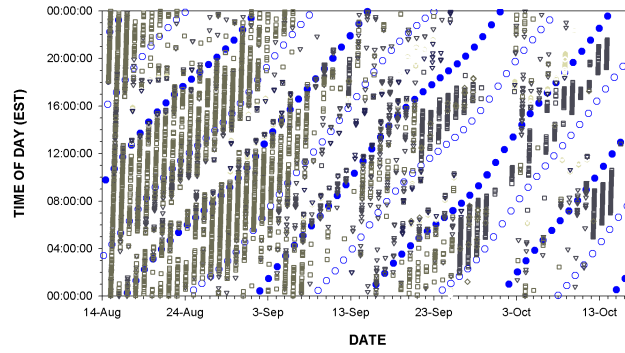
FISH-#26



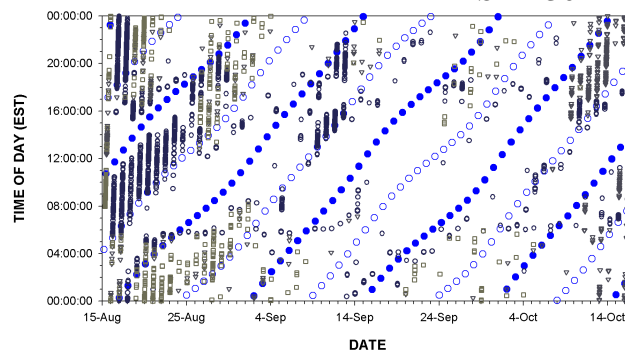
FISH-#27



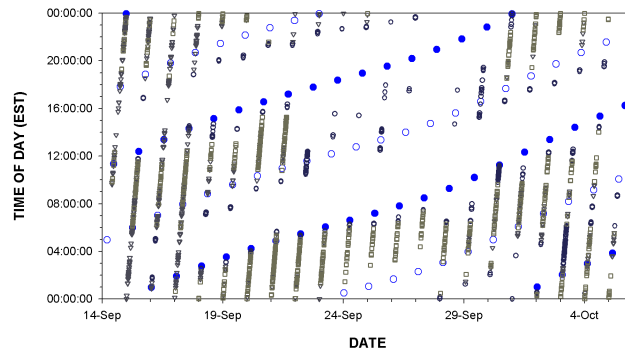
FISH-#28

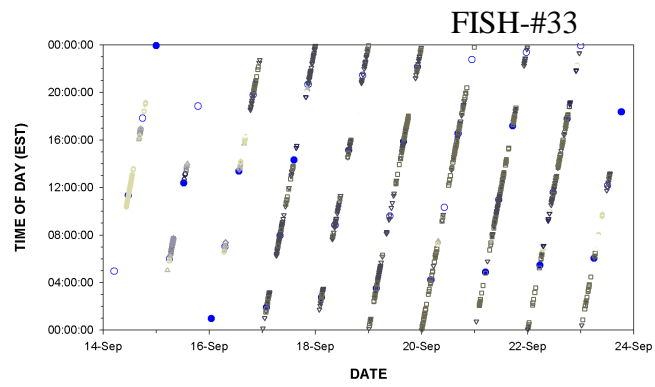


FISH-#30



FISH-#31





APPENDIX – H: FISH-TRACKER PLOTS, UPPER DUPLIN, SUMMER-AUTUMN
2002.

This section contains a set of time-series “fish-tracker” plots, which display movement patterns related to tidal and diel cycles. Tidestage and sunrise/sunset are overlaid onto each plot. The following is the caption that is applicable to all figures within this section, where “X”s replaced by the fish I.D.-#:

FISH-X: Individual fish detections (open circles) are plotted in a time series to indicate the location of a fish at any given point throughout the study period. Connecting lines between detections are drawn to show continuity between detections and should not be viewed as a direct pathway by the fish in its movements between any two sites. Sunrise (dotted vertical line), and sunset (dashed vertical line) times are indicated. Tidestage is represented by the sinusoidal line.

GRAPHS INCLUDED IN THIS SECTION, 1-PER PAGE (10 total pages)

- *FISH-21, FISH-TRACKER, UPPER DUPLIN*
- *FISH-23, FISH-TRACKER, UPPER DUPLIN*
- *FISH-24, FISH-TRACKER, UPPER DUPLIN*
- *FISH-25, FISH-TRACKER, UPPER DUPLIN*
- *FISH-26, FISH-TRACKER, UPPER DUPLIN*
- *FISH-27, FISH-TRACKER, UPPER DUPLIN*
- *FISH-28, FISH-TRACKER, UPPER DUPLIN*
- *FISH-30, FISH-TRACKER, UPPER DUPLIN*
- *FISH-31, FISH-TRACKER, UPPER DUPLIN*
- *FISH-33, FISH-TRACKER, UPPER DUPLIN*

