1CM 2007/ G:02

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Estuarine habitat dynamics and telemetered movements of three pelagic fishes: Scale, complexity, behavioral flexibility and the development of an ecophysiological framework.

John P Manderson, J. Pessutti, J Rosendale and B Phelan

Movements of fish across seascapes should reflect the ways the animals manage physiological and fitness requirements in the context of spatial habitat dynamics. From May, through September, 2006 we released ultrasonically tagged striped bass (*Morone saxatilis*; N=34), bluefish (*Pomatomus saltatrix*; N=29) and weakfish (*Cynoscion regalis*; (N=15) in a New Jersey, USA estuarine observatory (~900 hectares) in which moored ultrasonic receivers, hydrographic sensors and rapid hydrographic surveys allowed measurement of movement responses to habitat dynamics at space/time scales of 350m to 10km and 10mins to months. Age 1+ bluefish and striped bass used the observatory for a median of ~20d; weakfish and age-0 bluefish for ~36d. Individuals of all three species responded to habitat dynamics at two space/time scales. Individuals moved over distances of 350m to 2km at minute to 24hr time scales These fine scale movements within established home ranges frequently entrained tidal and/or day-night cycles. Animals often moved from deep habitats to ecotones defined by steep gradients in salinity and primary productivity or into marsh creeks. However, new cycles of movement within daily home ranges, home range expansions, or broad scale searches and establishments of daily home ranges in new locations occurred during episodes when seasonal temperature, freshwater and freshwater discharge, were high. Our observations suggest that animals adapted to meet fitness requirements on seascapes in which critical habitat resources are spatially dynamic show a high degree of behavioral flexibility. We develop an ecophysiological framework integrating behavioral physiology and spatial habitat dynamics to account for behavioral flexibility at individual, ontogenetic and species levels.

Keywords: Spatial habitat dynamics, fish movements, ecophysiology, ultrasonic telemetry

Contact Author: John P. Manderson: Behavioral Ecology Branch NEFC/NOAA/NMFS, James J. Howard Marine Sciences Laboratory, 74 Magruder Rd, Highlands, New Jersey 07732, USA [Tel : +1 732 872 3057, Fax : 732 872 3128, Email: john.manderson@noaa.gov]

Introduction

Movements of fish across seascapes should reflect the ways animals manage vital rates in the context of the spatial dynamics of important habitat resources affecting those rates. From late spring through the fall many commercially and recreational important fishes reside in shallow temperate estuaries in which environmental factors regulating, masking, or limiting rates of growth, survival and reproduction are highly dynamics in space and time at scales of meters to 10's of km's and minutes to months. On the east coast of the United States shallow temperate estuaries serve as important habitats for a variety of species including Striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*) and weakfish (*Cynoscion regalis*). While these species support large recreational fisheries supporting local human economies, they also enhance the transfer of energy and materials between pelagic and benthic compartments of estuarine food webs and, thus may play an central role in regulating the "stability" of estuarine ecosystems (Krause et al. 2003). A number of studies using traditional approaches have shown that these fishes are abundant in certain regions of estuaries during specific periods of the year (Jung and Houde 2003, Scharf et al. 2004). However traditional strategies using nets cannot repeatedly sample distributions of individual fish and key habitat features at temporal scales and spatial grains fine enough to resolve individual residency times and movement responses to spatial habitat dynamics. Repeated sampling of individuals and habitat resources at fine spatial and temporal scales should allow us to more accurately assess the potential importance of specific estuarine habitat resources and can serve as the basis for future assessments of functional habitat quality.

Recent developments in passive ultrasonic tracking technology allow investigators to establish relatively low cost "acoustic observatories" in marine and estuarine systems in which relatively small fishes can be individually tagged with ultrasonic tags and released (e.g. Heupel et al. 2004, Dresser and Kneib 2007). These observing systems enable investigators to collect data describing movement patterns at spatial scales of 100's meters to 100's km's and temporal scales of minutes to years, and have begun to revolutionize our understanding of patterns of movement, and habitat use of fish. Observatories containing sensors and surveys measuring spatial and temporal variation in potentially important biotic and abiotic environmental variables well known to affect fish physiology, fitness and thus habitat selection at space and time scales matching movement data present opportunities to develop hypotheses about ecological responses to environmental heterogeneity. These systems should allow us to better understand the functional characteristics of areas where animals establish home ranges as well as the extrinsic factors driving relocations of individual home ranges and migration.

In this paper we present preliminary results of the first year of a two year ultrasonic telemetry study of the movements and habitat use of age-0 and age 1+ bluefish, age 1+ striped bass, and age 1+ weakfish in a small estuarine system with characteristics typical of many riverine estuaries in the northeast coast of the United States. We use descriptive and statistical analysis to determine estuarine residency time, and the potential effects of the spatial dynamics of important estuarine habitat gradients on movement patterns at diel to seasonal time scales. We develop an ecophysiological framework that integrates behavioral physiology and spatial habitat dynamics to account for the behavioral flexibility at individual, ontogenetic and species levels apparent in the movement data.

Materials and Methods

Study Area

Movements and habitat use of age-0 and age 1+ bluefish, age 1+ striped bass, and age 1+ weakfish were examined using passive ultrasonic telemetry in the Navesink River, New Jersey, USA (Fig. 1). The Navesink River is a small tributary of the Hudson Raritan estuary with characteristics typical of riverine systems in the northeastern USA. The Navesink extends ~12 km east from the confluence with its primary freshwater source, the Swimming River, to the Shrewsbury river and Sandy Hook Bay which connects the system to the Atlantic ocean. The river is approximately 1000 hectares in surface area, 1.5 km wide at it's widest point and has a partially dredged channel ~4 m deep at mean low water (MLW) along its axis. Deep habitats are located in the main channel of the lower river (Fig. 1, location A; max. depth~ 6m), in the middle river (location B; max depth ~7m), and in the upper river (Location C; max depth ~ 9 m). Semidiural tides average 1.4 m in the system and salinities range from as low as 0.08‰ at the river head to ~27‰ at the rivers mouth. Tidal currents are flood dominated and attenuate in the middle and upper river which is generally deeper [$\bar{x}$ depth (D) = 1.5 m at MLW], has finer grained sediments, and more vegetation (*Ulva lactuca*, *Gracilaria* spp.) than the lower river ($\bar{x}$ D = 1.0 m at MLW). In the lower river, channels are flanked by sandbars and coves vegetated with sea lettuce and eelgrass. Many of these coves and other small tributaries of the river are fringed with *Spartina alterniflora* and *Phragmites* marsh.

Components of the estuarine observatory

Ultrasonically tagged fish were detected using an array of 30 omnidirectional ultrasonic receivers (Vemco VR-2) moored 1 meter above the bottom throughout the study area (Fig. 1). Each mooring consisted of anchor, an ultrasonic receiver (model VR2, Vemco Ltd., Shad Bay, Nova Scotia), a lobster float located 1 meter above the receiver, and a surface float connected with low stretch, 9,800-lb test line (Amsteel, Samson Rope Technologies, Ferndale, WA). The nearest neighbor distance between moorings averaged 498 meters (SD=138, Range 216-788). We deployed three receivers that served as "gates" to Sandy Hook Bay, the Shrewsbury River, and the oligohaline portion of the Swimming River. The receivers continuously "listened" for coded ultrasonic transmitters (Vemco Ltd.) from May 15 through October 3, 2006.

Habitat characteristics were measured continuously with moored hydrographic instruments (Fig 1) as well as frequent mobile hydrographic surveys. The moored instruments measured water characteristics ~ 20 cm above the bottom at 20 minutes intervals throughout the study and included StarOdi temperature, salinity, pressure sensors (N=3); YSI temperature, salinity, pressure and dissolved oxygen sensors (N=3); and an Andreaa RCM-9, which measured current speed and direction, temperature, salinity, pressure, and optical backscatter. One StarOdi and one YSI sensor were moored in the lower, middle and upper portions of the river while the RCM-9 was deployed in a deep channel connecting the lower and middle river which serves as the pathway for Sandy Hook Bay water which is typically cooler and more saline (Chant and Stoner 2001, Fugate and Chant 2005).

Mobile hydrographic surveys were performed on a 19 ft vessel ~ once per week using an onboard computer system that integrated a geographic information system (GIS) with a global positioning system (GPS), a Hydrolab Datasonde probe with temperature and salinity sensors mounted 0.5m below the surface, and a Seabird SBE-25 CTD with temperature, conductivity, pressure, dissolved oxygen, PAR, turbidity (NTU), and flourometer sensors. Data collected by the GIS/GPS, and the Hydrolab datasonde were continuously recorded at 1 second intervals throughout each cruise. During each cruise we performed cross-sectional transects of the river that intercepted all receiver moorings. CTD casts were performed to profile the water column at each mooring. After completing the cross-sectional transects, we often performed a single axial transect of the river in the channel. Simultaneous hydrographic and small mesh gill net (46 meters long; 6- 8 meter panels: 4 cm, 2 cm, 1cm , 1.3 cm, 0.6 cm, 2.5cm) surveys for prey fishes were performed along with passive acoustic tracking (unpubl. data) in 2007 in the deep habitat and salinity front in the upper river (Locations C & D, Fig 1.) near the end of sequential daytime flood and ebb tides. The same mobile hydrographic survey equipment described above was used to identify the salinity front, locations for net deployments and to map the structure of important gradients during net sampling. Three replicate nets were deployed in the deep habitat and in the vicinity of the salinity front and fished for one hour. Seven temperature probes (Onset TidbiT; ±0.2 ˚C) positioned 1 meter apart on a line with an anchor and surface buoy were periodically deployed in the deep habitat to record temperatures across the depth profile. Daily freshwater discharge measured at the USGS station in the swimming river (http://nwis.waterdata.usgs.gov/nj/nwis/monthly/?site_no=01407500&agency_cd=USGS) was also used in the analysis of movement patterns.

Fish tagging

Striped bass, age 1+ and age-0 bluefish and weakfish were collected by hook and line within the observatory based on seasonal availability from May 14 to September 8, 2006 and returned to the laboratory for tagging (Table 1) . In the laboratory, fish were anaesthetized with Aqui-S (Aqui-S New Zealand Ltd., Lower Hutt, New Zealand) at concentrations of 54 mg/L which provided rapid anaesthesia induction times (mean = 3.3 min; n=127). Once a fish was anaesthetized, we made an incision dorsal to the ventral midline with a sterile scalpel, and a sterilized individually-coded ultrasonic transmitter was inserted into the body cavity (V9-6L 69 kHz with a 40-120 second repetition rate; 9mm x 20mm, 2g in water, 83 day battery life; Vemco Ltd, Halifax, Nova Scotia Canada). We used non-absorbable monofilament nylon sutures (Ethilon® 3-0 and 4-0 with FS-1 cutting needle, Ethicon, Somerville, NJ) in a simple interrupted suture pattern to close incisions. Incisions were closed with two or three sutures. Each fish was then measured for length (mm), and two individually numbered anchor tags were inserted into the dorsal musculature. Recovery of fish required 3 to 9 min. Fish were placed in continuous flow-through tanks (2.5 m diam x 0.35 m deep) supplied with ambient seawater pumped from Sandy Hook Bay and closely monitored for at least 2 hrs after surgery (but less than 48 hrs) before they were released into the estuarine observatory. Fish were released at randomly selected locations throughout the observatory to determine whether initial movements of tagged fish reflected active or passive habitat selection. Less than 5 individuals of a species class were released per week in order to expose each class to the widest possible range of estuarine conditions.

Striped bass, weakfish and bluefish (N> 5 for all species classes) subjected to the surgical implantation of ultrasonic tag replicas showed exceptional survival for as long as a year in the laboratory (Phelan and Rosendale, unpublished data). None of the striped bass, weakfish and age-1+ bluefish tagged with replica tags died in <120 days. Several age-0 bluefish < 170mm died following the implantation of replica tags. As a result, age-0 bluefish implanted with active ultrasonic tags and released in the field were larger in size.

Analysis of dispersal probability:

We estimated the probability of dispersal of tagged fish from the Navesink River from May through September, 2006 using the Kaplan-Meier (KM) estimator (Bennetts et al. 2001). The variance of the KM estimator is well described and makes no assumptions about the underlying hazard function (Pollock et al. 1989a). The probability of not dispersing is estimated as the proportion of tagged fish that did not disperse relative to the total number of tagged fish (alive and status known) available to disperse during the specific time interval. A tagged fish of known status is considered uncensored. Censoring occurs if the experiment is terminated or when the acoustic signal is 'lost'. We censored a number of individuals on the basis of movement histories. Several striped bass (N=4) disappeared from the upper estuary as a result of angling or their movement patterns indicated they probably died shortly after release. Two weakfish and 10 age-0 bluefish were censored because they were detected in the system < 2 days before the array of ultrasonic receivers was removed from the estuary in early October, 2006 and therefore probably remained in the estuary longer than the sampling period.

Movement data was analyzed at fine sub-daily to daily time scales to determine movement patterns within established daily home ranges as well as at coarser daily to monthly time scales to examine shifts in daily home ranges and emigrations from the system. Ten day segments of movements of fish remaining in established daily home ranges were analyzed to determine fine scale patterns. To examine coarse scale movements and the possible causes of shifts in daily home range, daily centroids of tagged individuals were calculated and related to time series of potentially important environmental forcing variables. We examined the effects of extrinsic variables including temperature, freshwater discharge, and time in the spring neap tidal cycle on mean daily position of tagged fish in the estuary using generalized additive models (GAM; Wood & Augustin 2002, R Development Core Team 2004). Distance up-stream of daily centroids for each fish served as the dependent variable. Cubic spline smooths of average daily temperature at the RCM-9 meter, log transformed freshwater discharge from the swimming river, and time in the spring neap cycle were included in initial models. We also included a linear factor term for tagged individuals as well as the number of days since release in the models. We performed backward selection of significant terms using analysis of deviance of nested models (Venables & Ripley 1997). We replaced smoothed terms with linear terms if estimated nonparametric degrees of freedom were close to 1 and deviance plots indicated that dependent and independent variables were linearly related. We attempted a similar hybrid GAM analysis of sub-daily to daily patterns of movement within established home ranges with respect to tide stage and diel period. However, this analysis was not pursued further because important between and within individual variation in movement behavior was evident for all 4 species classes at these fine space and time scales and not described sufficiently well using the hybrid GAM approach.

Results and Discussion

Physical characteristics

Temperatures at the RCM-9 (see Fig. 1 for location) increased from 15^0 C in early May to over 30^0 C in early August before declining later in the summer (Fig. 2). Maximum daily temperatures in the lower river in the vicinity of location A in Figure 1 were similar to those measured at the RCM-9 ($\bar{x}_{\Delta}$=-0.02^0 C, -0.47-1.21) while minimum temperatures were slightly cooler ($\bar{x}_{\Delta}$=-0.50^0 C, -3.9- 0.04). In contrast, temperatures upstream at location D were typically 1 degree warmer than those measured at the RCM-9 ($\bar{x}_{\Delta}$ daily max=1.25^0 C, -0.56-3.93; $\bar{x}_{\Delta}$ daily min =0.80^0 C, 1.36-5.69). Temperatures mid-river reached a maximum of 32^0 C on days 214 and 215 (Aug 2 & 3). Six episodes of significant freshwater discharge from the swimming river occurred in May and June and in September (day 154, 6/3; 159, 6/8; 176, 6/25; 187, 7/6; 246, 9/3; 259, 9/16; Fig. 2). During periods of low freshwater discharge a salinity front formed in the upper river (location D in Fig. 1) at certain stages of the tide (Fig 2). A strong gradient in Chlorophyll-A concentrations with high values upstream was usually associated with this salinity front. The salinity front moved downstream and was often established south of location C during episodes of high discharge (Fig. 2). During several high discharge events, Chlorophyll-A concentrations were higher in the lower river than in the middle and upper river. These reversals of the spatial structure of the Chlorophyll-A gradient may have been caused by the influx of water from the Raritan and/or Hudson Rivers which are much larger in size and in discharge volume than the Navesink (Geyer and Chant 2006).

Residency in estuarine observatory

We tagged and released 78 fish into the Navesink River between mid-May and early September 2006 (Table 1; Fig 3). Striped bass (N= 34, 359-630 Tl mm) and most age-1+ bluefish (N= 14, 310-390 Tl mm) were released in May and June, while weakfish (N= 15, 224-535 Tl mm) and age-0 bluefish (N= 15, 175-270 Tl mm) were released from July through September.

Preliminary analysis of dispersal probabilities indicated that individuals of all species classes used the Navesink River for relatively long periods of time (Fig. 4). Age-1+ bluefish used the estuary for a median of 19.5 days (range=10-48d) while striped bass used the system for a median of 20 days (range=2-57d; Table 2, Fig. 4). The long residency times for age 1+ bluefish were particularly surprising given their rapid swimming speeds, high prey resource requirements, and highly migratory nature (Buckel et al., 1999; Olla et al., 1970; Shepard et al., 2006). More than half the age-0 bluefish (range=5 to >37d) and weakfish (range=3-63d) used the estuary for > 30 days before dispersing. Dispersal probabilities were significantly different among the four classes of tagged fish (Table 2; Log ratio test χ^2=9.6 , 3 d.f., p=0.0224). The long estuarine residency times of tagged individuals suggests that small estuarine systems, like the Navesink River, provide resources necessary for the maintenance growth and survival of the three species for significant periods of time. Long residencies and highly localized movements could result in substantial uptake of chemicals including contaminants unique to specific small, shallow water, coastal systems. Thus, our results may be particularly relevant to future studies using chemical microconstituents in calcified bony structures as geographic markers (Gillanders and Kingsford 2003, Thorrold and Shuttleworth 2000, Wells et al. 2003) and in estimates of contaminant uptake for resource species using such systems.

Fish released generally remained in the estuary continuously and did not return following dispersal (Fig 3). Most of the striped bass emigrated by the beginning of July and all had dispersed by the beginning of August (Fig 3). However, three striped bass emigrating in July returned to river habitats in late August and September following absences of 49 to 183 days. The ingress of several striped bass back into the Navesink in the fall, following a mid-summer emigration from the system is consistent with recent observations of seasonal and inter annual homing of individual striped bass to locations within specific estuaries (Able and Grothues). Most weakfish emigrated before early October. Three weakfish emigrating from the system in early September returned in late September following absences of 12 and 26 days. Most age 1+ bluefish dispersed from the estuary in July and all had emigrated by the beginning of September. Four bluefish returned to the river after absences of 1 to 21 days. Most age-0 bluefish released in August and September used the estuary continuously from date of release until the receivers were removed from the estuary in the beginning of October. Our results are consistent with previous studies using traditional sampling methods to document the seasonal abundance the three species in small temperate estuarine systems including the Navesink River (Manderson et al. 2006, Martino and Able 2003, Scharf et al. 2004).

Descriptive patterns of movement

All species and size classes of fish appeared to establish daily home ranges in which they moved 1-3 km's at minute to hourly time scales and exhibited episodic movements > 2.5 km that were followed by the establishment of daily home ranges in new locations or a return to old home ranges (Fig 5a,b,c,d). All of the species classes used habitats in the middle and upper reaches of the river. Only striped bass consistently used habitats in the lower river. Nearly all tagged striped bass, weakfish, and age-1+ bluefish established daily home ranges in areas that included deep habitats near locations A, B or C (Fig. 1).

Most striped bass released in late May and early June spent some time in the upper part of the estuary within, or near the mouth of the swimming river (Fig 1 location E, Fig 5a) before moving downstream > 2 km to establish daily home ranges in the middle and lower river in mid to late June (Fig. 5a). Weakfish showed two patterns of habitat use related to timing of release (Fig 5b). More than half of the tagged fish (N=8) established daily home ranges that included the deep habitat near location B (Fig.1) but rarely included habitats upstream of point C. Most of these fish were released in July when temperatures exceeded 25^0 C. Six weakfish, released in mid-August after the highest temperatures were recorded, established home ranges that included the deep habitat at location C, as well as shallower areas upstream. On the basis of this difference, weakfish were divided into upriver and down river groups for analysis of home range shifts over day-monthly time scales. Most Age-1+ bluefish (10 of 14 fish) used parts of the seascape that included the deep habitat near location C (Fig 5c). In general, bluefish spent significantly more time upstream of point C than in the lower estuary. Most age-0 bluefish (10 of 14) established daily home ranges in the upper river in the vicinity of location D (Fig 5d). In mid September, a few individuals migrated downstream and established new daily home ranges in the lower estuary.

Home range shifts and environmental forcing.

Movements of fish at day-weekly time scales varied with temperature and in most cases freshwater discharge, as well as among individuals and with the number of days following release (Table 3; Fig. 6a,b,c,d,e). Spring-neap cycles did not appear influence the coarse scale movements of any species class. Locations of daily centroids varied among individuals and, as expected, fish moved downstream as the number of days following release increased. While much of the individual variation in the location of daily centroids was related to the period of time animals were resident in the estuary, there were a number cases for each species class in which differences in the location of individuals occurred during the same periods. This suggests that multiple areas in the estuary contained adequate resources to support individuals of the same species class.

Daily home range shifts and other large scale movements were most strongly associated with changes in temperature (Table 3; Fig. 6a,b,c,d,e). Daily home ranges of striped bass and age 1+ bluefish shifted downstream when temperatures at the RCM-9 exceeded 24^0 C (Fig 6a,b). Age-0 bluefish were located furthest upstream when temperatures ranged between 21^0 C and 23^0 C and moved downstream at warmer and cooler temperatures (Fig 6c). Positions of weakfish in the down river group were furthest upstream when temperatures were less than 26^0 C (Fig 6d). At higher temperatures these fish moved into the lower river. The relationship between temperature and upstream position was weak for the upriver group of weakfish released in mid-August after the highest bottom temperatures were recorded (Fig 6e).

Water temperature is considered to be the most important factor controlling metabolic rates in aquatic poikilotherms (Brett and Groves 1979, Fry 1971, Neill et al. 1994) and all tagged fish moved downstream when temperatures in the middle and upper estuary exceeded species specific and ontogenetic thresholds. The universality of downstream movement with increasing temperatures may indicate that habitat characteristics in upstream portions of the estuary are preferred by all 3 species and that the spatial distributions of thermal refuge habitats are a critical component of estuarine seascape quality. Conceivable there are certain seasonal periods when temperatures are within optimal ranges throughout the estuary and animals are free to exploit feeding and other important resources without regard to thermal regime. However, as temperatures increase during the spring and summer and decrease in the fall, animals find regions providing thermal refugia as well as habitats meeting other essential physiological and survival requirements. Such regions must have volumes that fall within limits defined by the cost of movement and species and size specific movement scales of the animals. The seasonal evolution of the “thermal seascape” probably results in important seasonal changes in volumes and distributions of optimal habitat and thus the carrying capacities of small temperate estuarine systems.

Freshwater discharge from the swimming river also affected the location of daily home ranges for all tagged fish except those in the down river weakfish group which were released in July and not exposed to substantial discharge events (Table 3; Fig. 6a,b,c,d,e). Striped bass, age 1+ bluefish, and weakfish with upriver home ranges responded to freshwater discharge by moving downstream (Fig 6a,b,e). The relationship between freshwater discharge events and daily home ranges of age-0 bluefish was complex (Fig 6c). Many of these fish moved upstream during periods of high discharge. Examinations of individual movement tracks showed that ~ 50% of tagged age-0 bluefish moved upstream into the swimming river for at least a few days following discharge events.

Exposure to sub-optimal salinities results in the mobilization of metabolic energy toward osmoregulation and away from growth (Fry 1971, Neill et al. 1994) and presumably results in the movement of animals toward regions where salinities are optimal. The downstream movement of tagged striped bass, age-1+ bluefish and upriver group of weakfish may have represented shifts to habitats with optimal salinities as the salinity gradient moved downstream during high discharge. However a significant number of striped bass and age 1+ bluefish moved out of the receiver array up into the swimming river where they were "disappeared" for a few days. Salinities measured upstream during these excursions were periodically low (<10 ppt) even when river discharge was low. Thus movements in response to episodes of freshwater discharge may be more directly related to other factors also influenced by freshwater discharge. One possible explanation is that freshwater discharge events produce changes in the salinity, nutrient input and turbulence structure that temporarily destabilize the structure of the pelagic food web in the system. The reversal of the spatial structure of the chlorophyll-A gradient with high discharge indicates that such food web destablization may occur (Fig. 2). This could make significant short term relocations for feeding necessary during and immediately following major discharge events. Many fish returned to previous daily home ranges a few days after episodes of high freshwater discharge. Movement responses age-0 bluefish to freshwater discharge were certainly not related to the direct effects of changes in salinity structure and osmoregulatory requirements since more than half of the individuals tagged moved upstream into the swimming river during discharge events.

Movements within daily home ranges at subdaily to daily time scales

The daily range of movement varied among species classes and among individuals within classes (Table 4. Fig. 7). Age 1+ bluefish had the largest daily ranges of upstream-downstream movement ($\bar{x}$ = 2570 m, SE= 95) in established home ranges while age-0 bluefish had the smallest ($\bar{x}$ = 1637 m, SE= 109). Weakfish had slightly larger ranges of movement ($\bar{x}$ = 1853 m, SE= 84) in daily home ranges than striped bass ($\bar{x}$ = 1700 m, SE= 92). However, there was significant individual variation in daily ranges of movement within each class that was not related to body size. Body size and movement capabilities are believed to determine the limits of home range size in terrestrial animals and marine animals (Blackwell 1997, Comiskey et al. 2002, Heupel et al. 2004, Powell 2000). However we found a high degree of individual variation in daily movement ranges within all species classes nearly as large as the species differences. Many between individual differences in the home range size were probably related to differences in spatial and temporal distribution of required habitat resources during the time periods when animals were in specific home ranges. However there were a number of cases in which individuals of the same species and size showed dramatically different home range sizes during the same time periods and areas. Presumable these differences were related to individual preferences (e.g.diet) and the spatial distribution of specific resources used by specific individuals within the locations. Alternatively, individuals may have varied levels of activity and proclivity for movement.

All four classes of tagged fish made upstream-downstream excursions within established daily home ranges at day to sub-daily time scales that were directly or indirectly related to diel period and/or tidal rhythms (Fig. 8a, b, c, d). Preliminary GAM modeling indicated that diel period, tide stage and the interaction of diel period and tide stage were important in determining positions upstream for all classes of fish. However detailed examination of individual movement histories indicated many important exceptions to mean patterns both between and within individuals in each species class (e.g. Fig 8. a 1460; b 2264, c 2265, d 2296). As a result, the modeling is not included here. Behavioral flexibility both within and between individuals suggests that the spatial and temporal dynamics of important physical and biological resources (e.g. temperature, prey and predators) forced by tide stage, diel period and other factors may have had greater effects movement patterns than tide stage and diel period.

Many tagged individuals of all 4 species classes established daily home ranges in the upper part of the estuary and made daily excursions between the deep habitat at location C and habitats upstream of C during some period (Fig. 1). Strong salinity and chlorophyll-A gradients form during periods of low freshwater discharge from the swimming river in the region just upstream of C (Fig. 2). Presumable this portion of the estuarine seascape can contain physical and biological resources that meet the physiological requirements of all three species of fish for significant periods of time. Examination of records from a thermistor string deployed in deep habitat C during a particularly warm period showed that bottom temperatures can be as much as 5 C lower than on the surface where temperatures exceeded 31 C during daytime ebb tides (Fig. 9). Temperatures throughout the water column were more similar during flood tides and during the night time at all tide stages. Thus, this deep habitat can form a daytime thermal refuge for fish in the upper estuary during particularly warm periods. On average, small fish prey (*Menidia menida*, *Anchoa mitchelli*) frequently eaten by all species classes of fish are generally more abundant upstream in the area where the salinity and chlorophyll-A front forms during periods of low freshwater discharge (Fig 8). Similar upstream salinity fronts form highly productive areas in similarly sized and larger estuaries (Jung and Houde 2003, Roman et al. 1997, Roman et al. 2001). We suggest that many tagged individuals used this region because thermal and prey resources are distributed across the seascape within the daily movement ranges of all 4 species classes of animals for relatively long periods of time. However, these conditions can be transitory as temperatures in the deepest water can exceed thermal limits and/or the prey field shifts in composition in response to forcing by other factors including freshwater discharge.

Conclusions

Our preliminary analysis of movement data collected in the Navesink River, New Jersey, US in the first year of a two year telemetry study indicates:

1: Individual striped bass, bluefish and weakfish, which are important taxon bridging pelagic and benthic compartments of estuarine food webs (Krause et al. 2003), are resident in small estuarine tributaries for relatively long periods of time and thus such systems must contain the resources to support the maintenance growth and survival of individuals.

2: The spatial structure of estuarine seascapes evolves seasonally resulting in dynamic changes in the spatial and temporal distribution of resources required for the maintenance, growth and survivorship of fish species. Individuals maintain positions in relatively small home ranges as long as required resources fall within the animals movement scales and movement costs don't out way metabolic and fitness benefits. However, individual animals are adaptable and show complex changes in movement behavior that may be related to changes in the fine scale spatial distribution of required habitat resources within established home ranges.

3: While tagged fish used most habitats in the estuary, individuals of all species established home ranges for relatively long periods of time in the upper estuary which included an area where salinity and chlorophyll-A fronts form and prey production is frequently high. Residence time in this area appeared to be controlled by the availability of thermal refuge habitats near this frontal area. Seasonal changes in temperature and river discharge probably directly and indirectly affect the distributions of resources in this area and thus the volumes of optimal habitat. The carrying capacity of this region probably also changes dramatically over time

4: Estuaries are highly dendritic networks of small tributaries and the upper portions of these tributaries may provide a significant portion of the volume of optimal habitat available in large estuarine systems. Warmer estuarine temperatures and/or changes in the seasonal trajectory of temperature with climate change could reduce the quality and carrying capacity of these upstream estuarine habitats and reduce stock sizes over relatively large portions of the ranges of species that depend on them.

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Table 1. Number and sizes of striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) tagged with ultrasonic transmitters and released in the Navesink River, New Jersey, USA observatory in 2006.

Species Year	Number	Total length range (mm)	Dates of release
Striped bass	34	359-630	May 15 - Jun 28
Bluefish			
Age-0	15	175-270	Aug 27 - Sep 9
Age-1	14	310-390	Jun 5 - Aug 16
Weakfish	15	224-535	Jul, 13 - Aug, 16

Table 2. Kaplan-Meier survival analysis of the number of days tagged fish used the Navesink River observatory. Individual fish were censored if movement patterns indicated that they may have died, been removed from the estuary by fisherman, or if they were detected ≤ 2 days before the ultrasonic receiver array was removed from the estuary. Log-ratio test: Chisq=9.6 on 3 degrees of freedom, p= 0.0224. O=observed, E= expected, V=variance

Species	Censored N	Median days	95% CI	$(O-E)^2/E$	$(O-E)^2/V$
Age-0 Bluefish[1]	5	∞	27-∞	2.88	3.76
Age-1 Bluefish	14	19.5	16-42	10.4	1.64
Striped Bass	30	20	9-29	2.88	4.77
Weakfish	12	36	26-∞	2.06	3.20

[1] The receiver array was removed from the estuary before 50 percent of age-0 bluefish emigrated in the fall.

Table 3. Preliminary hybrid GAMs of relationships between daily centroids of individual tagged fish and environmental forcing variables. Terms included with spline smooth indicated with s(parenthisis), otherwise linear terms were included. Factor term for individuals significant (P<0.01) in all cases.

Species	expected degrees of freedom	T or F	p-value
Striped bass			
discharge		-2.243	0.025453
s(days since release)	7.497	29.844	< 2e-16
s(temperature)	6.448	2.722	0.00435
Deviance explained = 71.8%			
Weakfish (downstream group)			
s(days since release)	6.294	7.370	3.10e-09
s(temperature)	2.236	8.068	6.12e-07
Deviance explained = 37.2%			
Weakfish (upstream group)			
temperature		-2.039	0.043123
s(discharge)	4.04	2.161	0.0276
Deviance explained = 38.2%			
Age 1+ Bluefish			
s(days since release)	5.995	21.119	< 2e-16
s(discharge)	7.705	7.903	3.84e-10
s(temperature)	3.105	5.143	1.90e-05
Deviance explained = 80.2%			
Age 0+ Bluefish			
s(days since release)	4.739	3.516	0.000368
s(discharge)	8.699	5.222	1.29e-06
s(temperature)	3.882	6.153	2.29e-07
Deviance explained = 56.1%			

Table 4. Repeated measures analysis of variance of daily ranges movement on 5 consecutive days for classes of tagged fish in established home ranges.

Source	SS	Degrees of Freedom	Mean Square	F	P
Between Subjects					
Species classes					
Hypothesis	3.86×10^7	3	1.29×10^7	3.11	0.041
Error	1.28×10^8	31			
Within subjects					
Species Hypothesis	7.61×10^6	12	6.34×10^5	1.174	0.309
Error	6.70×10^7	124	5.41×10^5		
Days Hypothesis	2.86×10^6	4	7.14×10^5	1.321	0.266
Error	6.70×10^7	124	5.41×10^5		

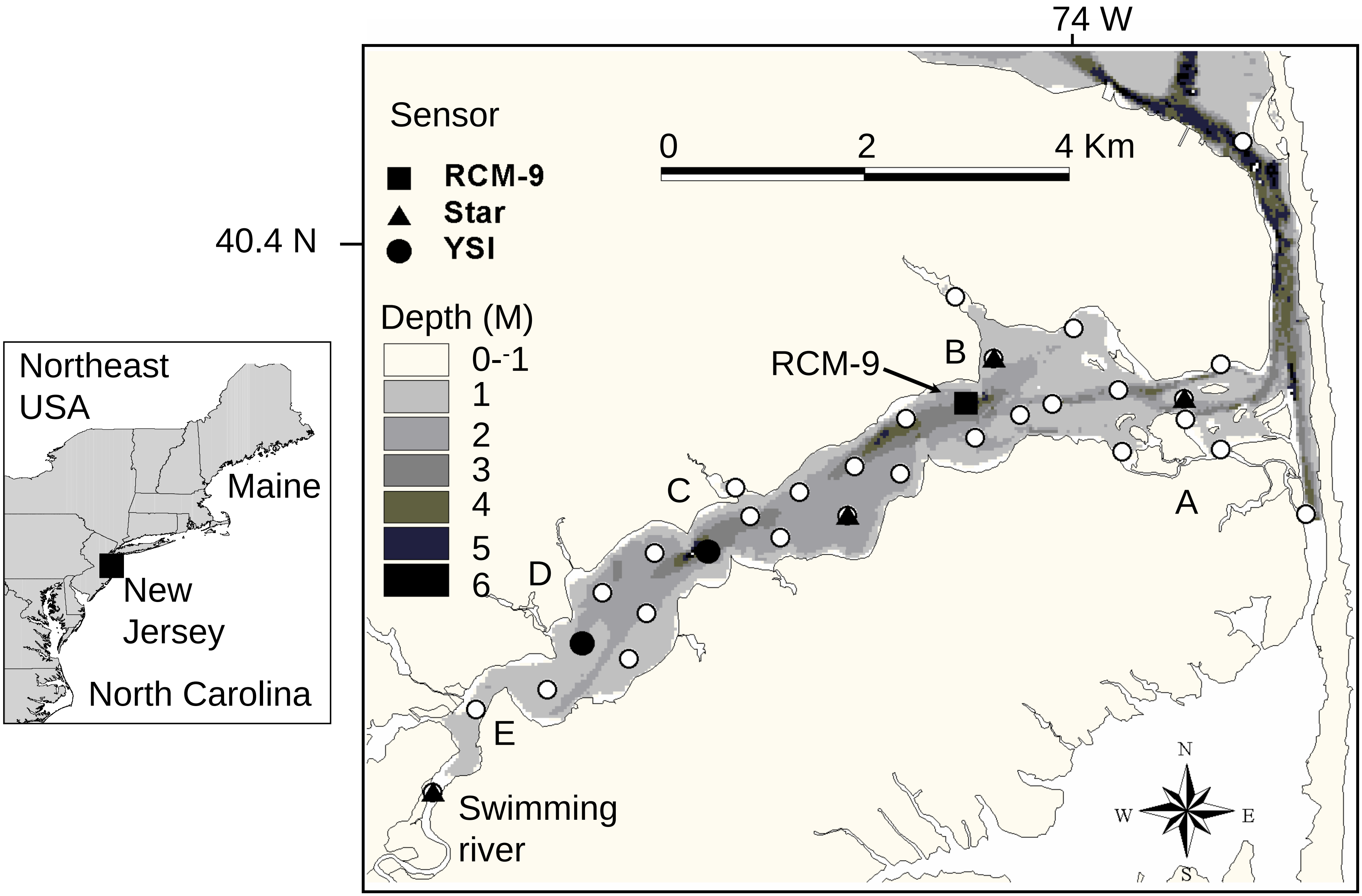


Figure 1. Location of the Navesink River, New Jersey on the northeast coast of the United States and of the 30 moorings with ultrasonic receivers (all moorings) and physical sensors (dark symbols). Locations A - E are reference points referred to in the text.

Figure 2. Bottom water temperatures measured at the RCM-9 mooring (see Fig. 1), freshwater discharge from the USGS station in the swimming river, and the typical spatial structures of salinity and chlorophyll-A gradients during periods of high and low freshwater discharge.

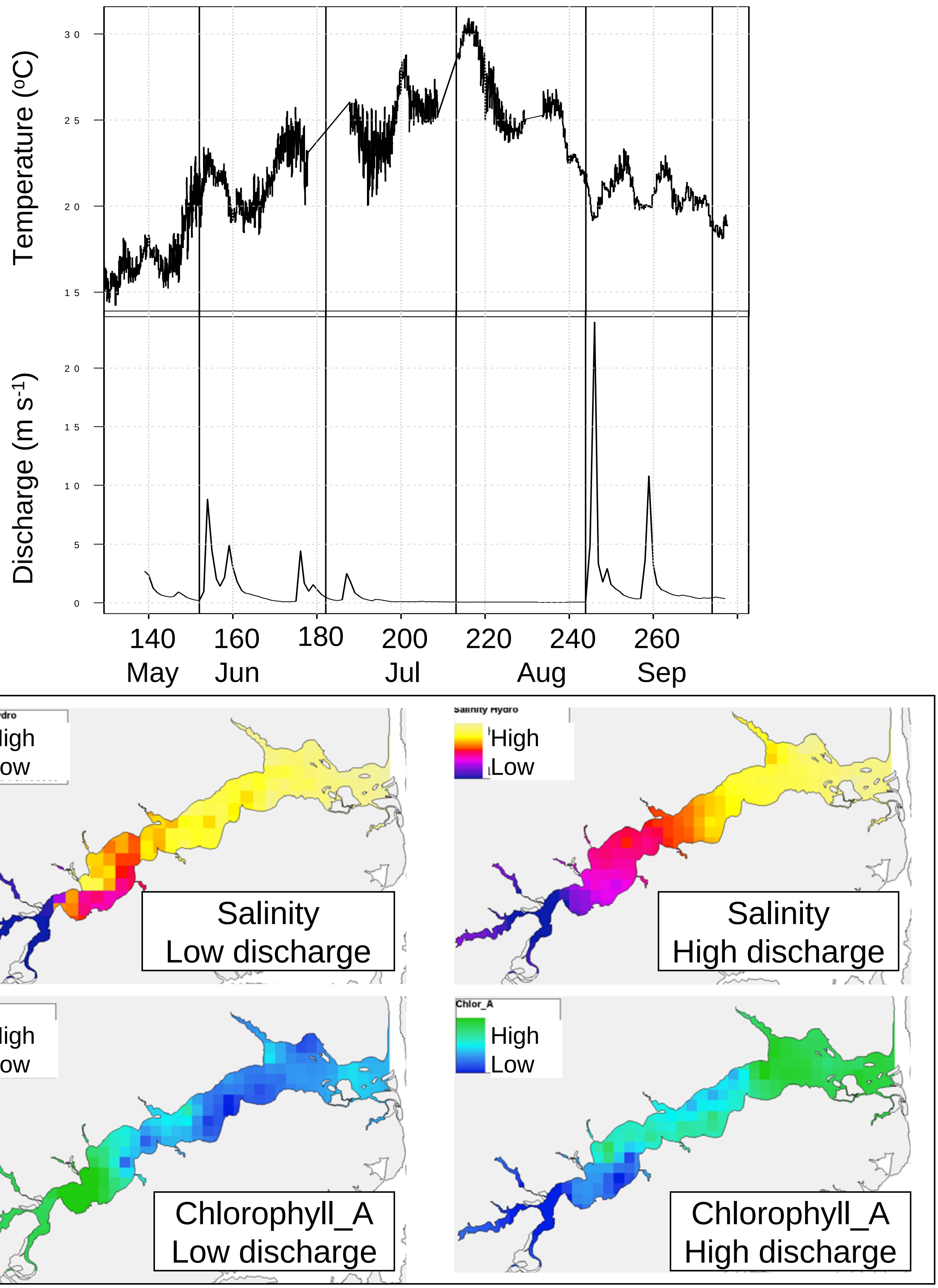
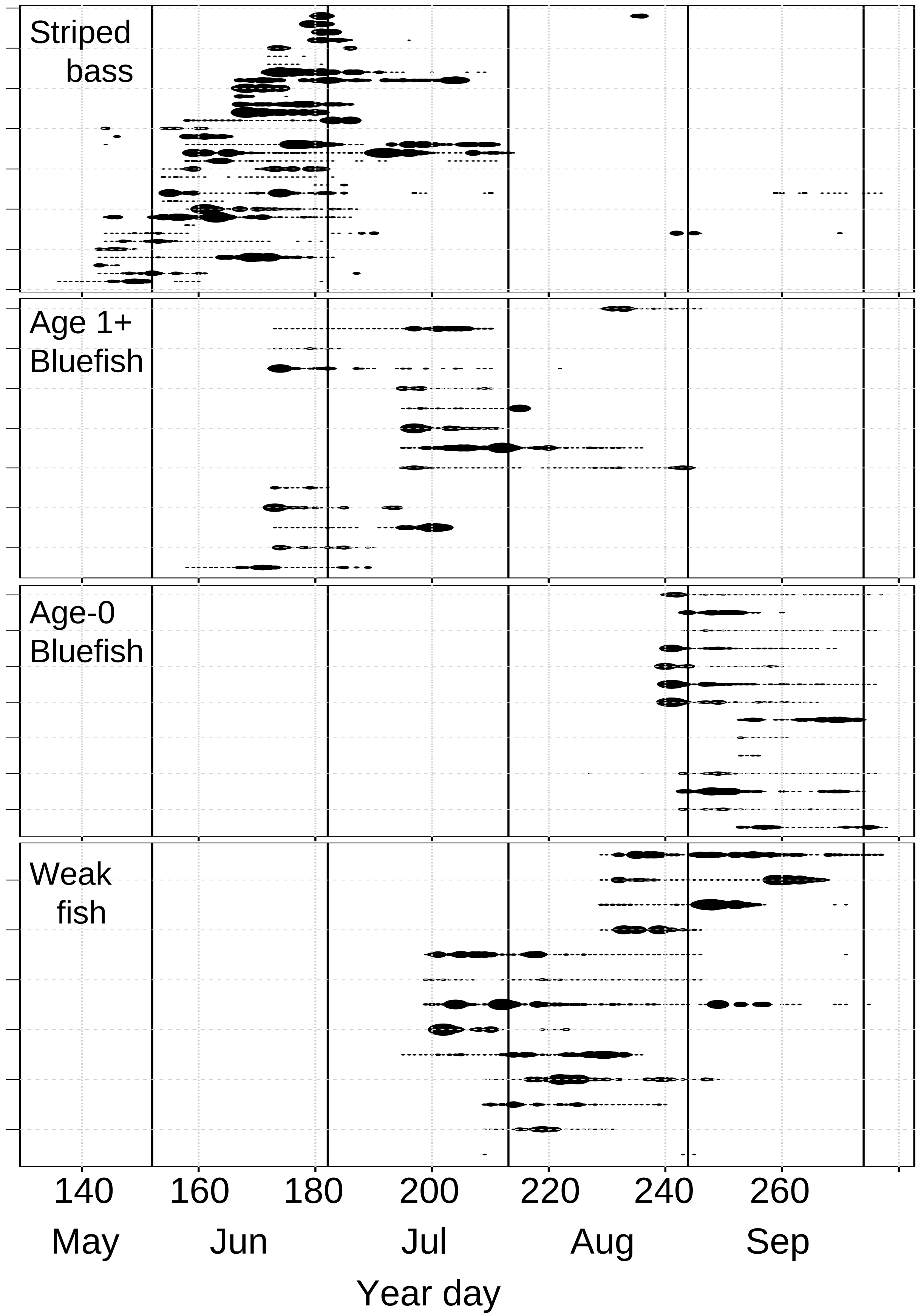


Figure 3. Records of daily receiver detections (pooled) for ultrasonically tagged striped bass, bluefish and weakfish released in the Navesink River in 2006. Symbol sizes indicate relative number of detections per day.



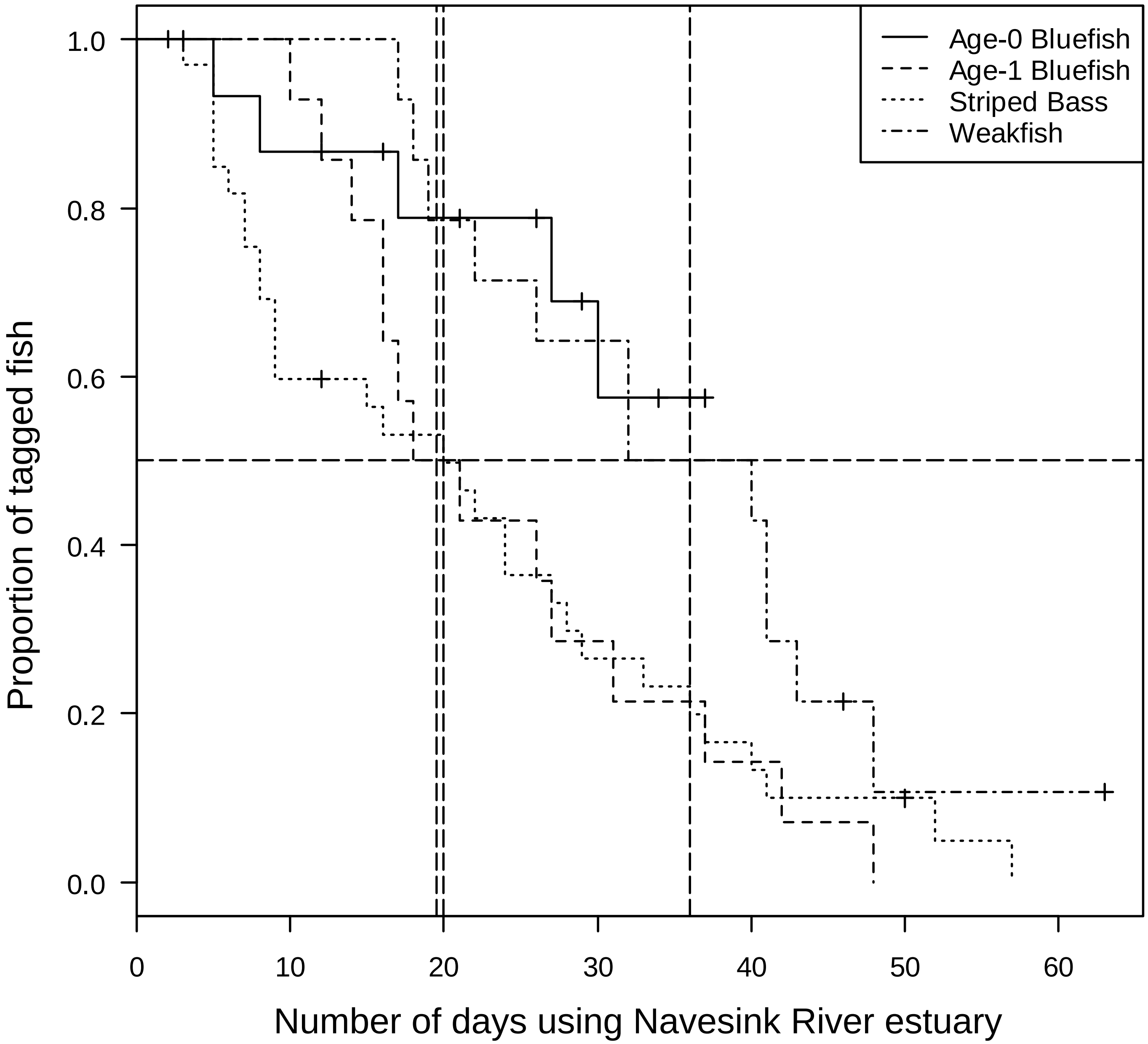


Figure 4. Dispersal probabilities calculated using Kaplan-Meier estimator for fish tagged and released into the Navesink River. Striped bass ad Age 1+ bluefish used the estuary for a median of ~20 days while median residence times for weakfish and age-0 bluefish were > 35 days. + symbols indicate censored individuals.

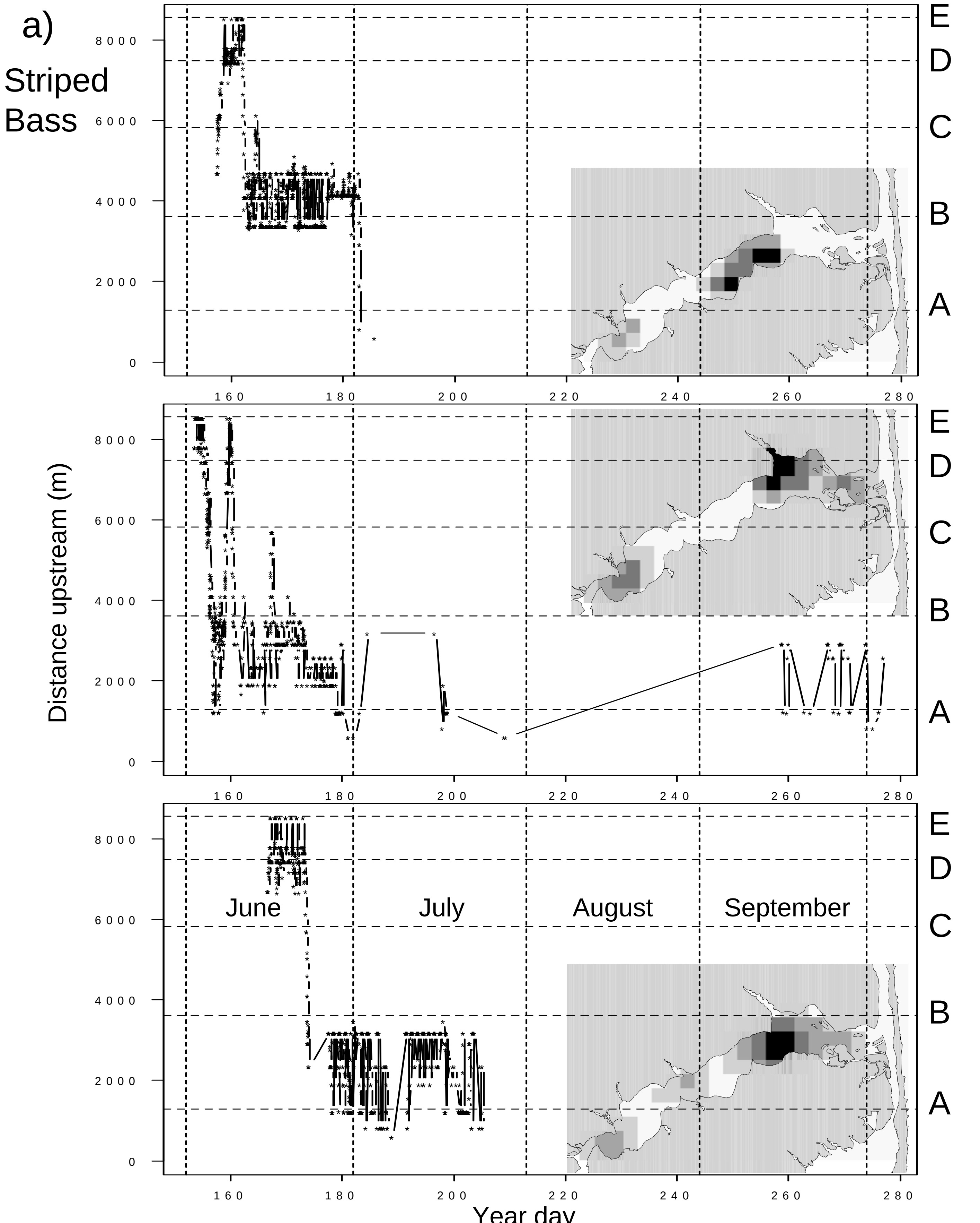
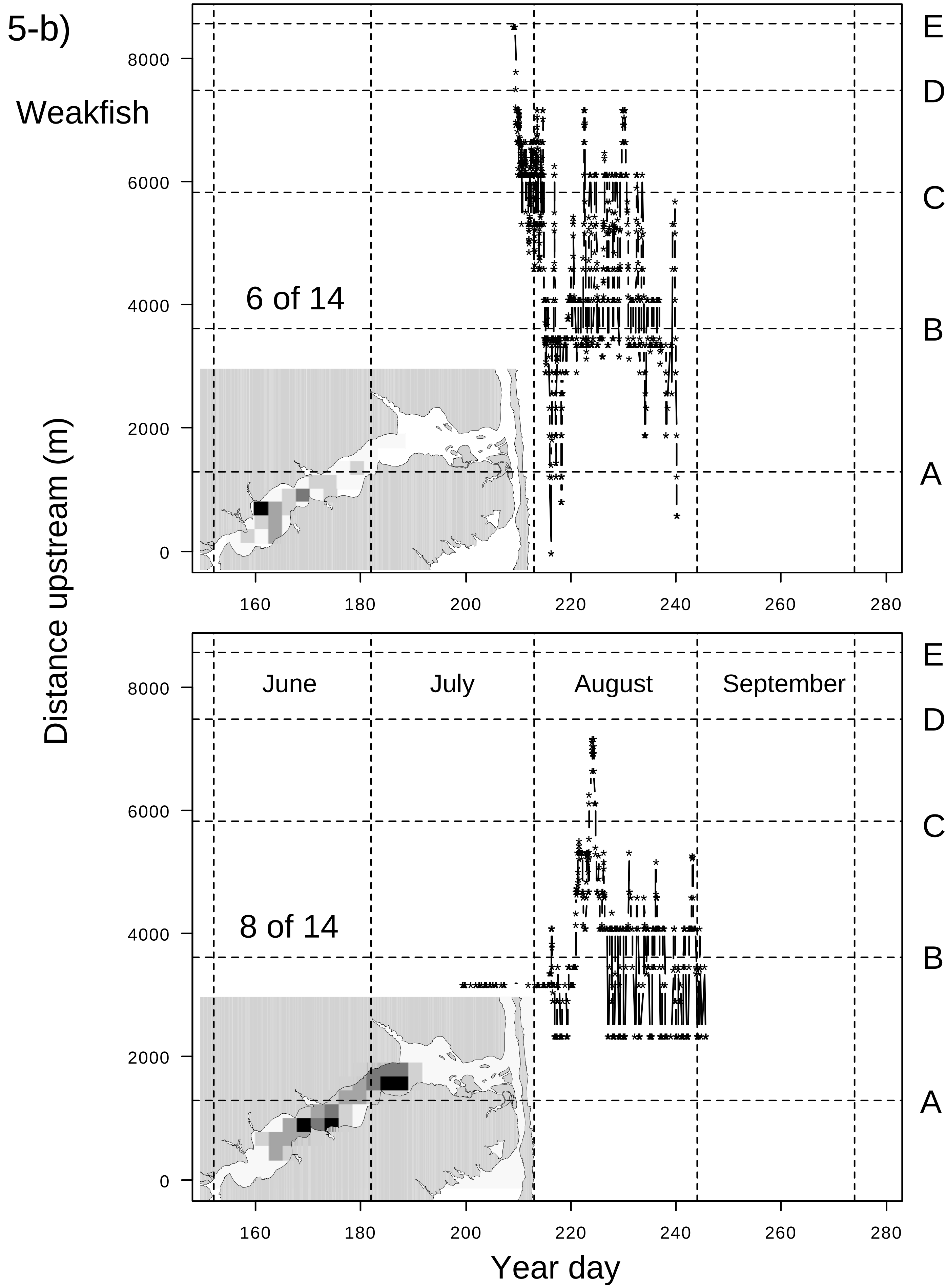
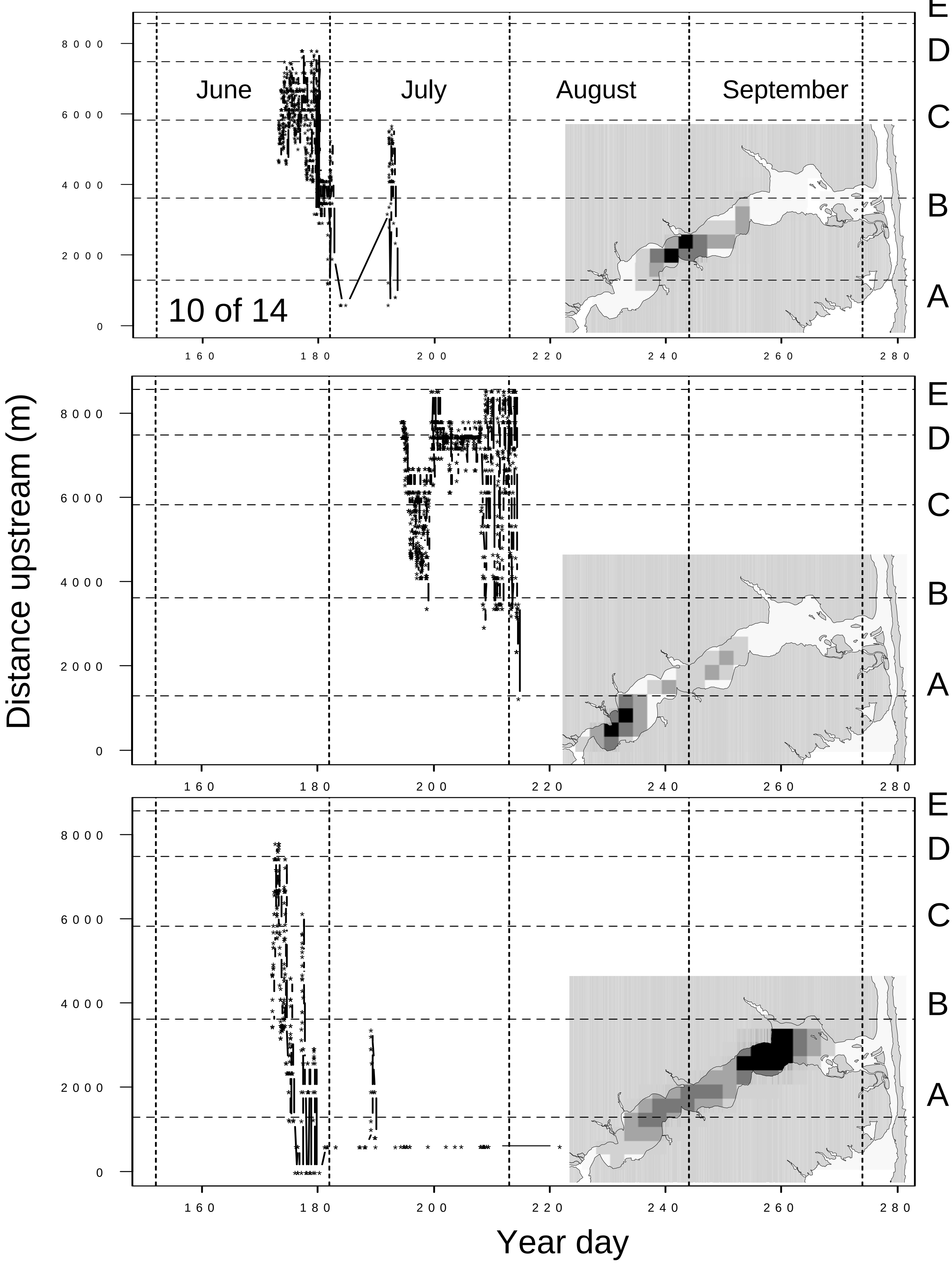


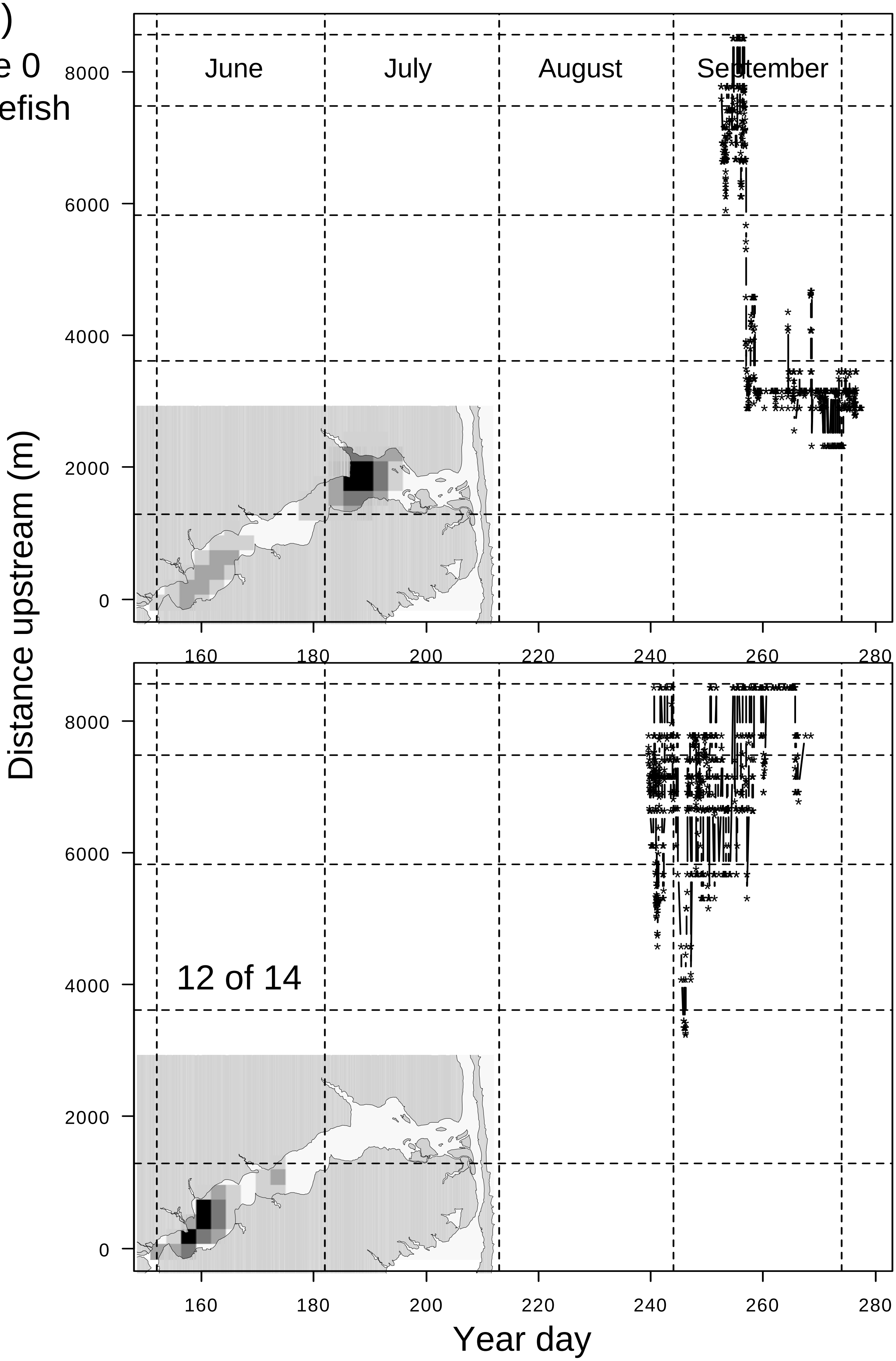
Figure 5. Maps of utilization distribution (UD) and plots of upstream-downstream movements for representative a) Striped bass, b) weakfish, c) age 1+ Bluefish, and d) age-0 Bluefish. Numbers indicate number of individuals with similar UD's and patterns of movement. Letters along y-axis are locations in Figure 1.


5-b)
Weakfish
6 of 14
8 of 14
June
July
August
September
E
D
C
B
A
Distance upstream (m)
Year day
0
2000
4000
6000
8000
160
180
200
220
240
260
280

5 c) Age 1+ Bluefish

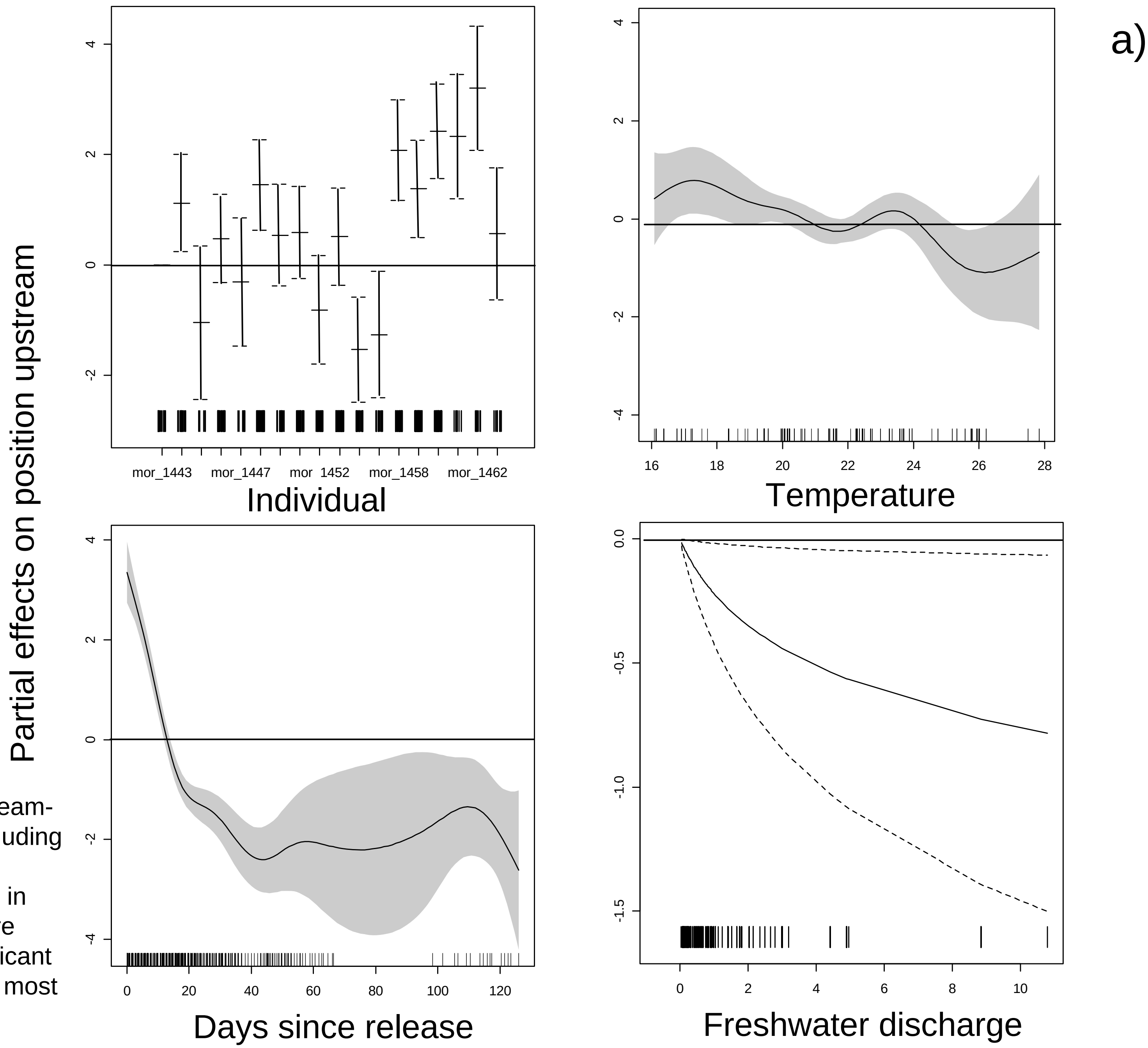


5 d)
Age 0
Bluefish

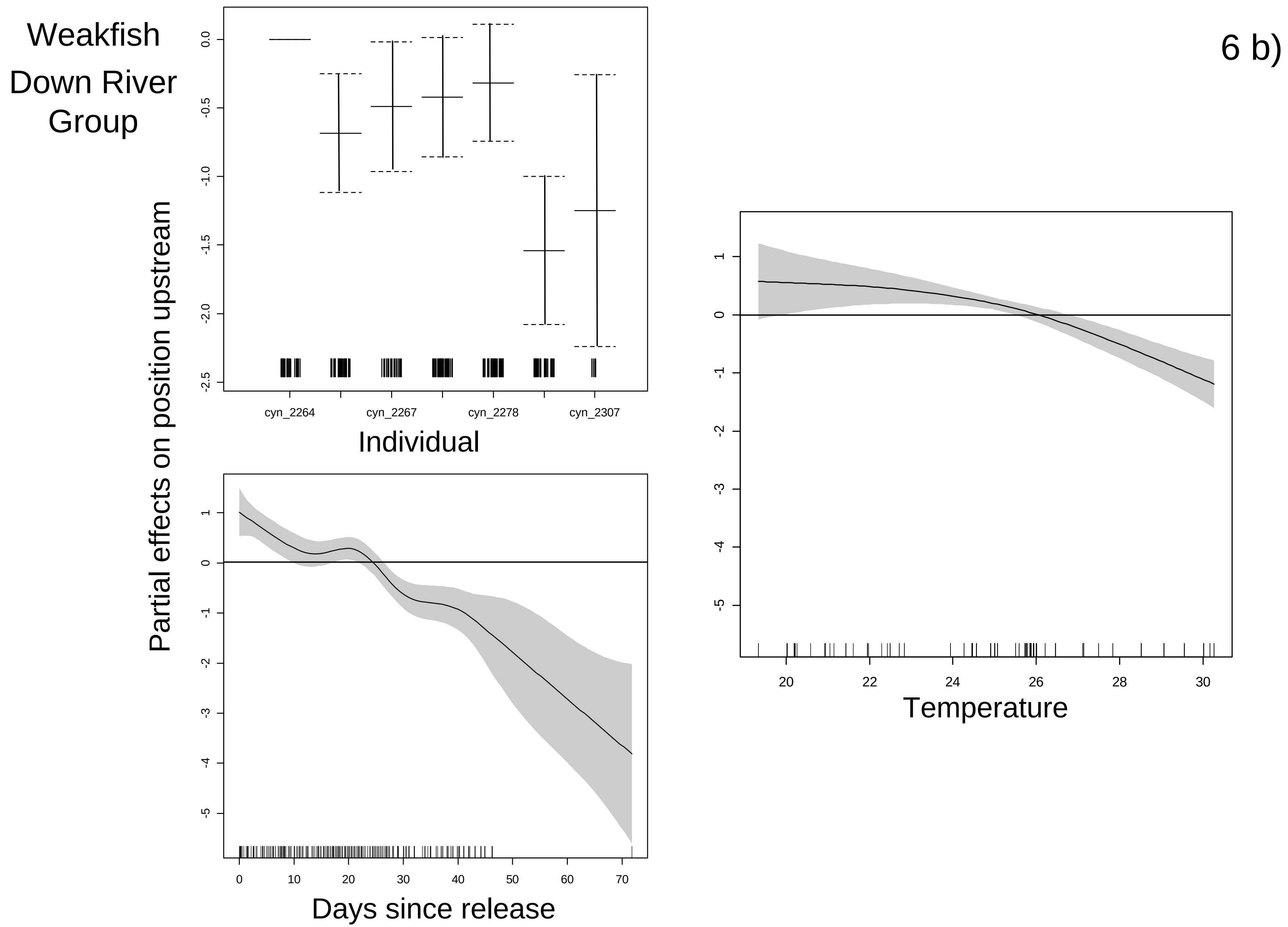


Striped Bass

Figure 6. Results of hybrid generalized additive modeling of changes in daily centroids of ultrasonically tagged a) striped bass b) weakfish with downriver distributions c) weakfish with upriver distributions, d) age 1+ bluefish and e) age-0 bluefish in response to environmental forcing.

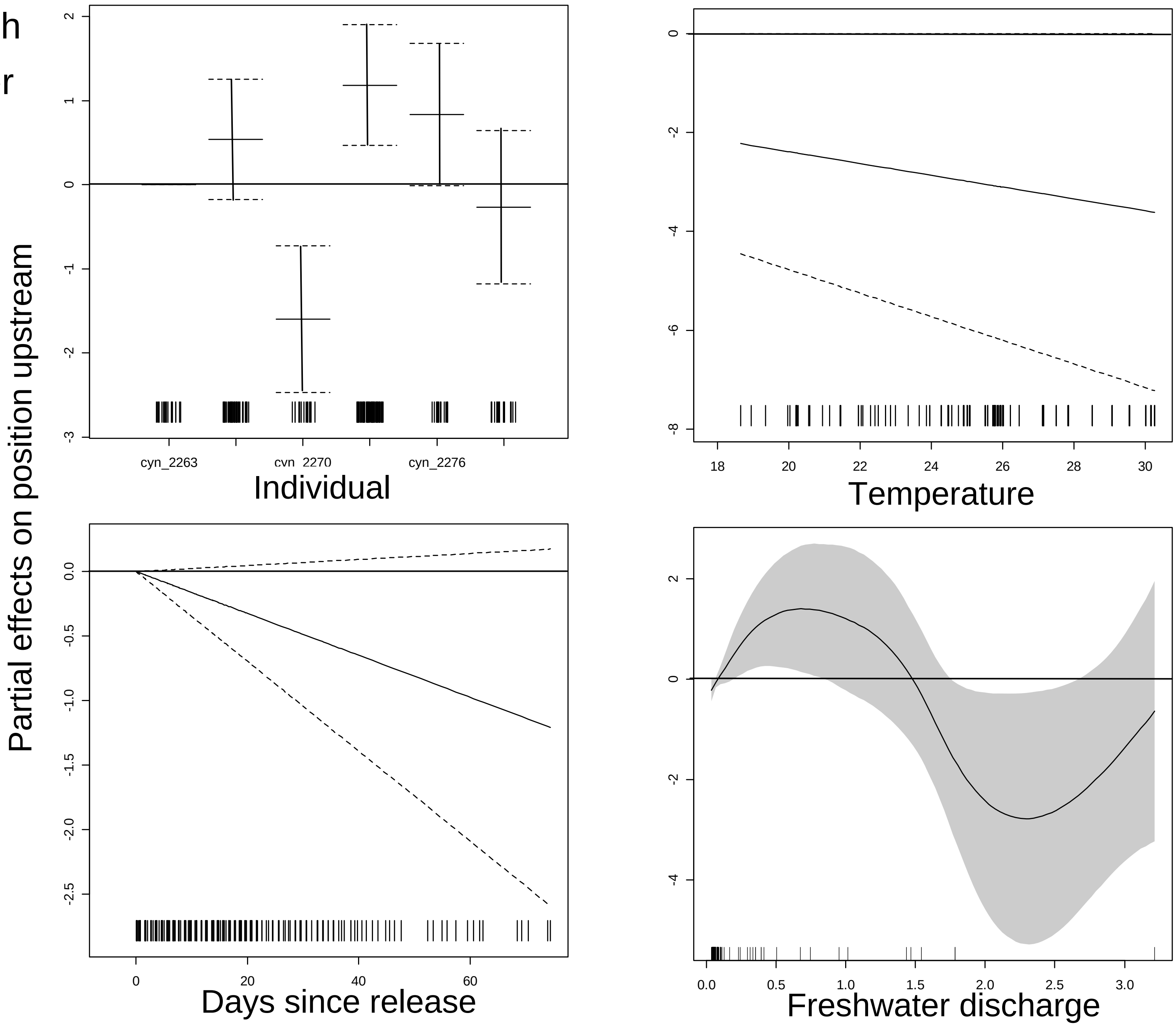


Large changes in upstream-downstream position including home range shifts were associated with changes in bottom water temperature and/or episodes of significant freshwater discharge for most individuals.


Weakfish
Down River
Group
6 b)
Partial effects on position upstream
cyn_2264
cyn_2267
cyn_2278
cyn_2307
Individual
Days since release
Temperature

Weakfish

Up River Group



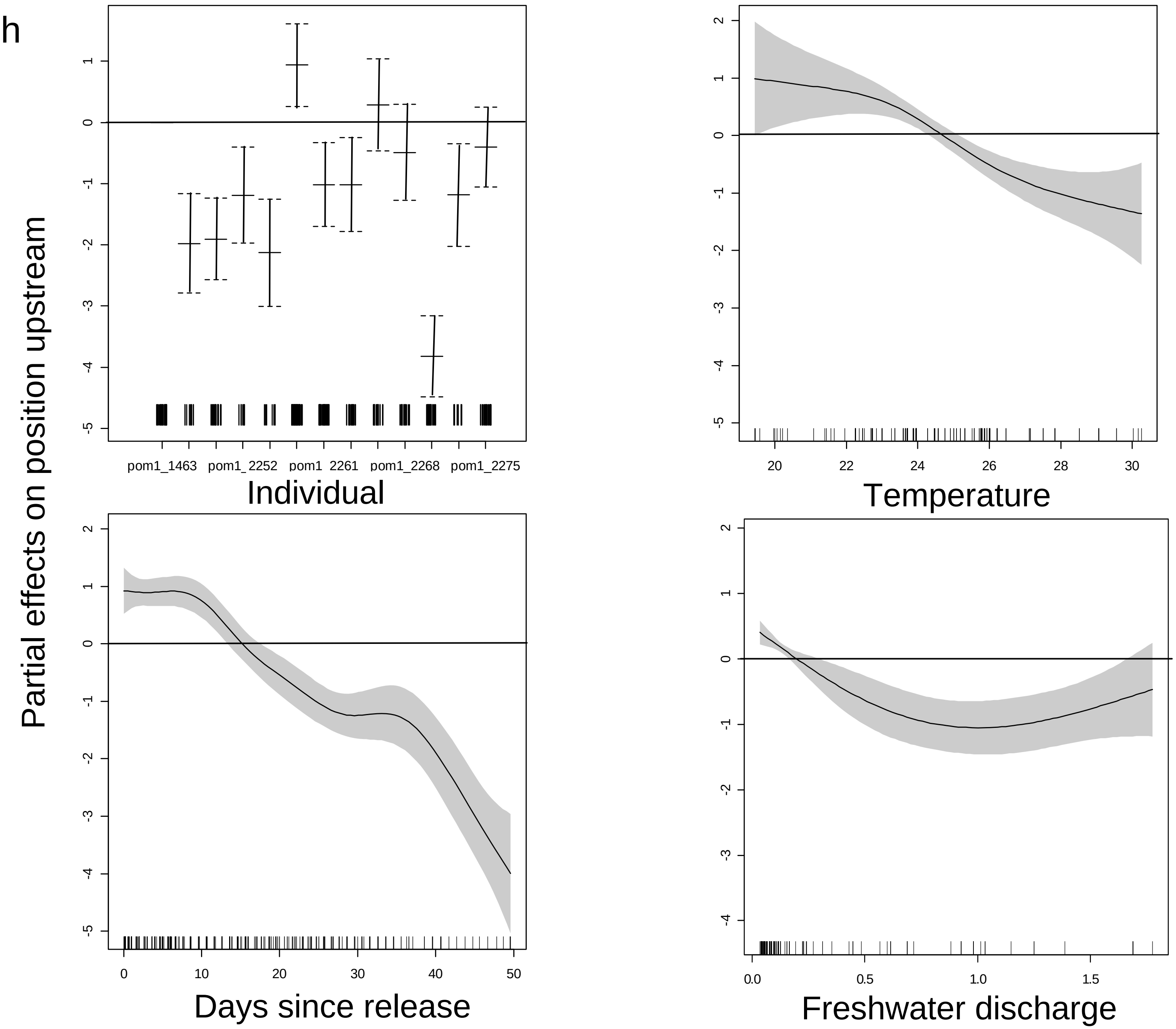
6 c)

Bluefish

Age

1+

6 d)



Bluefish
Age
0

6 e)

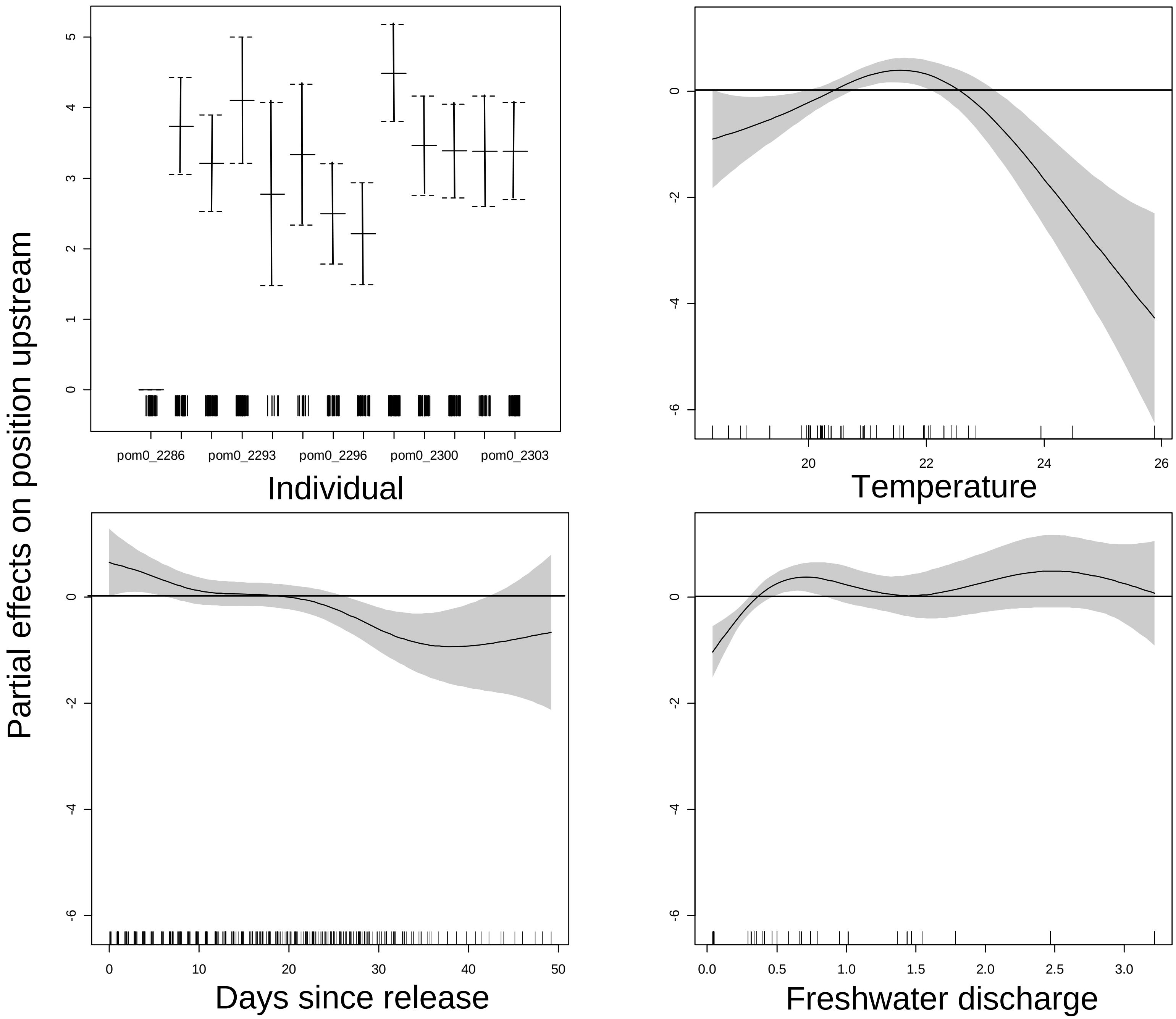


Figure 7. Daily ranges of upstream-downstream movement for individual tagged fish in established daily home ranges. While the mean range of daily movement for age 1+ bluefish was significantly larger than the other 3 species classes, all species classes showed substantial and significant individual variation.

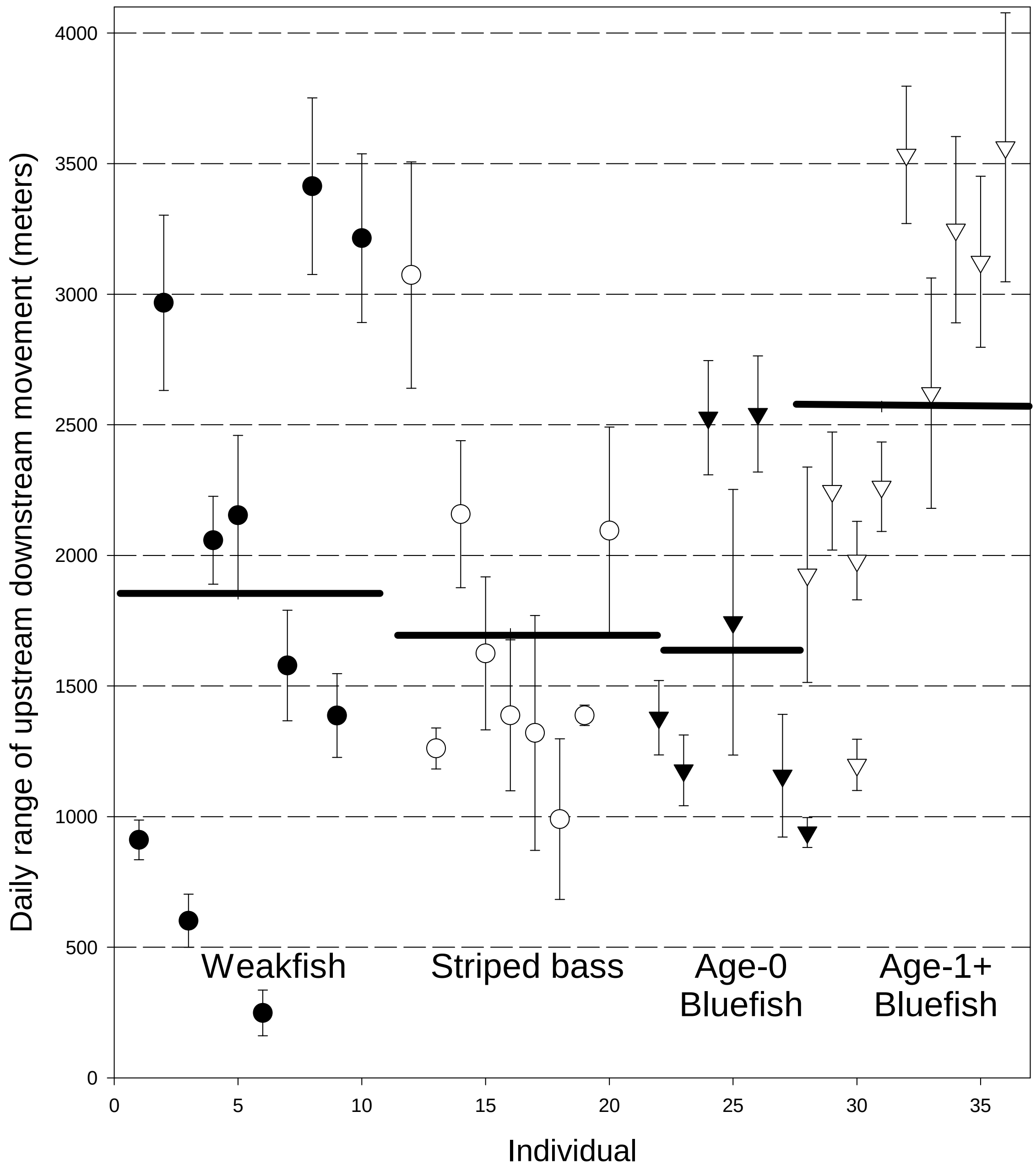
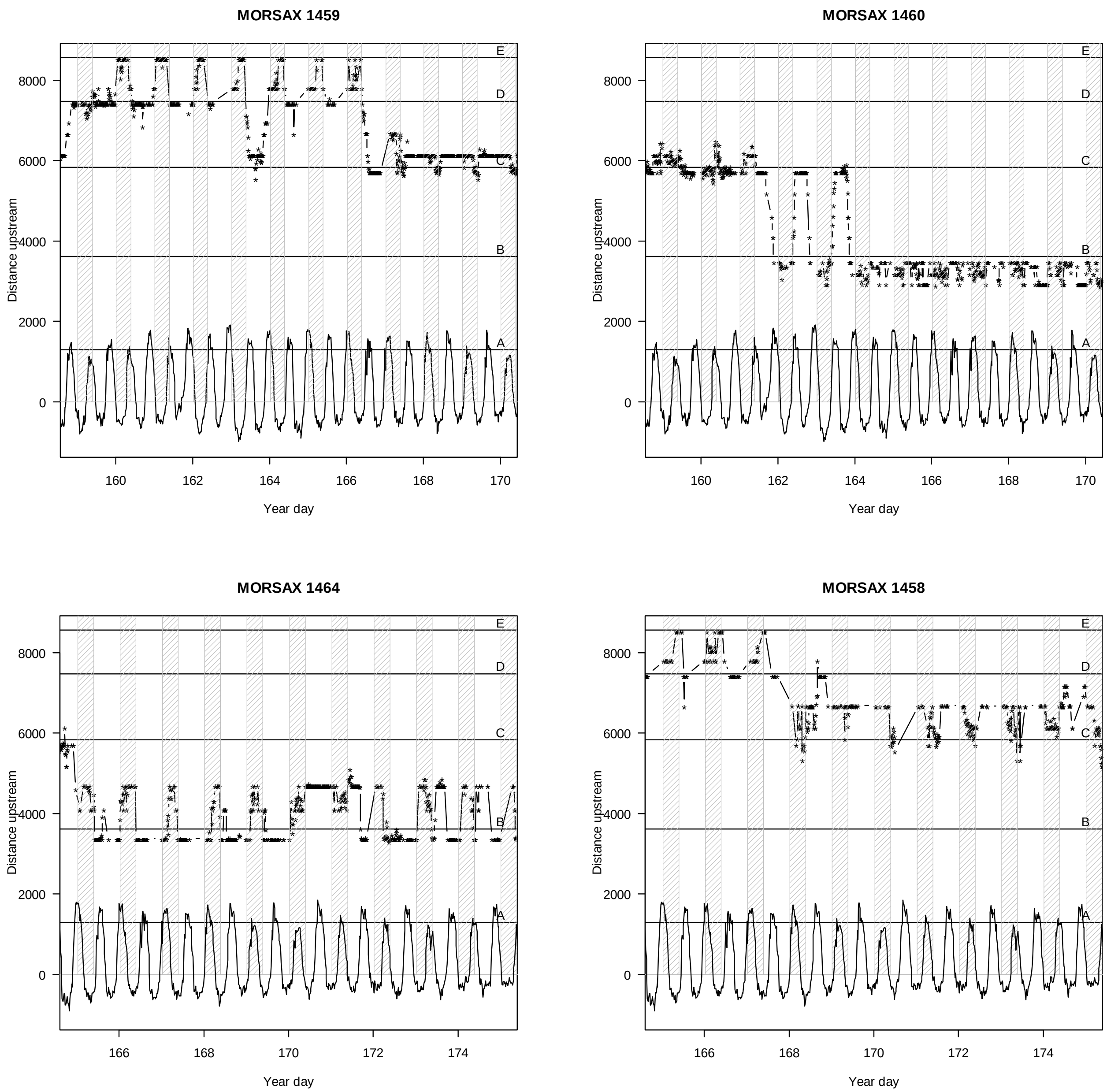


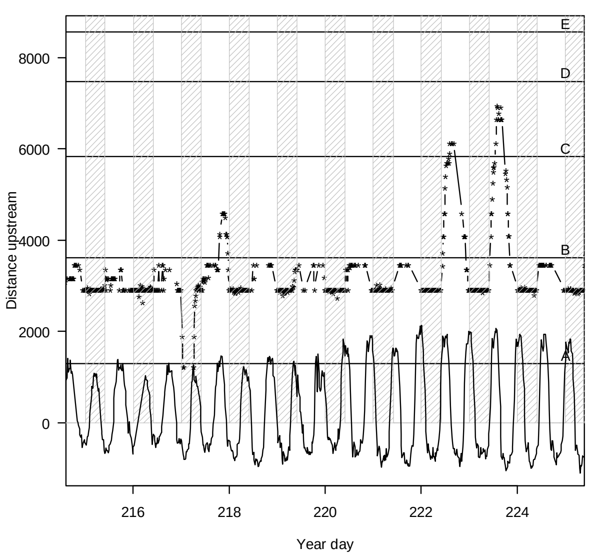
Figure 8. Daily and sub-daily patterns of upstream-downstream movement for tagged a) striped bass, b) weakfish, c) age 1+ bluefish and d) age-0 bluefish in home ranges. Most individuals of all classes exhibited daily rhythms in movements related to day-night cycling (hatched bars indicate nighttime periods) and/or tidal current circulation (solid line = upstream-downstream current velocity at the RCM-9, Fig. 1) but these patterns often varied among individuals during the same time period, and within individuals during different times in movement histories.

a) Striped Bass

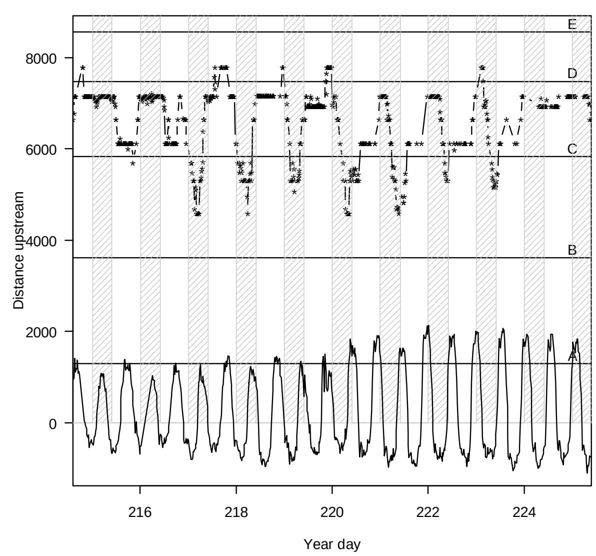


8 b) Weakfish

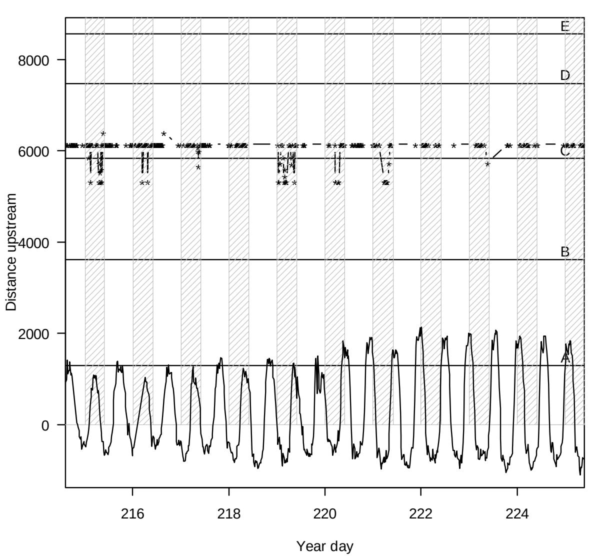
CYNREG 2278



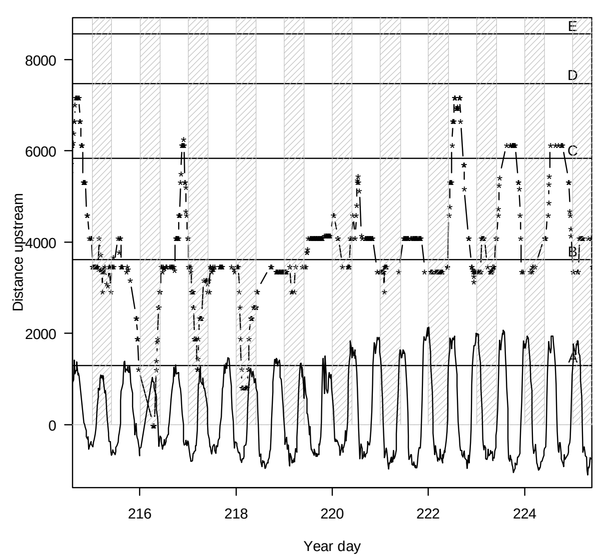
CYNREG 2272



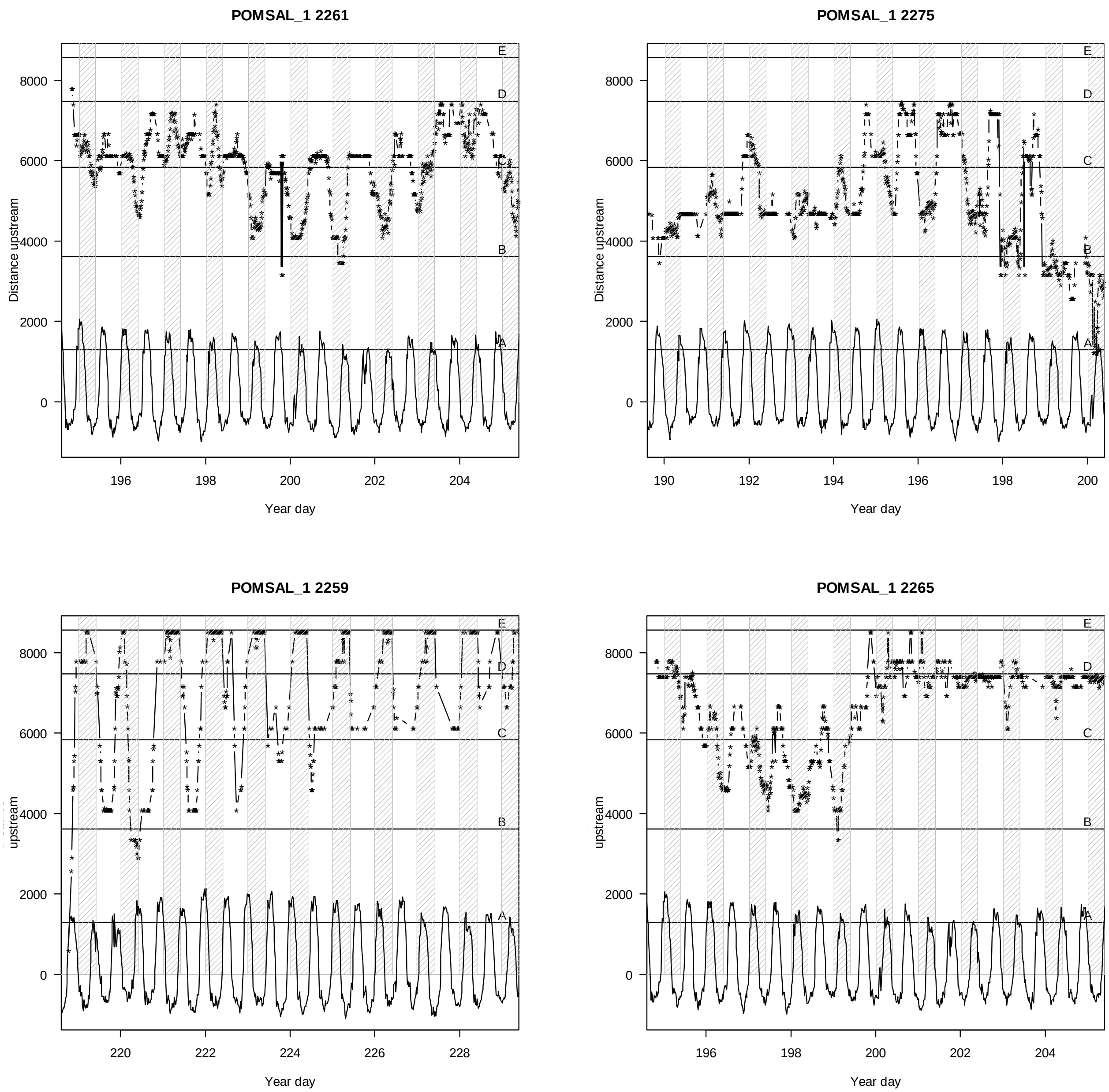
CYNREG 2269



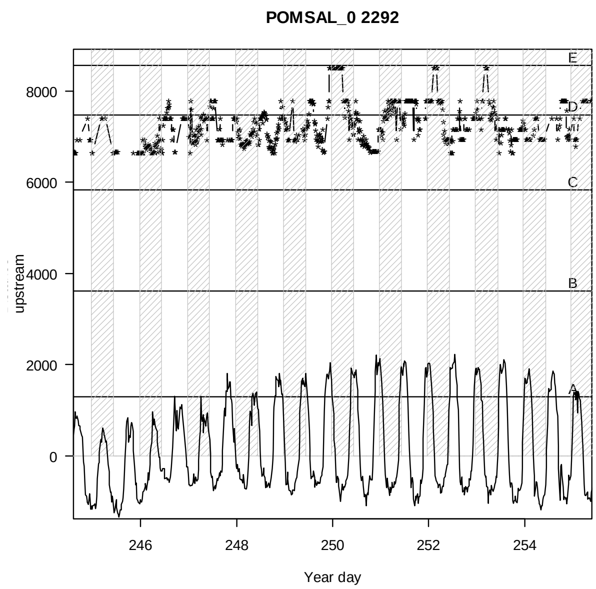
CYNREG 2264

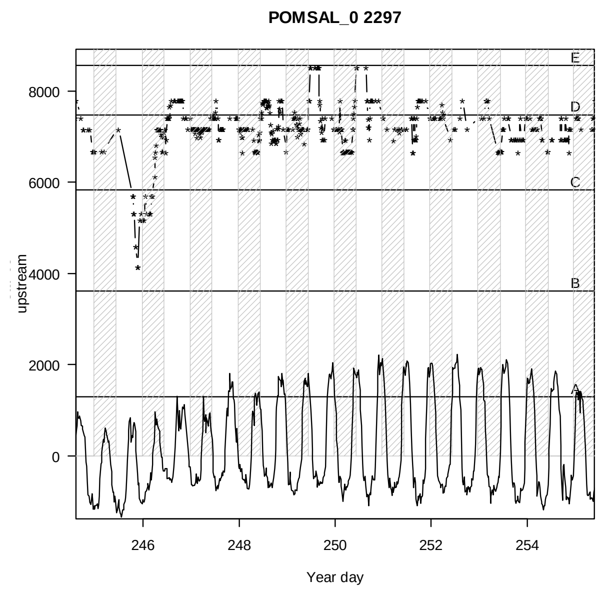


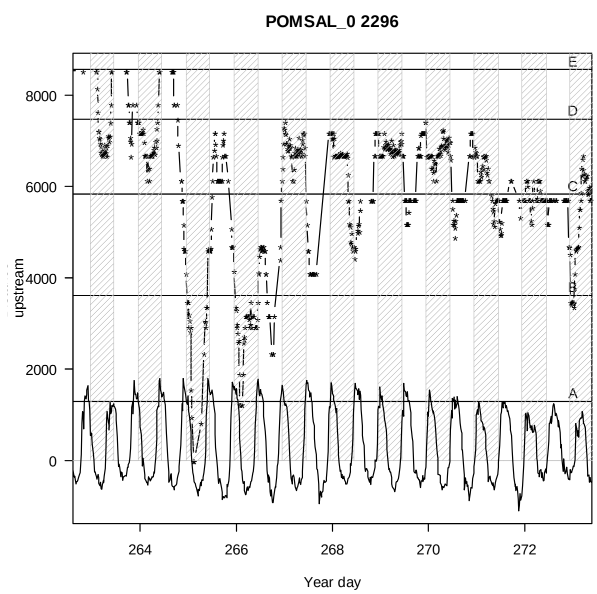
8 c) Age 1+ Bluefish

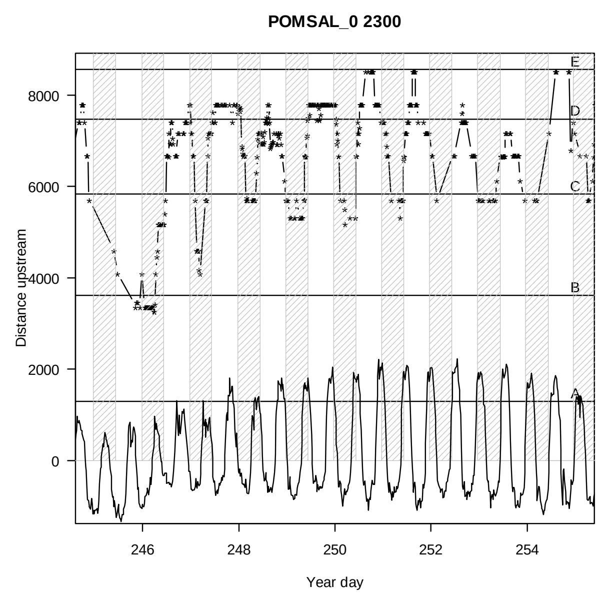


8 d) Age 0 Bluefish









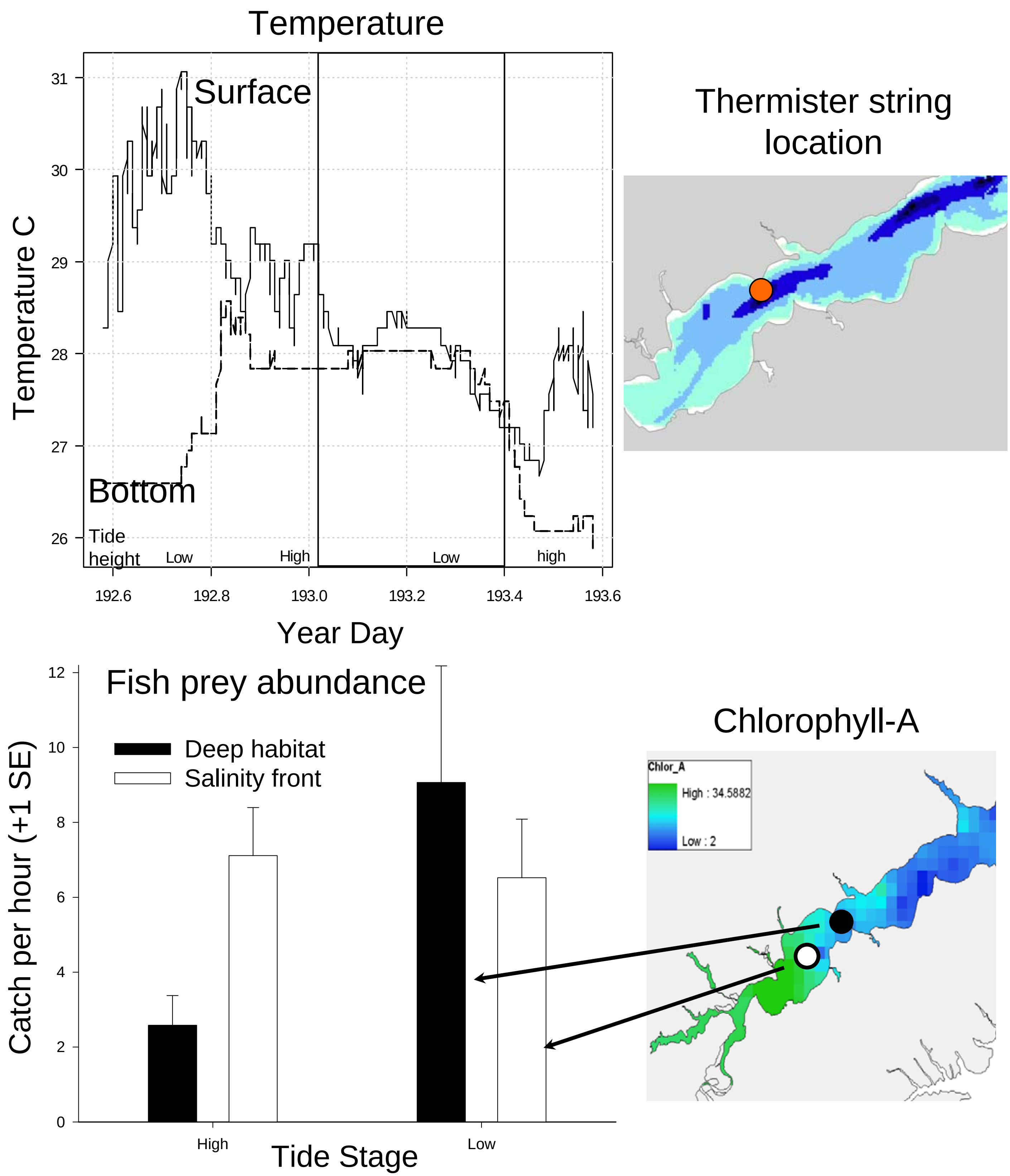


Figure 9. Twenty four hour history of surface and bottom (~8m) temperature measured with a thermistor string in the deep habitat located at location C which may provide a thermal refuge for fish during certain periods (hatched area indicates nighttime). Bottom water can be as much as 5o C cooler than surface water during daytime ebb tides. Mean abundance of small fish prey (Anchoa mitchelli, Menidia menidia) collected with small mesh gill nets during daytime high and low tides in the deep habitat and salinity front in the upper Navesink River. Plot shows a typical location for the Chlorophyll-A front and the location of net sampling during a period of low swimming river discharge.