DISCARD MORTALITY, RECRUITMENT, AND CONNECTIVITY OF RED SNAPPER (LUTJANUS CAMPECHANUS) IN THE NORTHERN GULF OF MEXICO

A Dissertation

by

JUDSON MATTHEW CURTIS

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This dissertation meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Red Snapper (*Lutjanus campechanus*) is the most economically important reef fish species in the Gulf of Mexico. Despite being intensively managed, stocks have been slow to recover from overharvest and the population is still rebuilding. One possible reason is that Red Snapper experience high discard mortality after catch-and-release. Additionally, there is a decoupling of the stock-recruit relationship in the fishery with high levels of recruitment despite low spawning stock biomass. This dissertation addressed these gaps in knowledge in three principal chapters.

In Chapter II, I evaluated if certain release methods reduced discard mortality of Red Snapper at different depths and temperatures. I used acoustic telemetry to determine the best-release practices for enhancing survival and to estimate the extent of delayed mortality. Venting and rapid recompression release methods were more beneficial for enhancing survival, and delayed mortality events occurred within a 72-hour time period.

In Chapter III, I used novel acoustic transmitters to analyze the post-release behavior and activity patterns of Red Snapper that survived catch-and-release. Red Snapper had different acceleration and depth activity over diel time periods, and increases in acceleration were correlated with higher depth in the water column. Release treatments did not affect long-term behavior and activity.

In Chapter IV, I examined the stock-recruit relationship for the Red Snapper fishery by assessing whether localized cryptic spawning stock biomass is responsible for maintaining high recruitment levels. Acoustic telemetry and catch data were used to show that large, sow Red

Snapper have high site fidelity and residency patterns in the western Gulf of Mexico, suggesting high recruitment observed in the stock may be originating locally from non-targeted sites.

By identifying the source of the high spawning stock biomass, protection measures and regulations can be implemented to ensure that the current high recruitment to the fishery is sustained. Determining the best-release practices to enhance survival of discarded fish will result in larger stock sizes. Ultimately, implementation of findings from this dissertation into the management process will further assist and expedite the rebuilding of Red Snapper stocks and promote the recovery towards sustainability in this historically important Gulf of Mexico fishery.

DEDICATION

In dedication to the most inspiring and passionate marine biologist I know, my sister, Anna; and to my California coast-raised parents, Tom and Linda, for passing down the love of the ocean to us both.

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CHAPTER I:

INTRODUCTION AND BACKGROUND TO THE RED SNAPPER FISHERY IN THE NORTHERN GULF OF MEXICO

World fisheries have received much attention over the past several decades because of severe over-exploitation that has left many stocks overfished worldwide (Jackson et al. 2001, Pauly et al. 2002, Myers & Worm 2003, Worm et al. 2006). Historically, the majority of this attention has focused on large commercial fisheries and the impacts of stock depletion (Thrush & Dayton 2002). Recently, however, substantial increases in recreational fishing effort have driven an increase in the proportion of total harvest from the recreational sector for 71% of marine species in the U.S. (Sutinen & Johnston 2003, Ihde et al. 2011). Additionally, there are pronounced regional differences across the U.S. in the proportion of recreational to commercial landings. For example, in the Gulf of Mexico (GOM), recreational fisheries make up 64% of total landings, the largest proportion for any region (Coleman et al. 2004). This figure conceivably may be much higher as this estimate does not incorporate catch-and-release, which has become increasingly prevalent as a management tool and conservation strategy in recreational fisheries (Cooke & Suski 2005). The success of catch-and-release as a management strategy depends directly on fish experiencing high post-release survival (Bartholomew & Bohnsack 2005, Cooke & Schramm 2007, Arlinghaus et al. 2007). For some demersal, deep-water species, this may be difficult to achieve as post-release survival may be severely compromised by pressure-related injuries caused by the rapid ascent to the surface associated with fishing activity (Rummer 2007). A prime example of this problem is presented by Red

Snapper (*Lutjanus campechanus*) in the GOM, where short recreational fishing seasons and strict bag limits result in large numbers of discarded fish with a high risk of post-release mortality. Finding effective release practices that minimize injury, mortality, and sub-lethal effects, and maximize the chance of post-release survival is critical to the sustainability of this fishery. Thus, this species is an ideal candidate to test the hypotheses developed for this dissertation.

Red Snapper is considered the most economically important reef fish species in the Gulf of Mexico. The Red Snapper fishery has been heavily exploited for decades and was first classified as overfished in 1988 (Goodyear 1988, Hood et al. 2007). According to recent estimates from the Southeast Data Assessment and Review (SEDAR), overfishing may no longer be occurring, although the stock is still overfished (SEDAR 2013). Red Snapper represents a vital economic commodity for coastal communities along the GOM, supporting valuable commercial and recreational fisheries; thus, effective management strategies are critical to ensure the sustainability of this resource for future generations. In the GOM, Red Snapper are currently managed as a single stock by the Gulf of Mexico Fisheries Management Council (GMFMC) under the Reef Fish Fishery Management Plan enacted in 1984. Conflicting perceptions among stakeholders, scientists, and managers concerning the health of the Red Snapper fishery has created many controversies with regard to how the stock should be managed (Cowan et al. 2010). Regulatory measures have included a combination of bag limits, minimum size limits, catch quotas, seasonal closures, and total allowable catches for both the recreational and commercial fisheries. The cumulative effect of these regulations has only recently alleviated the overfishing status of Red Snapper populations and they are still in the rebuilding phase. At the current rate, stock recovery is expected by 2031 (SEDAR 2013). However, these recovery patterns are heavily debated because of a lack of scientific understanding of some key population parameters (Cowan et al. 2010). Clearly, to increase the recovery rate of this species, better understanding of the factors affecting the fishery, such a mortality resulting from regulatory discards (i.e., release) and its associated barotrauma, understanding site fidelity and movement patterns of adult spawners, and better explanatory models of population connectivity, will help toward better management and recovery of this fishery.

Minimum size limits have been a regulatory strategy employed by fishery managers in a variety of fisheries worldwide and similarly have been used in the GOM Red Snapper fishery since 1984 (Hood et al. 2007). Currently, the recreational fishery minimum size limit for Red Snapper in federal waters of the GOM is 406 mm (16 inches); no maximum size limit exists. The consequence of setting a minimum size limit is that a large proportion of undersize fish are required to be released after capture (Coleman et al. 2004). This problem has been compounded by an increasingly shorter recreational fishing season, as snapper are commonly captured out of season as bycatch. These “regulatory discards” may represent an estimated 75 – 98% of the total catch in the GOM (Dorf 2003, Nieland, Fischer, et al. 2007). SEDAR (2009) estimates showed more than a 2:1 ratio in discards to total landings. In addition, new smartphone electronic reporting (i.e., “iSnapper”; Stunz et al. 2013) indicates even during the season as much as 40% of Red Snapper are discarded. Because of the depth preferences of these fish, individuals commonly experience reduced survival from a variety of factors including post-release predation, trauma from pressure-related injuries, and environmental conditions (e.g., thermal stress related to water temperature differences at depth and the surface). Total estimates of immediate post-release mortality have been highly variable, ranging from 20 – 66% (Campbell et al. 2013). Immediate post-release mortality of regulatory discards varies seasonally (Render & Wilson 1994) and with depth (Gitschlag & Renaud 1994, Burns et al. 2004). Once released, fish are presumed to survive but this may not necessarily be true, and delayed mortality may account for 36 – 64% of total mortality in regulatory discards (Gitschlag & Renaud 1994, Diamond & Campbell 2009). Delayed mortality may occur from reduced fitness, reduced predator avoidance ability, inability to forage, or lingering effects of internal organ trauma after release. The fate of regulatory discards remains highly ambiguous and merits further scientific study as accurate estimates of total mortality in the Red Snapper fishery represent essential information in determining overall catch and landings data.

Delayed fishing mortality is thought to occur from a series of pressure-related injuries, collectively referred to as “barotrauma” or “catastrophic decompression.” These symptoms are associated with bringing the fish to the surface rapidly from depth causing an overexpansion of the swim bladder. The effects of barotrauma inflicted injuries is highly variable and depth dependent (Burns et al. 2002, Rummer & Bennett 2005, Burns 2009a). Externally evident barotrauma symptoms include stomach and intestine eversion, bulging eyes, subcutaneous gas bubbles, external hemorrhaging, and hard swim bladders. Rummer & Bennett (2005) detected up to 70 different overexpansion injuries caused by barotrauma, including severe damage to vital organs. Regulatory discards suffering from barotrauma may be prevented from returning to depth because of increased buoyancy associated with an overinflated swim bladder, making them easy targets for predation by dolphins, sharks, barracudas, and other top predators (Burns et al. 2004). Federal requirements previously stipulated that fishermen must carry a venting tool on board their vessels to release excess gases that accumulate in the body cavity of the fish, but the efficacy of venting has recently been called into question (Wilde 2009), and managers recently rescinded this requirement in the GOM. One method to avoid venting upon release that has recently been developed is the use of rapid recompression devices such as weight-descended hooks, whereby the fish is placed on an inverted hook containing a heavy weight at the end of the line that quickly takes the fish back to depth and rapidly recompresses the swim bladder. These "descender hooks" were developed for the California rockfish fishery but conceptually would also serve the Red Snapper fishery. However, the effectiveness of this approach of the descender hooks has not yet been examined for Red Snapper in the GOM, and the utility of venting and use of recompression devices certainly merit further investigation.

In Chapter II, I focus on determining the fate of regulatory discards afflicted with barotrauma injuries using acoustic telemetry. I analyzed the effects of temperature and depth on Red Snapper mortality and assessed if venting and rapid recompression release strategies may increase survival. The many potential reasons for barotrauma-inflicted mortality (temperature, release method, hook type, depth, etc.) previously mentioned have never been examined using acoustic telemetry. Using this technology along with specialized tags that measure acceleration and depth in the water column, novel insights can be gleaned into Red Snapper mortality and behavior up to 45 days after fish are caught-and-released, thereby estimating delayed post-release mortality in ways not previously documented. These results will fill important gaps in stock assessments where this release mortality is often only a "best guess." Additionally, the "best practices" of release for maximizing the chance of survival in discarded fish for the recreational fishery will be determined.

In Chapter III, I extend the utility of these acceleration and depth sensors to document behavior patterns of Red Snapper that survived the catch-and-release process from a long-term mortality standpoint. The focal point of this chapter is to determine if the method of release has longer-term ramifications for fitness, behavior, and other sub-lethal effects beyond immediate survival after catch-and-release. A secondary objective is to use acceleration and depth sensors to examine diel movement patterns and build an ethogram that classifies the activity and behavior of Red Snapper over a period of time. Advances in transmitter technologies have made it possible to examine extremely fine-scale (spatial and temporal) movement patterns and have enabled novel areas of study in the areas of physiology and behavior. Conclusions from this chapter provide further insight into the post-release behavior of discarded Red Snapper over a longer time period and help determine the best-release practices of maximizing survival in fish subject to catch-and-release.

In Chapter IV, I examined whether localized cryptic spawning stock biomass is responsible for maintaining high recruitment levels seen in the Red Snapper fishery while adult populations are at all-time lows. I tagged and tracked large “sow” Red Snapper to determine if they use different habitats compared to smaller, younger Red Snapper. If habitat preferences are determined to be different for sow snapper, this finding would lend support to the “Mother Lode” hypothesis, suggesting that significant localized recruitment is occurring and is responsible for the large proportion of overall recruitment witnessed in the face of declining population size and spawning stock biomass. To complement the tagging studies, I also analyzed data from a series of catch-per-unit-effort trials to determine if certain site or structure characteristics have differential abundance and/or size of Red Snapper. The life history characteristics of Red Snapper are first described to provide the context for the Mother Lode hypothesis and how the experimental design for this chapter was conceived.

Red Snapper belong to the family Lutjanidae in the order Perciformes (Allen 1985). Geographically, Red Snapper have a wide distribution, ranging along the eastern Atlantic from Massachusetts to Brazil but are most commonly found in the GOM. The temperature range of this species is between 14 and 30°C with the optimal temperature determined to be 18°C (Moran

1988). Depth range varies seasonally with summer depths ranging from 20 – 30 m and winter depths ranging from 30 – 65 m, although adult individuals may exist as deep as 256 m (Moran 1988). Post-settlement juveniles are generally found in shallower depths of 10 – 35 m (Gallaway et al. 2009). Individuals initially grow rapidly in the first year and continue to grow quickly until approximately age 10 when the growth rate starts to level off. While increases in total length become asymptotic, significant increases in weight still occur (Wilson & Nieland 2001). Red Snapper are a long-lived species with a reported maximum age of over 50 years in the GOM (Wilson & Nieland 2001, Fischer 2007).

Red Snapper reach sexual maturity at two years of age and spawn offshore in the GOM between the months of April and September with the peak spawning period occurring in June through August (Collins et al. 1996). Red Snapper are heterochronal (batch) spawners with indeterminate annual fecundity (Collins et al. 1996, Porch et al. 2007, Brulé et al. 2010). Egg production in female Red Snapper increases exponentially such that larger female Red Snapper contribute a disproportionate amount of eggs relative to smaller Red Snapper. At age 10, a female Red Snapper can produce 60 million eggs (Collins et al. 1996, SEDAR 2005). Larvae spend 22 – 28 days in a pelagic larval stage before settling on the benthos on soft, mud bottoms in open areas (Geary et al. 2007, Gallaway et al. 2009). Juveniles seek a variety of benthic substrates with small-scale complexity, including mud flat habitats, and structured habitats such as shell ridges and rock outcroppings occurring both inshore and offshore (Szedlmayer & Howe 1997, Rooker et al. 2004, Patterson et al. 2005, Geary et al. 2007, Piko & Szedlmayer 2007, Wells & Cowan 2007). In the late fall, juveniles move to more structured habitats that include natural and artificial reefs. At age 2, individuals recruit into the directed fishery where they are caught by commercial and recreational fishermen on artificial and natural structured habitats.

Age 2 – 3 fish represent the most abundant size class on artificial reefs in the directed fishery (Gitschlag et al. 2003, Nieland & Wilson 2003). They are thought to use these habitat types for the remainder of their adult life, although recent evidence indicates that older fish might move off these reef areas in favor of open areas with mud bottoms containing small, less structured relief (Nieland & Wilson 2003, Gallaway et al. 2009).

Red Snapper are carnivorous, feeding primarily on shrimp, copepods, and squid as juveniles (Szedlmayer & Lee 2004). As individuals grow and move toward structured habitats, diet preferences shift towards feeding more frequently upon fish and squid as adults (Szedlmayer & Lee 2004, McCawley & Cowan 2007, Wells et al. 2008). Large adults are thought to be nearly exclusively piscivorous, and diets vary with diel feeding period (Ouzts & Szedlmayer 2003, McCawley et al. 2006). Predators of Red Snapper include larger, piscivorous pelagics such as dolphins and sharks. At larger sizes, however, Red Snapper are presumed to have few predators. Red Snapper tend to aggregate together in dense populations associated with reef structures and exhibit high site fidelity to these structures once there (Patterson & Cowan 2003, Szedlmayer & Schroepfer 2005, Strelcheck et al. 2007, Westmeyer et al. 2007, Topping & Szedlmayer 2011a), and they co-occur with a number of other species that also associate with these structured habitats.

Despite declines in overall population size and spawning stock biomass of Red Snapper, the overall number of recruits is increasing. One purpose of this dissertation was to test the Mother Lode hypothesis, which states that there is an unfished portion of the Red Snapper population that consists of larger female sow Red Snapper (> 686 mm) that contribute a disproportionate amount of recruits to the population because of their associated high fecundity. These larger fish may escape harvest because of differential habitat use. I hypothesize that these sow snappers may use different habitats than smaller, younger Red Snapper. Instead of inhabiting large artificial reef structures (i.e., oil/gas platforms) widely known to attract Red Snapper (Patterson & Cowan 2003, Westmeyer et al. 2007) and heavily targeted by fishermen, these larger sow snappers reside off-structure in relatively unknown areas where they escape fishing pressure (Mitchell et al. 2004). These unknown habitats acting as a refuge from harvest serve as a source of localized recruitment for the overall population and explain why recruitment levels have been higher than previously seen despite low spawning stock biomass.

Chapter V summarizes the overall conclusions of each of the findings of the previous chapters as they relate to the implications for fishery management and provides some discussion regarding the future direction of the Red Snapper fishery based on current data projections.

CHAPTER II:

QUANTIFYING DELAYED MORTALITY IN DISCARDED RED SNAPPER USING ACOUSTIC TELEMETRY

ABSTRACT

Red Snapper (*Lutjanus campechanus*) is the most economically important reef fish species in the Gulf of Mexico. Despite being intensively managed, the stock remains in a state of recovery. One possible reason for the slow recovery of this long-lived fish is that Red Snapper are susceptible to pressure-related injuries (i.e., barotrauma) that compromise the chance of survival post catch-and-release, and discard mortality is high. Barotrauma afflicted fish may not only experience immediate mortality at the surface but also delayed mortality after returning to depth. This unknown drives uncertainty in stock assessment models. To determine the extent of delayed mortality and post-release behavior, we tagged Red Snapper across a variety of treatments with ultrasonic acoustic transmitters and recorded acceleration and depth data for approximately 45 days. Unique behavior profiles were generated for each fish allowing classification of survival and delayed mortality events. The severity of barotrauma and likelihood of survival were influenced by sea surface temperatures, depth of capture, and release treatment. Survival was higher at cooler versus warmer temperatures and at shallower depths compared to deeper depths. Additionally, venting and rapid recompression strategies had higher survival than non-vented, surface-released fish suggesting these methods may increase the probability of post-release survival. Acoustic profiles showed that fish suffering from delayed mortality perished within a 72-hour period. Overall, we experienced 70% survival, 19% immediate mortality, and

11% delayed mortality across all treatments. Results from these experiments enhance the understanding of delayed mortality and post-release behavior of Red Snapper and provide conclusive information documenting the fate of regulatory discards. Estimates of delayed post-release mortality from this study can be integrated into stock assessment models to reduce uncertainty in discard mortality estimates.

INTRODUCTION

Catch-and-release has become an important fisheries management tool, but clearly this strategy is only effective when released fish have high survival (Bartholomew & Bohnsack 2005). For many offshore reef fish species this may be difficult to achieve as they tend to live at deep-water depths and routinely experience pressure-related injuries when brought to the surface (Rummer 2007). These coupled characteristics have historically contributed to high release mortalities in many important fisheries including Gulf of Mexico Red Snapper (Campbell et al. 2013). Certainly, development of techniques that avoid or minimize injury or mortality associated with pressure-related injuries has the potential to significantly improve the management of deep-dwelling species.

Demersal, physoclistous fishes in deep-water environments suffer an increased risk of discard mortality in catch-and-release fisheries because of barotrauma – a combination of pressure-related injuries associated with the rapid ascent to the surface from depth associated with fishing. These injuries are caused by the initial displacement and subsequent compression of internal organs by gas expansion in the swim bladder and other body cavities because of the inverse relationship between gas pressure and volume (i.e., Boyle’s Law). Rummer and Bennett (2005) documented over 70 symptoms of barotrauma in Red Snapper from necropsies of fish afflicted with barotrauma using hyperbaric chamber experimentation and X-ray imaging. Common and observable external effects include everted stomachs, exopthalmia (eyes forced from orbits), intestines protruding from anus, formation of subcutaneous gas bubbles, and bleeding from gills. Barotrauma severity increases with capture depth and can also be affected by hydrographic variables such as sea surface temperatures, thermoclines, and dissolved oxygen (Gitschlag & Renaud 1994, Patterson et al. 2001, Rummer & Bennett 2005, Rummer 2007, Alós 2008, Diamond & Campbell 2009, Brown et al. 2010, Campbell et al. 2010, Sumpton et al. 2010, Butcher et al. 2012).

Red Snapper is considered the most economically important reef fish species in the Gulf of Mexico and, consequently, has been heavily managed since the fishery was first classified as overfished in 1988 (Goodyear 1988, Hood et al. 2007). Management strategies enacted by the Gulf of Mexico Fishery Management Council (GMFMC) for the recreational fishery have included reducing bag limits, shortening fishing seasons, and setting minimum size limits with the goal of reducing fishing pressure and allowing stocks to rebound (see Hood et al. 2007 for comprehensive fishery management history). However, with the stocks not fully rebuilt and almost a two-decade horizon in the rebuilding phase remaining, management strategies have become increasingly stricter. An unintended consequence of these tightened regulations has been the increase in the amount and frequency of “regulatory discards” – fish that are required by law to be released because they do not meet size, season, or bag requirements. This species commonly experiences severe barotrauma, and the large number of discards with associated high release mortality due to barotrauma, may represent a large portion of overall mortality in the fishery and substantially impact annual catch limits for future years.

Studies attempting to quantify discard mortality in the Red Snapper fishery have been extensive, yet remain inconclusive and highly variable. The latest estimate of discard mortality from a meta-analysis of studies ranges from 0 to 91% (Campbell et al. 2013), and this wide range is influenced by season, fishery sector, geographical region, water depth, among other factors, and is further complicated by interactions among these factors (Gingerich et al. 2007). Moreover, the majority of these studies have only included immediate discard mortality, or mortality that is observed from surface observation within several seconds post-release, and delayed mortality is unknown. Although fish that are capable of re-submerging unassisted are presumed to survive, this assumption is largely untested, and there is some evidence that the ability to swim away is unrelated to survival (Bettoli & Osborne 1998, St John & Syers 2005, Diamond & Campbell 2009). A substantial proportion of fish may undergo delayed mortality hours to several days after a purported successful release. At depths between 20 and 50 m, delayed mortality estimates using cage experiments ranged from 20 to 71% (Gitschlag & Renaud 1994, Render & Wilson 1994, Diamond & Campbell 2009). While cage studies allow the ability to track post-release survival over longer time periods, they have an inherent bias because they exclude predatory effects, prevent foraging, and restrict natural movement (Campbell et al. 2013).

One method to overcome the biases associated with cage studies in estimating delayed mortality in the field is through the use of ultrasonic acoustic telemetry. Acoustic transmitters send out uniquely coded high-frequency signals that are detected by an array of acoustic receivers. This technique has already been extremely successful in tracking movements, long-term residency, and site fidelity of Red Snapper (Szedlmayer & Schroepfer 2005, Peabody & Wilson 2006, Westmeyer et al. 2007, Topping & Szedlmayer 2011a) but has not yet been used to quantify discard mortality. Recent advances in tag technology have now made this possible.

Transmitters are equipped with sensor technologies allowing researchers to monitor post-release survival and behavior of fish via acceleration and depth. For fish experiencing barotrauma, these tags can provide presence/absence data, mortality (no acceleration), post-release depth preference, and activity level compared to fish not experiencing barotrauma. There have been no published tagging studies that used these advanced acoustic tags to examine physiological responses of Red Snapper, particularly as they relate to regulatory discards and examining delayed mortality. Using this tagging methodology not only allows us to avoid cage artifacts but also replicate post-release fishing practices most reflective of the actual fishery.

Despite highly variable and inconsistent estimates of discard mortality, minimizing death after release is a common goal for fishery managers. Because pressure differences from seafloor to surface cause exponential increases in swim bladder volume, one management strategy adopted was a requirement to “vent” the swim bladder to release the excess gas, thereby returning the fish to neutral buoyancy prior to release. This practice involves puncturing the swim bladder of the fish by inserting a hypodermic needle (venting tool) into the abdomen posterior to the pectoral fin and became a GMFMC implemented requirement for the Red Snapper fishery in 2008. Recently, the venting regulation has been rescinded to allow the use of descender devices (e.g., SeaQualizer^{TM} and Shelton Descender Hook^{TM}) along with some skepticism over the efficacy of venting in reducing discard mortality (Wilde 2009). Results specific to Red Snapper observed by Wilde (2009), however, were inconsistent, with one study showing positive (Gitschlag & Renaud 1994), two studies showing neutral (Render & Wilson 1994, 1996), and one study showing negative (Burns et al. 2002) effects of venting on survival. An alternative to venting and potentially more effective method of release is rapid recompression using descending devices. This technique involves rapidly descending the fish back to depth on a weighted line prior to release to rapidly recompress the swim bladder and alleviate any barotrauma symptoms without having to vent the fish. Additionally, this method also avoids releasing the fish at the surface where increased risk of predation exists (Burns et al. 2004). Few studies have examined the efficacy of using rapid recompression techniques to reduce discard mortality in catch-and-release fisheries, and this remains an unexplored area warranting further research.

The inconclusive estimates of discard mortality in the Red Snapper fishery necessitate further study. Additionally, determining which release treatments are most effective is imperative for increasing survival rates. Coupling surface observations with acoustic telemetry can provide estimates of both immediate and delayed mortality of discarded fish. Thus, the primary goal of this study was to determine the fate of discarded Red Snapper and to quantify the extent of delayed mortality using acoustic telemetry. Specifically, I tested whether: (i) certain release treatments are more favorable for increasing post catch-and-release survival and if rapid recompression strategies are a better alternative to venting, (ii) season of capture associated with differences in water temperatures and presence of thermoclines influence survival, and (iii) if depth of capture influences survival. This study will help managers better understand how delayed mortality estimates may factor into overall discard mortality and refine models aimed towards rebuilding Red Snapper populations.

METHODS

Study area

The northwestern Gulf of Mexico continental shelf contains predominantly soft, silty-clay benthic habitat with small areas of isolated natural hard-bottom substrate. The other major source of hard structure is provided by artificial reef habitats comprised primarily of oil and natural gas platforms, concrete culverts and other structures, and relict ships. Oil and gas platforms are popular fishing structures; thus, standing oil and gas platforms approximately 50 km east of Port Aransas, Texas were selected as study sites for these experiments. Sites MU-762-A and MU-759-A (approximately N27°45’, W96°35’) reside at 50 m water depth and sites MI-685-B and MI-685-C (approximately N27°55’, W96°35’) at 30 m water depth (Figure 2.1).

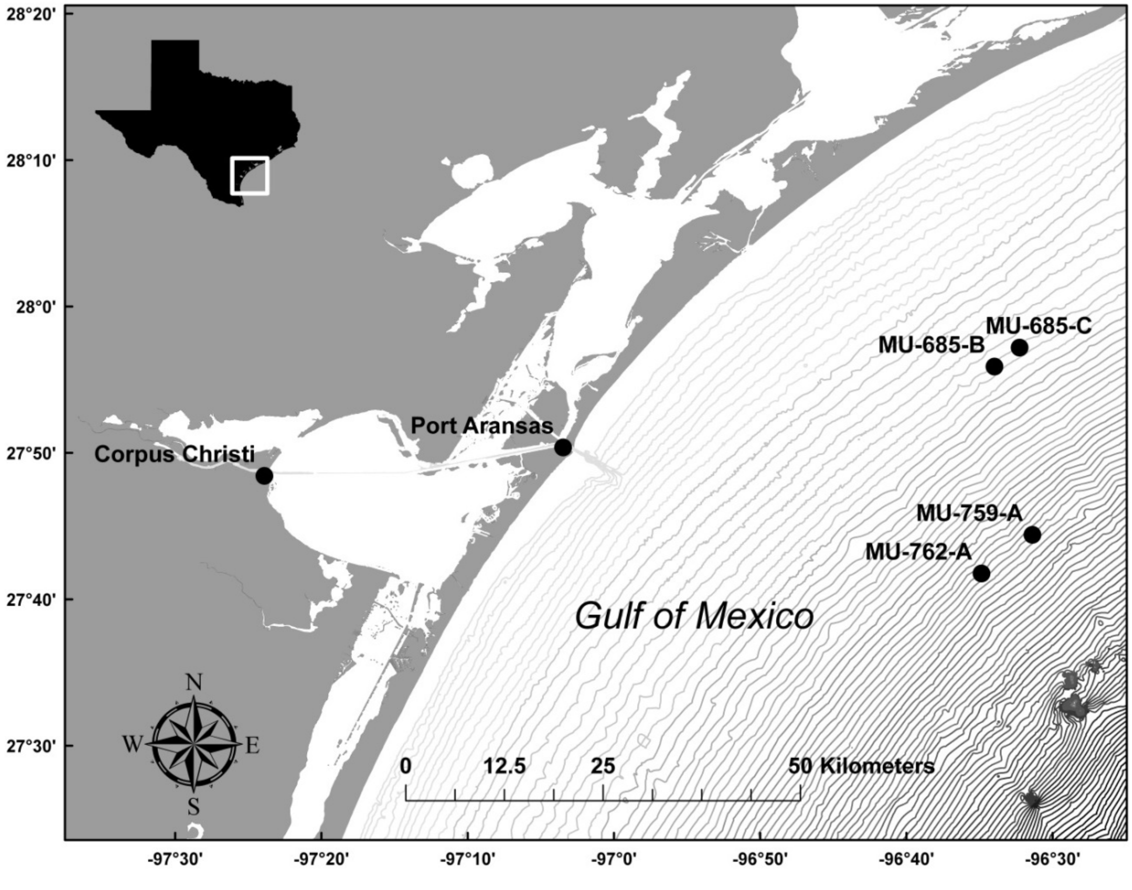


Figure 2.1. Study sites (standing oil/gas platforms) in the Gulf of Mexico off the South Texas coast where field tagging experiments occurred. Sites MU-685-B and MU-685-C reside at water depths of 30 m and sites MU-762-A and MU-759-A at 50 m.

Fish tagging

Red Snapper were captured at each site using hook-and-line sampling gear using 5/0 circle hooks baited with squid (*Loligo sp.*), scad (*Trachurus sp.*), or sardines (*Sardinella sp.*). Data recorded during fishing operations included hooking time, landing time, and release time allowing us to calculate overall fight time and handling time for each fish. Once landed, fish were measured for maximum total length (mm) and assessed (presence/absence) for six externally visible barotrauma symptoms: everted stomachs, swollen and hard abdomen, exopthalmia (eyes forced from orbits), intestines protruding from the anus, formation of subcutaneous gas bubbles, and bleeding from the gills. A barotrauma impairment score (scale: 0-1) was calculated by the sum of visible symptoms divided by the total number of possible symptoms (Diamond & Campbell 2009). Fish that appeared obviously moribund from severe barotrauma or deep hooked were not tagged.

Red Snapper were externally tagged with Vemco© V9AP ultrasonic coded transmitters (V9AP-2H, 46x9 mm, 69 kHz, random delay interval: 30-90 s, estimated battery life: 45 days) containing built-in acceleration and pressure (i.e., depth) sensors. To measure acceleration, the V9AP tags calculate a value (m s^{-2}) that represents the root mean square acceleration on three axes (X, Y, and Z) averaged over a fixed time interval:

$$m\,s^{-2} = \sqrt{x^2 + y^2 + z^2}\ averaged\ over\ time\ (T) \tag{1}$$

Depth is calculated by an algorithm that coverts pressure sensors to a depth value (max depth < 100 m). Because one goal of our study was to explore survival under a variety of release treatments, fish were rapidly (< 3 min) tagged externally without anesthesia (IACUC AUP #02-11) to best replicate normal fishing and release practices and minimize artifacts associated with tagging related surgeries (i.e., venting and use of only survivors). One challenge was to prevent unavoidable venting associated with traditional incision and suture internal tag implantation; therefore, we developed and validated a protocol to attach tags to fish externally in the lab (Johnson et al. 2014). In preliminary trials, tag presence did not impair fish behavior and tag retention using our external attachment method was 100% through 25 days. Tags were positioned below the anterior (3rd-6th) dorsal spines approximately 2-3 cm below the dorsal edge. Fish were punctured between pterygiophores below the anterior dorsal spines using a sterile stainless steel hollow surgical needle. Surgical grade suture monofilament was passed through one hollow needle, attached to the tag, and passed back through the second hollow needle and secured so that the orientation of the tag was parallel to the fish and on the opposite side as the secured monofilament. Fish were held in a tagging cradle with gills submerged in oxygenated water throughout the tagging process. An externally visible dart tag containing identification and reward information was also inserted into the posterior dorsal spine region.

Release treatments

Prior to tagging, fish were randomly assigned to one of four release treatments: (1) vented surface release; (2) nonvented surface release; (3) descended bottom release; and, (4) control (no barotrauma). Fish were released at the surface into an open-bottom 1.0 m^3 holding cage with mesh walls to protect fish from predation and enable retrieval of fish (and transmitters) that experienced immediate mortality at the surface. During all trials the number of immediate surface mortalities post catch-and-release was recorded and incorporated into the analyses. Vented surface-released fish were punctured in the abdomen posterior to the pectoral fin using a venting tool (Team Marine USA™ pre-vent fish venting tool) to allow escape of excess gas built up in the swim bladder. Once all residual gas had been vented, these fish were tagged and released at the surface. Nonvented surface released fish were not vented prior to tagging and released at the surface. Descended bottom released fish were not vented prior to tagging but, instead of being released at the surface, were forced back to depth quickly using a weighted line with an inverted barbless hook (Shelton Fish Descender^{TM}) attached to the fish's jaw and released at the bottom. This setup is one of several rapid recompression tools that quickly return the fish to depth to counteract the effects of barotrauma through rapid gas recompression without venting. Control fish had no barotrauma prior to tagging and release. To achieve this, fish were captured at the study sites prior to experimental trials, transported to the Texas A&M AgriLife Research Mariculture Laboratory in Port Aransas, Texas, and held in 6400 L tanks for three weeks. Fish were treated for parasites using copper (II) sulfate and were fed three times weekly to satiation with a diet of squid and sardines. Fish recovered and began feeding quickly (typically within 24 h), and health and behavior of these fish were closely monitored. After a three-week holding period, fish were transported in oxygenated live wells to the study site where they were tagged and released along with fish assigned to the other release treatments in randomized order.

Experimental design

Three tagging trials occurred in different seasons: summer, winter, and spring. During each of these trials, we measured water temperature, salinity, dissolved oxygen, and conductivity using a Manta2 water quality multiprobe (Eureka Environmental Engineering). This unit was deployed to depth for each trial and recorded a data point at one second intervals. All drops were performed to a depth of 50 m at the same tagging site for each season: MU-762-A. Hourly sea surface temperatures for the duration of tagging trials (~ 45 days post tagging) were obtained from NOAA-NDBC station 42020 (N26°58', W96°42'). Summer and winter trials were performed at 50 m depth on site MU-762-A. Twenty fish were tagged and released on site using one of three release treatments: control, nonvented surface, or descended bottom release. However, because of repeated inability of nonvented fish to re-submerge during the summer trial and subsequent mortality, we were forced to modify our protocols and add a vented surface release treatment. Additionally, venting requirements were initiated by the GMFMC during the course of this study. Thus, the venting treatment was not always included to represent a balanced design. Because of expense, tags were limited for this study that prevented each treatment during every season. Thus, for spring trials, where survivorship was expected to be high, a second depth was incorporated into the experimental design to test for depth differences at two sites at 30 m (MI-685-B and MI-685-C) and two sites at 50 m (MU-762-A and MU-759-A). At each depth, 32 fish were tagged between the two sites (*n* = 64) and all four release treatments were included. Two Vemco VR2W-69kHz acoustic monitoring receivers were attached to platform cross beams by scuba divers at each study site. Receivers were placed at depths of approximately 20 and 30 m for 50 m sites and at 15 and 25 m for 30 m sites.

Fish survivorship classification

VR2W receivers were retrieved from study sites after approximately 60 days and data were uploaded to Vemco VUE$^{©}$ software and exported for analysis to R version 3.0.2 (R Development Core Team 2013). Acceleration and depth profiles for each fish plotting these values over time were generated using tag sensor data. Using these unique acoustic profiles, the fate of each individual was classified into one of three categories: survivor, delayed mortality, or unknown. Surface mortalities did not yield an acoustic profile but were counted towards estimates of total mortality. Fish classified as survivors had continuous detections after release, with frequent changes and bursts in acceleration and vertical depth movements in the water column. Delayed mortality events were classified by initially active acceleration and depth movements followed by a sudden drop-off to zero acceleration and depth equal to the seafloor. Fish that emigrated from the array and did not register sufficient detections to classify as either survivor or delayed mortality were classified as unknown. These fish are classified as unknown because it is not possible to decipher whether the end of detections are due to fish emigration from the array (i.e., survival event), or predation (i.e., mortality event). Because the fates of these unknowns were unclassifiable, these fish were omitted from subsequent analyses.

Survival analysis

Percent survival was calculated using the binomial distribution for two outcomes: survival and mortality. Fish classified as unknown were omitted from the model. Mortality, in this case, represents total mortality or the sum of immediate surface mortality witnessed during trials plus delayed mortality as indicated by acoustic returns. Survival estimates ($\hat{S}$) were calculated following equations in Pollock & Pine (2007):

$$\hat{S} = \frac{x}{n} \tag{2}$$

with a standard error of:

$$SE(\hat{S}) = \sqrt{\frac{\hat{S}(1-\hat{S})}{n}} \tag{3}$$

where x is the number of survivors, and n is the total number of tagged fish minus the fish classified as unknown (i.e., survivors + surface mortalities + delayed mortalities).

The probability of survival post catch-and-release was calculated using the product limit estimate (Kaplan & Meier 1958) built into the ‘survival’ package in R (Therneau & Grambsch 2000). At each time interval (day), survival probability is calculated by dividing the number of survivors (x_i) by the number of individuals alive at that interval (n_i). The Kaplan-Meier estimate of total survival probability ($\widehat{K}$) is calculated by multiplying all probabilities of survival at all time intervals preceding the time interval of interest:

$$\widehat{K}(i) = \prod_{i=1}^{j}(1 - x_i/n_i) \tag{4}$$

Survival probabilities were plotted for a time period greater than 10 days for each level of three factors: release method, season, and depth.

The Cox proportional hazards model (Cox 1972), also built into the ‘survival’ package in R (Therneau & Grambsch 2000), was used to examine the relationship between survival and multiple explanatory variables. This model has been used extensively in public health studies but has only recently been applied to survival analysis in fisheries (Sauls 2014). The Cox model is a semi-parametric regression method for survival data. It provides an estimate of the treatment effect on survival after adjustment for other covariates in the model and gives an estimation of the hazard ratio (in this case the proportional risk of death) among levels within each of these explanatory variables. For survival analysis, this method is advantageous over logistic regression models because it can account for survival times and censored data, whereas regression models do not. Additionally, hazard ratios between covariates may be estimated without needing to specify the underlying baseline hazard, which may not be known. The Cox proportional hazards model is given by:

$$h(t) = h_0(t)\exp(\textstyle\sum_{i=1}^{p} \beta_i X_i) \tag{5}$$

where $h_0(t)$ is an unspecified function representing the baseline hazard, β_i are regression coefficients, and X_i are the explanatory variables or covariates in the model. The three covariates used in the Cox proportional hazards model for this study were release method, season, and depth.

RESULTS

Temperature data

Hydrographic water data were collected during each of the three tagging days using a Manta2 water quality multiprobe. Temperature was plotted against depth to determine if thermoclines in the water column were present and if so, at what depths they ranged (Figure 2.2). During winter tagging, a thoroughly mixed water column at a constant 24°C and no thermocline was apparent in temperature data. The spring tagging date had a temperature range of 3.5°C (23.5°C at the surface to 20°C at the seafloor) with a thermocline beginning at a depth of 20 m. Water temperatures from 22 – 31°C occurred in the summer profile, with a steep thermocline observed beginning at 25 m depth and continuing to the seafloor. Sea surface temperatures for each season were recorded hourly from NOAA-NDBC station 42020 and reported for a period of 10 days after fish tagging (Figure 2.3). Winter temperature was relatively constant over 10 days and averaged 23°C ± 0.39 (mean ± SD). In the spring, temperature had a slight increasing trend over 10 days and averaged 25°C ± 0.68 (mean ± SD). Summer temperatures also remained constant for 10 days and averaged 30.5°C ± 0.39 (mean ± SD). Mean temperatures in each season were significantly different from one another (ANOVA, $F_{2,716} = 5102$, $p < 0.001$).

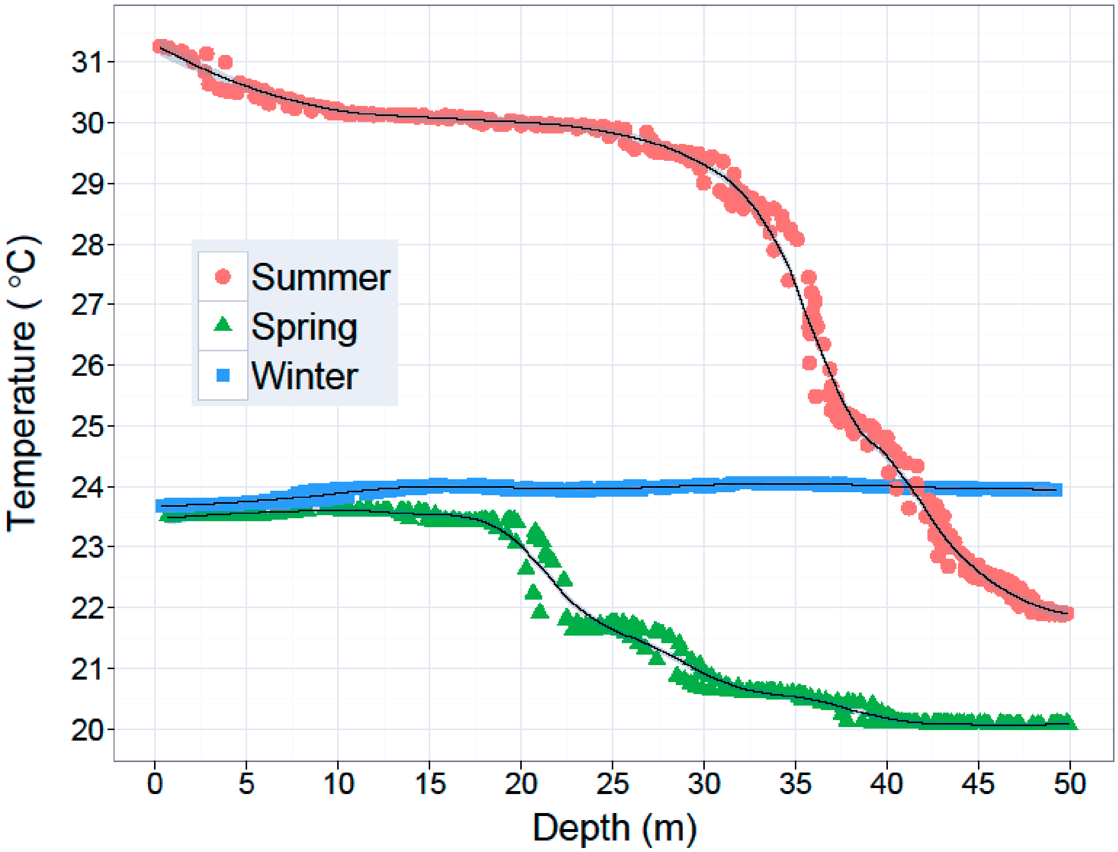


Figure 2.2. Temperature versus depth data collected using a Manta2 water quality multiprobe during three seasonal tagging trials at site MU-762-A (50 m). Black smoothing lines fitted to temperature data using loess model.

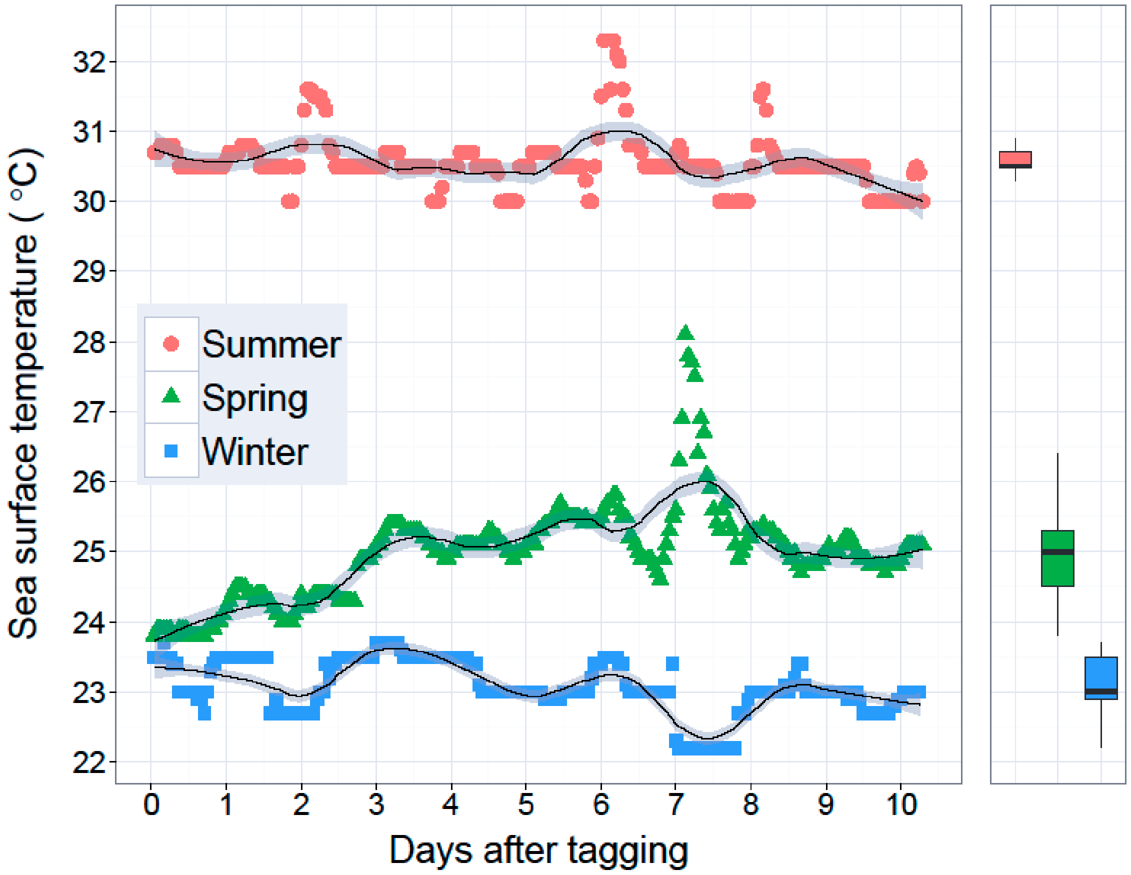


Figure 2.3. Sea surface temperatures (°C) during the first 10 days fish were at liberty for three seasonal tagging trials. Data obtained from NOAA-NDBC buoy 42020 (N26°58’, W96°42’). Boxplots show distribution of temperature data for each season. Black smoothing lines were fitted to temperature data using loess model.

Fish tagging

A total of 111 Red Snapper ranging from 280-651 mm TL (mean ± SE: 446 ± 7.8 mm) were caught and tagged over three seasonal trials (Figure 2.4). No significant differences existed in TL among release treatments (ANOVA, $F_{3,106} = 2.13$, $p = 0.10$). Fight time was positively correlated with TL (Pearson's $r = 0.327$, $p < 0.01$, $n = 111$). Handling time on deck was not correlated with TL (Pearson's $r = -0.050$, $p = 0.62$, $n = 111$). However, descended bottom release fish had marginally longer handling times (25.0 ± 11 s) than other release treatments (ANOVA, $F_{3,97} = 3.10$, $p = 0.03$), attributed to the extra time on the descender hook device as the fish was being descended from surface to seafloor. Handling time stopped recording only after the fish had been released from the descender hook at the seafloor. Fish were assessed for six externally visible barotrauma symptoms: everted stomachs, swollen and hard abdomen, exopthalmia (eyes forced from orbits), intestines protruding from the anus, formation of subcutaneous gas bubbles, and bleeding from the gills, and were given a barotrauma impairment score (scale: 0 – 1) upon catch, calculated by adding up visible symptoms and dividing by the total number of possible symptoms (six). Fish released under vented, nonvented, and descended release treatments had a mean score of 0.32 ± 0.02 (mean ± SE) and were not significantly different (ANOVA, $F_{2,89} = 0.41$, $p = 0.66$). All control treatment fish had a barotrauma impairment score of zero at the time of release.

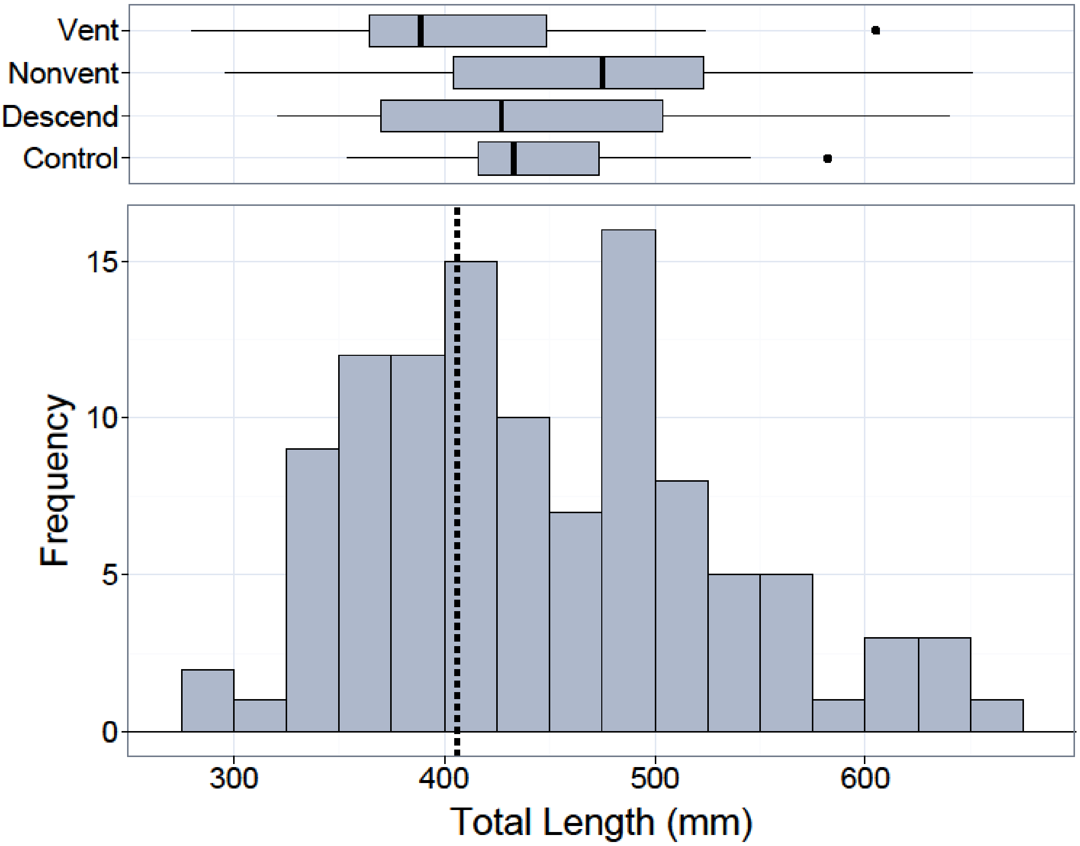


Figure 2.4. Distribution of total lengths (mm) for all Red Snapper caught during trials (*n* = 111) binned in 25 mm increments. Dashed line represents the federal minimum size limit for Red Snapper in the recreational fishery (406 mm, 16 inches). Top panel shows the size distribution of individuals by release treatment (vented, nonvented, descended, and control). Points represent outliers in the size distribution at each level. There was not a significant difference in total length among release treatments.

Fish survivorship classification

Each of the 111 fish tagged and released were classified into one of four categories: surface mortality, survival, delayed mortality, or unknown. Surface mortalities were immediate, and were likely the result of inability to re-submerge unassisted, typically because of overly positive buoyancy from gas expansion in the swim bladder in non-vented fish. Upon death, fish were retrieved and transmitters applied to a subsequent fish, and this mortality was factored into the analyses. Obviously, surface mortality fish did not have an acoustic profile. Metrics for classifying survivors were intentionally conservative. Survivors registered continuous detections for longer than three days and had active acceleration profiles with frequent changes in acceleration and vertical depth movements in the water column (Figure 2.5). Fish with delayed mortality had initial detections after release followed by a sudden drop-off to zero acceleration and depth of the seafloor (Figure 2.6). Fish that emigrated from the array and did not provide sufficient detection returns to confidently classify as either a survivor or delayed mortality were classified as unknown (Figure 2.7). These fish were omitted from further analyses. Fates from all trials are presented subdivided by season, depth, and release method (Table 2.1; see Appendices for acoustic profiles of each individual fish). To determine the average time elapsed to a delayed mortality event, the acceleration and depth acoustic profiles of all fish classified as suffering delayed mortality ($n = 8$) were plotted over time (Figure 2.8). Acceleration reached zero and depth reached the bottom depth at approximately three days (72 h) (generalized additive model fitted with a localized linear model smoothing curve). After this time period elapsed, there were no further delayed mortality events.

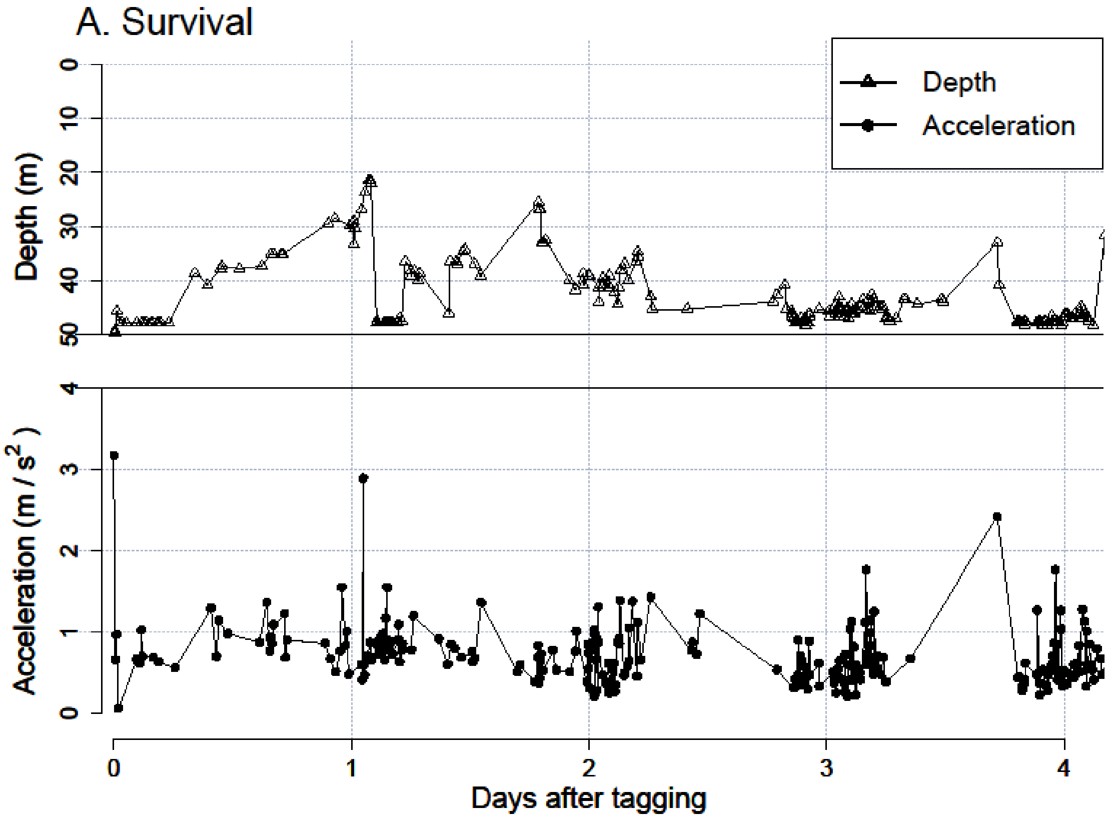


Figure 2.5. Acoustic telemetry acceleration (m/s^2) and depth (m) profile of one acoustically tagged Red Snapper classified as a survivor post catch-and-release < 4 days. Points represent individual acoustic detections and are connected by lines for visualization. Filled dots represent acceleration and reveal a healthy and active acceleration profile for this fish. Triangles represent the depth profile for this fish. Site depth was 50 m.

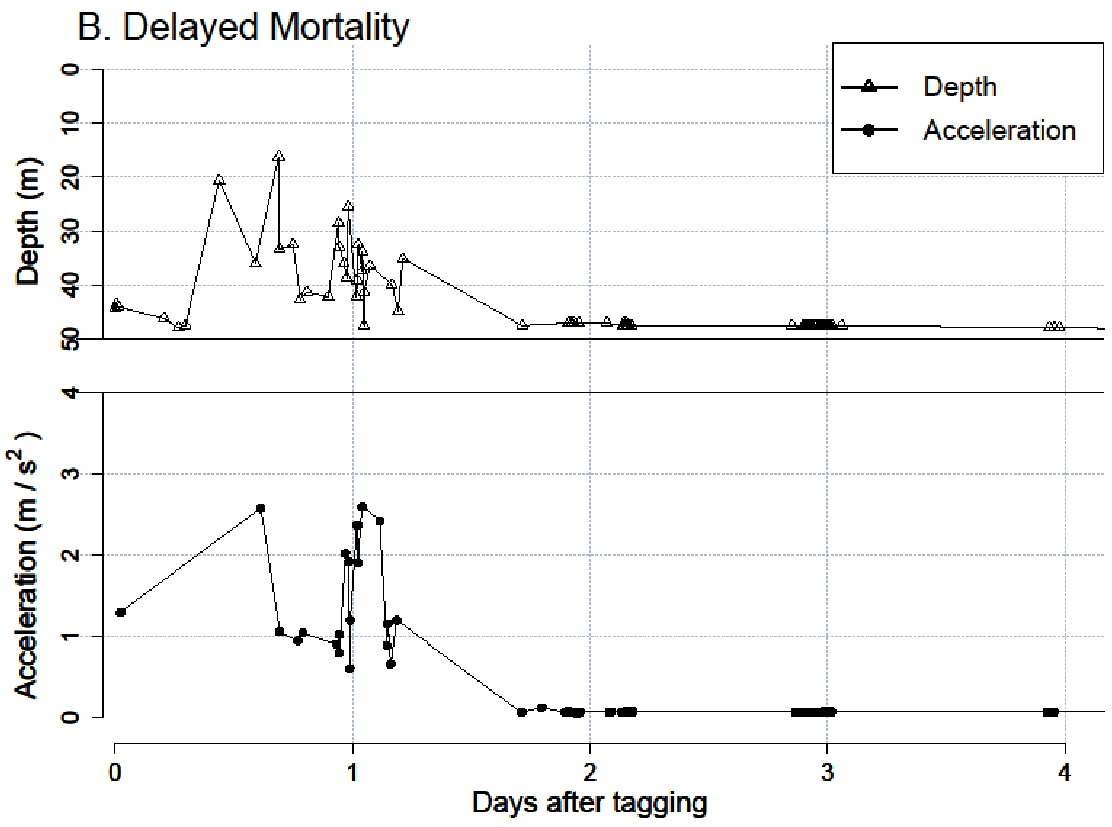


Figure 2.6. Acoustic telemetry acceleration (m/s^2) and depth (m) profiles of one acoustically tagged Red Snapper classified as delayed mortality post catch-and-release. Points represent individual acoustic detections and are connected by lines for visualization. Filled dots represent acceleration and show that after < 2 days the fish has perished, no longer exhibiting any acceleration or movement. Triangles represent the depth profile for this fish and show that after < 2 days the fish has fallen to the seafloor and perished, showing no further vertical movement. Site depth was 50 m.

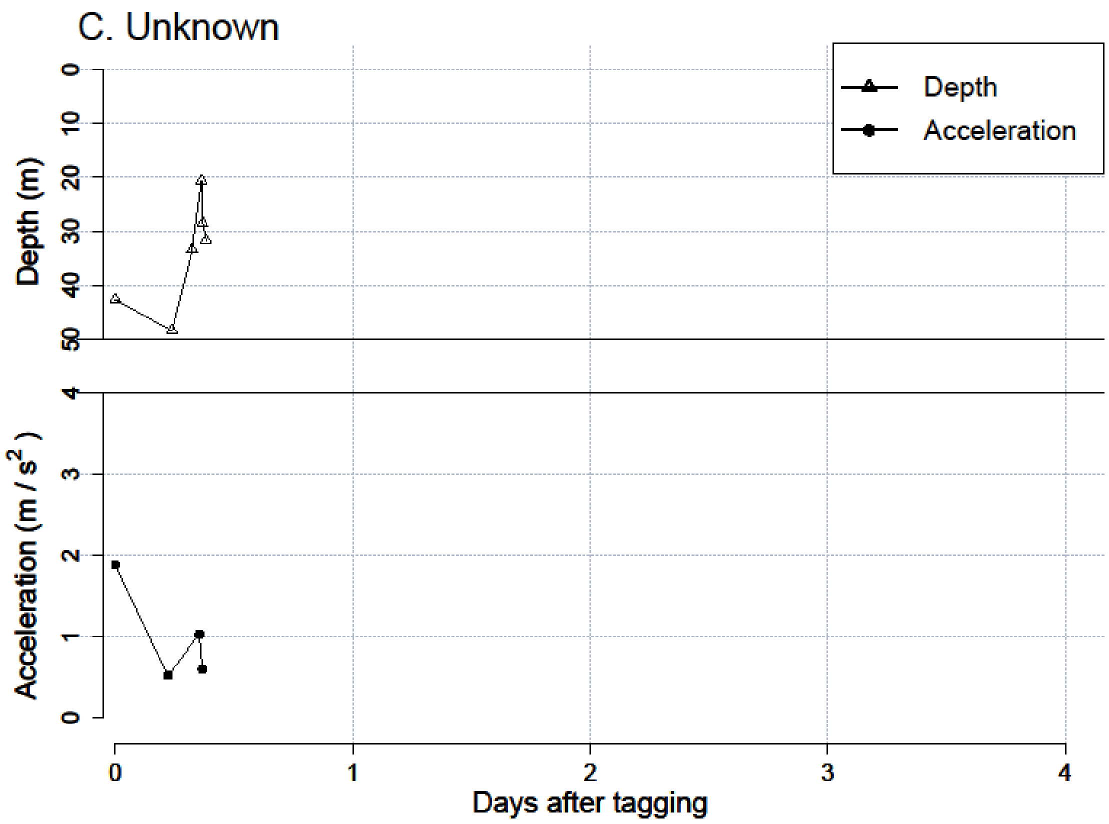


Figure 2.7. Acoustic telemetry acceleration (m/s^2) and depth (m) profiles of one acoustically tagged Red Snapper whose fate is unknown post catch-and-release. Points represent individual acoustic detections and are connected by lines for visualization. Filled dots represent acceleration and show active detections for 0.5 days before disappearing. Triangles represent the depth profile for this fish and show detections for 0.5 days before disappearing.

Table 2.1. Summary table of results of Red Snapper experimental trials. *Tagged*: number of fish tagged and released, including those that perished on the surface. *Fate unknown:* fish whose fate was unclassifiable as survive or mortality. *Surface mortality:* fish that perished at the surface. These fish were retrieved and tags were reapplied to subsequent fish. *Delayed mortality:* fish that exhibited delayed mortality (perished in < 3 days). *Survive*: fish that exhibited long term (> 3 days) survival.

	Tagged	**Fate Unknown**	**Surface mortality**	**Delayed mortality**	**Survive**
Winter					
Control	4	1	0	0	3
Descend	8	4	0	1	3
Nonvent	10	2	2	0	6
Vent	n/a	n/a	n/a	n/a	n/a
Subtotal	*22*	*7*	*2*	*1*	*12*
Summer					
Control	3	1	0	1	1
Descend	9	4	0	1	4
Nonvent	8	3	4	1	0
Vent	5	2	1	0	2
Subtotal	*25*	*10*	*5*	*3*	*7*
Spring - 50 m					
Control	6	4	0	0	2
Descend	8	3	0	2	3
Nonvent	10	2	3	1	4
Vent	8	4	0	1	3
Subtotal	*32*	*13*	*3*	*4*	*12*
Spring - 30 m					
Control	6	3	0	0	3
Descend	7	2	0	0	5
Nonvent	10	2	2	0	6
Vent	9	5	1	0	3
Subtotal	*32*	*12*	*3*	*0*	*17*
TOTAL	***111***	***42***	***13***	***8***	***48***

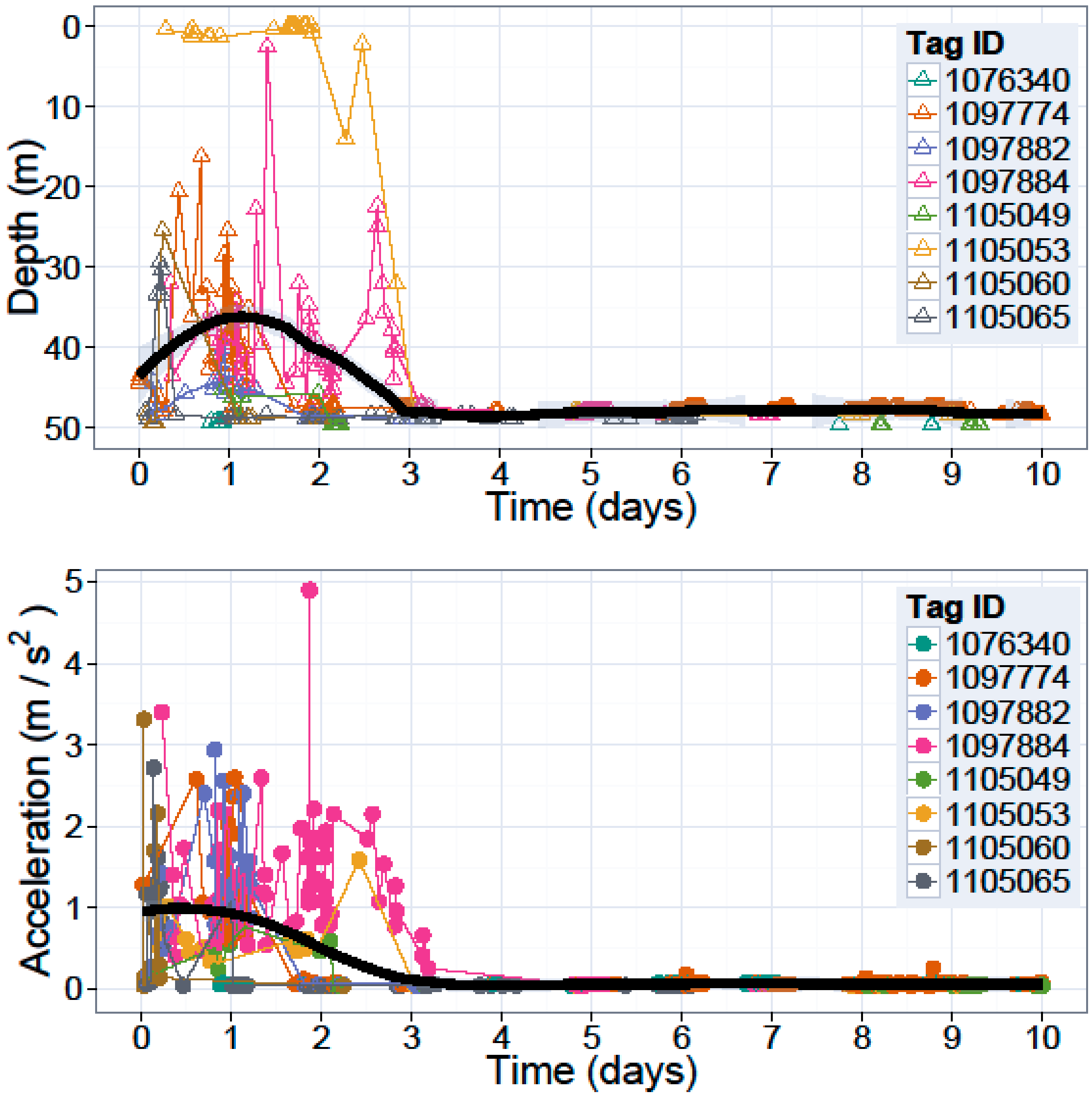


Figure 2.8. Acoustic telemetry acceleration (m/s^2) and depth (m) profiles (< 10 days) of all acoustically tagged Red Snapper classified as delayed mortality post catch-and-release. Points represent individual acoustic detections and are connected by lines for visualization. The thick black line represents a generalized additive model fitted with a loess smoother incorporating all eight delayed mortality fish. Filled dots in lower panel represent acceleration; triangles in upper panel represent depth. Site depth was 50 m.

Survival analysis

Percent survival was compared among release treatments over all the seasonal trials and depths (*n* = 69, Figure 2.9). Survival for control fish was 90% ± 9% (mean ± SE), followed by descended bottom release at 79% ± 9%, vented surface at 73% ± 13%, and lastly, nonvented surface at 55% ± 9%. Over all release treatments, survival was estimated at 70% ± 6%. Percent survival by individual season had seasonal and release method interactions. During the winter trial, there was 100% survival in control fish; descended (75% ± 22%) and nonvented (75% ± 15%) fish experienced similar survival (Figure 2.10A). The vented surface treatment was labeled 'n/a' because that treatment was not performed during the winter trial. During the spring trial (50 m only), there was 100% survival in control fish, the vented fish (75% ± 18%) experienced highest survival out of experimental release methods followed by descended (60% ± 22%), and lastly nonvented fish (50% ± 18%; Figure 2.10B). During the summer trial, control fish experienced only 50% survival because of a single mortality in a low sample size (*n* = 2). Among experimental release treatments, descended fish experienced highest survival (80% ± 18%), followed by vented fish (67% ± 27%; Figure 2.10C). The highest mortality occurred during warm summer trials, with nonvented fish experiencing 0% survival.

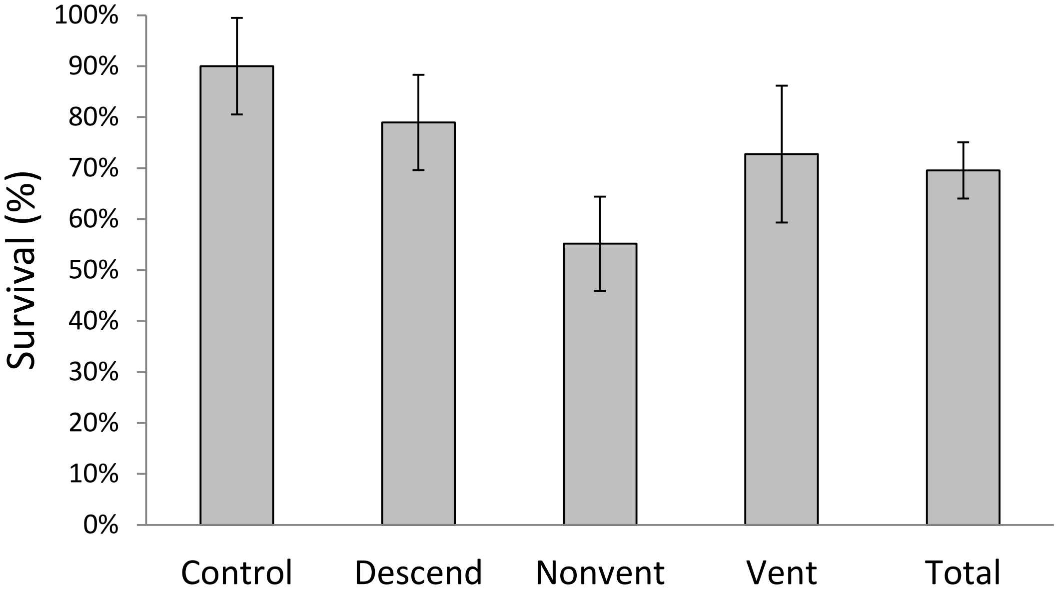


Figure 2.9. Percent survival (± SE) of Red Snapper classified by acoustic profiles over all seasons and depths (summer, winter, spring 50 m, spring 30 m). Fish classified as fate “unknown” from acceleration and depth profiles are omitted in analysis, therefore sample size (*n*) for each group is equal to the number of fish tagged minus the unknowns. Four release treatments: control fish (i.e., no barotrauma), descend (weighted descender hook), nonvent surface release, and vented surface release.

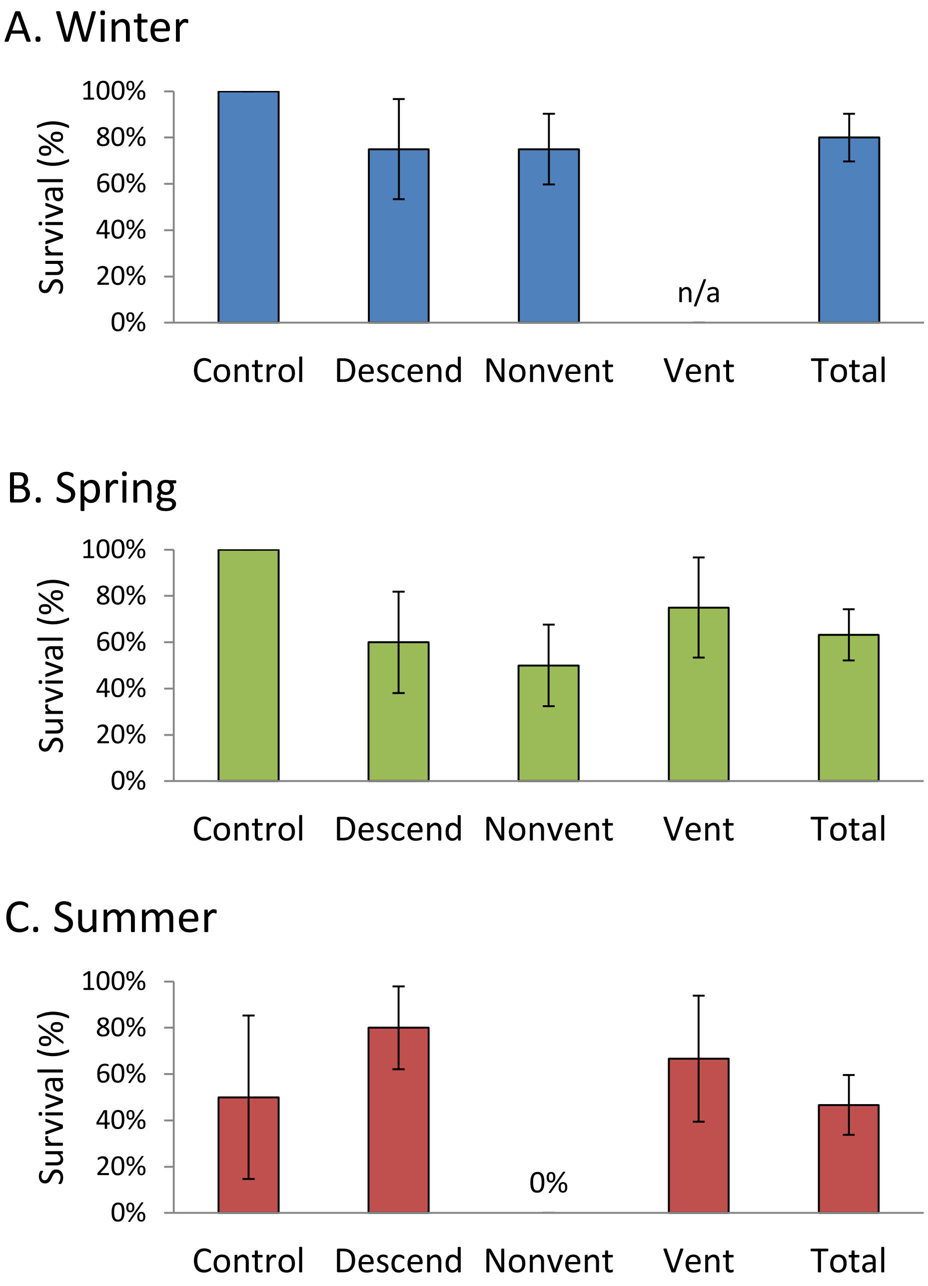


Figure 2.10. Percent survival (± SE) of Red Snapper during field trials for three seasons: winter, spring (50 m depth only), and summer. Fish classified as fate "unknown" from acceleration and depth profiles are omitted in analysis, therefore sample size (*n*) for each group is equal to the number of fish tagged minus the unknowns. Four release treatments: control fish (i.e., no barotrauma), descend (weighted descender hook), nonvent surface release, and vented surface release.

The effect of capture depth at 30 m versus 50 m on the fate of discarded Red Snapper was compared during the spring trial (Figure 2.11). All control fish at both depths experienced 100% survival. Within the experimental release groups at 30 m, descended fish had 100%, the vented group had 75% ± 22%, and the nonvented group 75% ± 15% survival. These percentages were all equal to or higher than the same release treatments at 50 m, with survival in descended fish 60% ± 22%, vented fish also 75% ± 22%, and nonvented fish 50% ± 18%. Over all release treatments, survival of discarded Red Snapper was higher at 30 m depth (85 ± 8%) than at 50 m depth (63 ± 11%).

The known fates of individuals by each season, classified by the acoustic profiles, were summarized in a cumulative bar graph (Figure 2.12). Winter trials had the highest survival in all 50 m treatments, with 80% survival, 13% surface mortality, and 7% delayed mortality. Summer trials fared the worst, with 47% survival, 33% surface mortality, and 20% delayed mortality. Spring 50 m trials had 63% survival, 16% surface mortality, and 21% delayed mortality. Lastly, spring 30 m trials had 85% survival, 15% surface mortality, and 0% delayed mortality. Combining all seasons had 70% survival, 19% surface mortality, and 11% delayed mortality.

Survival probabilities were calculated for each level of each explanatory variable (release, season, depth) based on the Kaplan-Meier product limit estimate (Figure 2.13). On the tenth day post-release, the probability of survival over all seasons for control fish was 0.900 ± 0.095 (mean ± SE), 0.769 ± 0.102 for descended fish, 0.727 ± 0.134 for vented fish, and 0.567 ± 0.091 for nonvented fish. Seasonally, fish experienced the highest chance of survival in winter (0.800 ± 0.103), followed by spring (0.744 ± 0.070; only 50 m depth), and lastly summer (0.400 ± 0.151). The probability of survival at 30 m (0.842 ± 0.084) was higher than at 50 m depth (0.637 ± 0.068) during the spring trial.

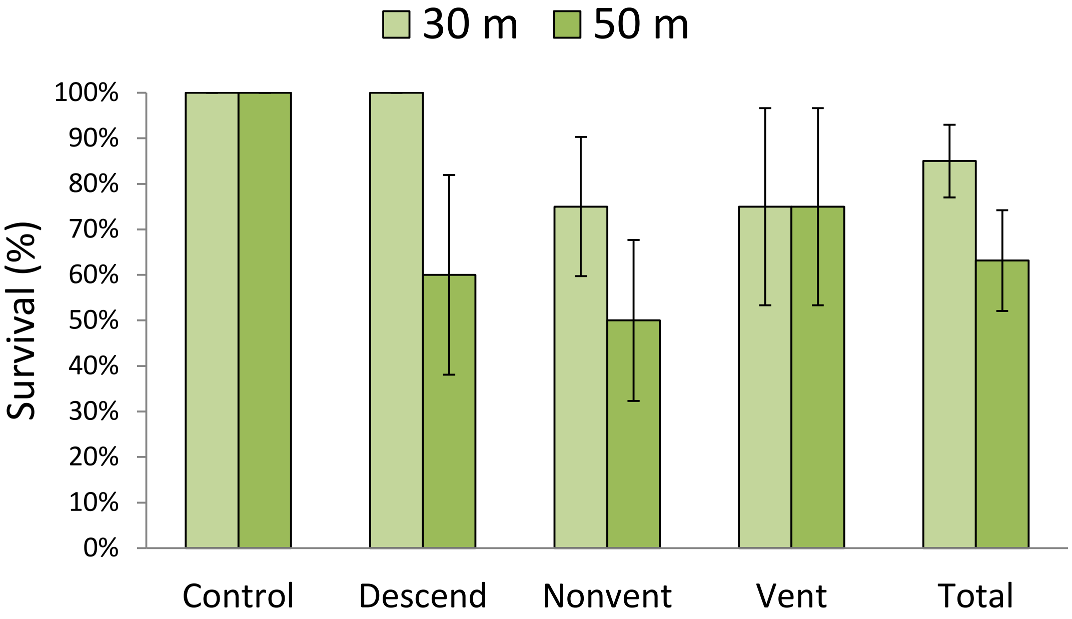


Figure 2.11. Percent survival (± SE) of Red Snapper during field trials for 50 m and 30 m depths during the spring season trial. Fish classified as fate “unknown” from acceleration and depth profiles are omitted in analysis, therefore sample size (*n*) for each group is equal to the number of fish tagged minus the unknowns. Four release treatments: control fish (i.e., no barotrauma), descend (weighted descender hook), nonvent surface release, and vented surface release.

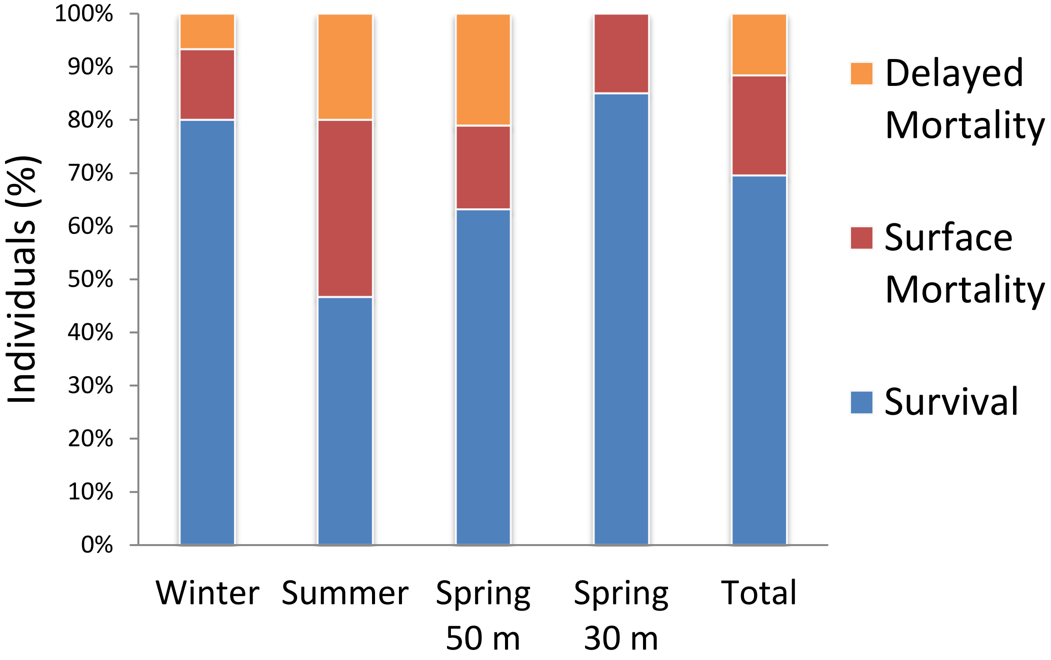
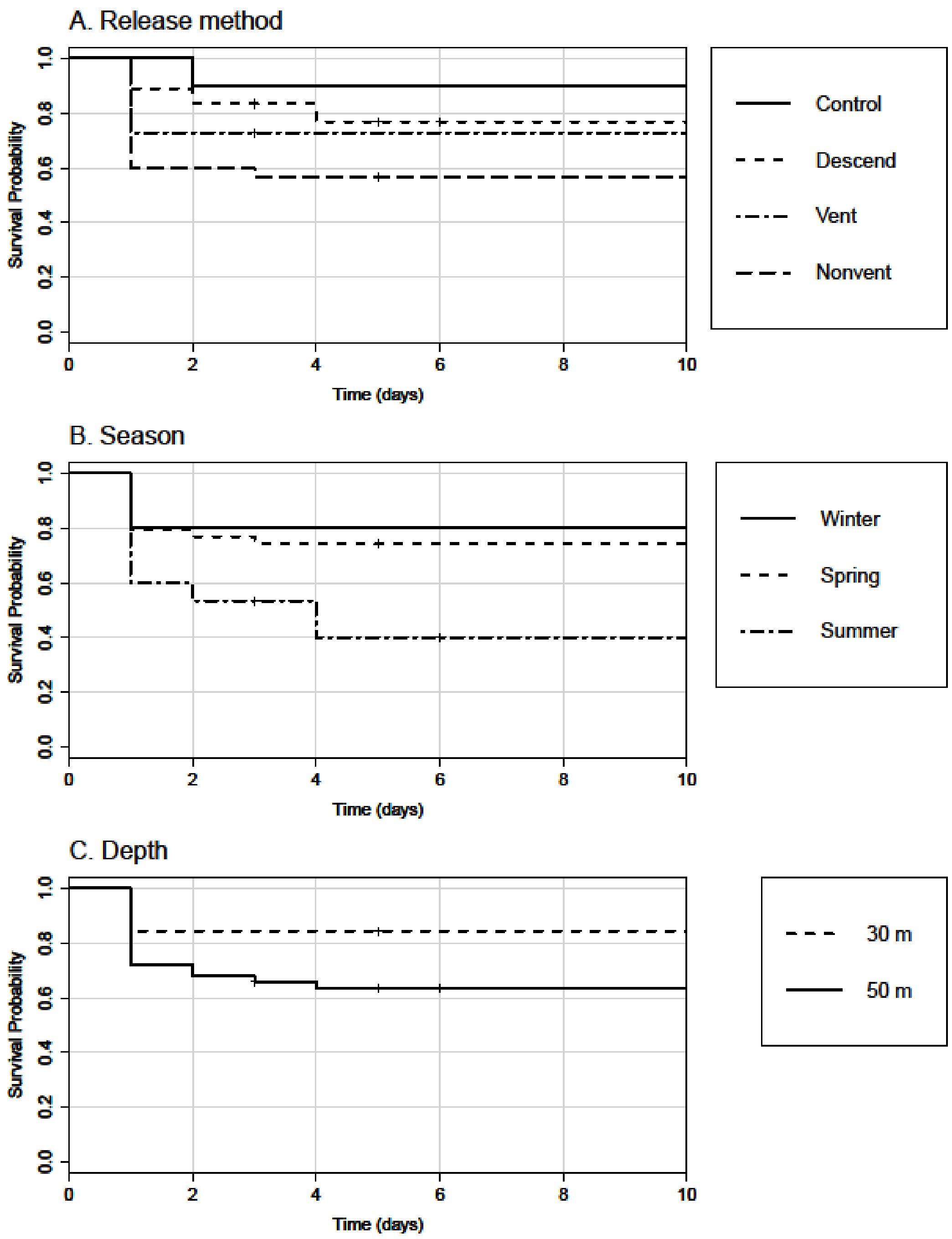


Figure 2.12. Cumulative bargraph showing known fates of individuals by season and overall based on acoustic profiles (survival, surface mortality, or delayed mortality). Each column reported as a percentage out of 100%. Winter and summer trials both performed at 50 m.



A. Release method

B. Season

C. Depth

Figure 2.13. Kaplan-Meier survival curves plotting survival probability over ten days by (A) release method, (B) season, and (C) depth. Survival probability calculated from all survivors, immediate moralities, and delayed mortalities (*n* = 69).

The Cox proportional hazards model was used to compare the relationship between survival and multiple explanatory variables and compute a hazard ratio, or proportional risk of death, for each covariate level (Table 2.2). For release method, the control was used as the baseline level to which experimental release treatments descend, vent, and nonvent were compared. Based on the calculated hazards ratio, descended fish were 1.9 times, vented fish 2.7 times, and nonvented fish 7.0 times as likely to perish as control fish. The winter trial was used as the baseline level against which spring (50 m only) and summer were compared. Spring-released fish were 1.9 times and summer fish 5.1 times as likely to perish as fish released in the winter. The 30 m depth was used as the baseline level against which the 50 m depth was compared. Fish released after capture from 50 m depth were 2.3 times as likely to perish as fish caught at 30 m depth.

Table 2.2. Cox proportional hazards model using treatment, season, and depth as covariates. The hazard ratio shows the proportional risk of each level of a particular treatment against the baseline risk of mortality (e.g., nonvented fish are 7.009 times as likely to perish as control fish).

Covariate	Coefficient (b)	S.E.	Hazard ratio (e^b)	95% C.I. for e^b	*P*
Control	*(baseline)*				
Descend	0.639	1.121	1.894	0.2106 - 17.028	0.569
Vent	1.008	1.160	2.741	0.2822 - 26.613	0.385
Nonvent	1.947	1.048	7.009	0.8985 - 54.671	0.063
Winter	*(baseline)*				
Spring	0.659	0.696	1.934	0.4941 - 7.568	0.344
Summer	1.636	0.717	5.132	1.2578 - 20.938	0.023
30 m	*(baseline)*				
50 m	0.829	0.690	2.291	0.5921 - 8.867	0.230

DISCUSSION

Using acoustic telemetry, I was able to determine discard mortality rates and examine the fate of discarded Red Snapper under a variety of conditions. This was the first study that documented and quantified the amount of delayed mortality occurring post release for the Red Snapper fishery using acoustic telemetry. Thus, these methods allowed examination of both immediate and delayed mortality. Overall, there was 70% survival, 19% surface mortality, and 11% delayed mortality for Red Snapper across all treatments. Discard mortality was influenced by season, release treatment, and depth of capture; the highest rates of mortality were observed in the summer season and when fish were released nonvented at the surface. Fish captured in deeper waters had higher mortality than fish captured in shallower waters. Fish suffering delayed mortality perished within a 72-hour period. This appears to be the critical time threshold whereby fish that survive this vulnerable short-time period will likely experience long-term survival. Researchers examining mortality in future studies should consider potential for delayed as well as immediate mortality.

There has been considerable debate regarding the best release practices for increasing survival in catch-and-release fisheries with mixed results that differ depending on species, season, depth of capture, angler experience, fish size, and other factors. For Red Snapper in the Gulf, the question of venting or not venting has recently been at the forefront of this debate with contradictory results in different studies (Wilde 2009). This uncertainty has subsequently contributed to the GMFMC rescinding the requirement of venting prior to release after establishing this requirement only five years prior. In this study, venting had a clear positive effect on survival. Fish that were not vented were over two and a half times as likely to perish as fish that were vented prior to release. However, this effect was highly dependent upon season.

Render & Wilson (1994) observed a similar interaction between season and release treatment. While the majority of nonvented fish survived catch-and-release during the winter and spring trials, zero fish survived during summer. Additionally, the largest number of immediate surface mortality events occurred in summer and the bulk of those mortalities were from fish unvented and released at the surface. With the recreational fishing season occurring during summer months, the threat of immediate surface mortality is magnified by the number of anglers fishing for Red Snapper. Thus, using appropriate release methods to reduce the risk of mortality is imperative for increasing post-release survival.

Two-thirds of offshore reef anglers in the northern Gulf practice venting prior to releasing fish and most perceive venting to be beneficial (Scyphers et al. 2013). Opposition to venting practices assert that the increases in handling time necessary to vent the fish negate the potential benefits of the practice and minimizing handling time (surface interval) may be more critical to fish survival (Burns et al. 2002, Jarvis & Lowe 2008, Pribyl et al. 2012). A second argument against venting is the inconsistency in proper technique by untrained anglers, and even trained scientists, which may cause additional and irreversible damage to vital organs that assuredly result in fish mortality. The regulatory transition away from venting requirements places accountability upon the individual angler to make educated and responsible decisions regarding the best release practices. It is important that education and outreach programs provide the appropriate knowledge of release methods, conditions, and techniques to increase fish survivability.

A relatively new alternative to the practice of venting is rapid recompression, which aims to return the fish quickly to depth, thereby rapidly recompressing the swim bladder without the need for venting. Rapid recompression improved survivorship for Red Snapper in this study.

Fish rapidly recompressed by descending and bottom release were nearly four times as likely to survive as fish that were similarly unvented but released at the surface. Previous studies involving rapid recompression devices support that these methods are beneficial for increasing post-release survival in several species of Pacific rockfish (Jarvis & Lowe 2008, Hochhalter & Reed 2011, Rogers et al. 2011, Hannah et al. 2012, Pribyl et al. 2012) and Australian snapper (Sumpton et al. 2010, Butcher et al. 2012). Descended fish in this study were also one and a half times more likely to survive than vented fish. Furthermore, survival of descended fish experienced less seasonal variability than other release treatments. While sea surface temperatures during tagging trials significantly differed seasonally, water temperatures at the seafloor were more temporally stable. Returning the fish to these cooler water temperatures by using descending devices enhances post-release survival and appears to be particularly important when seasonal thermoclines create large surface to bottom temperature differentials.

Fish tagged and released in the summer season were five times as likely to perish as fish tagged in winter and two and a half times as likely as fish tagged in spring. Thus, increases in water temperature negatively influenced fish survival. Extreme and particularly high water temperatures have been correlated with increased probability of mortality (Cooke & Suski 2005, Gingerich et al. 2007, Gale et al. 2013). Thermal stress caused by elevated water temperatures causes numerous physiological and behavioral changes that can have profound effects on cellular function and metabolic activity (Fry 1971, Prosser 1991, Cooke & Suski 2005). Additionally, levels of dissolved oxygen are depressed at higher water temperatures so that there may be inadequate availability of oxygen at the surface and this may cause additional physiological problems in catch-and-release fisheries (Arlinghaus et al. 2007). The increased risk of mortality associated with higher sea surface water temperatures during the summer is likely exacerbated by large temperature differentials produced by the summer thermocline. High surface to bottom temperature differentials decrease survival in rockfish (Hannah et al. 2012) and Red Snapper (Diamond & Campbell 2009). Fish caught and released in the summer were brought from bottom temperatures of 22°C to 31°C at the surface, a differential of 9°C. In contrast, spring fish experienced a much smaller 3.5°C differential and winter fish experienced 0°C differential with maximum temperatures between 23 to 24°C for both seasons. Thermal stress occurs when captured fish are displaced and released in water temperatures that extend beyond their temperature tolerance range or in temperatures in which they are not acclimated (Diamond & Campbell 2009). Surface water temperatures during the summer approached the 33°C upper tolerance limit of Red Snapper (Moran 1988). Coupled with the additional physiological stress accompanied by a 9°C water temperature change because of the presence of a thermocline, the warmer surface waters in summer seemingly were instrumental in reducing Red Snapper survival post catch-and-release.

One challenge encountered when using acoustic telemetry and transmitters is the variability in detection efficiency under different environmental conditions. Specifically in this study, the mean number of acoustic detections per fish collected in winter and spring trials were much higher than in summer. This could be an artifact of the depth placement of acoustic receivers in relation to tagged fish in the presence of developing thermoclines. Acoustic detection efficiency varies significantly depending on environmental conditions (Mathies et al. 2013). Westmeyer et al. (2007) witnessed a near complete truncation of detections coinciding with the movement of a thermocline below receiver depth. There may have been a similar effect during the summer trial that substantially reduced the number of detections. Acoustic receivers were placed at depths of 20 and 30 m during each of the trials for 50 m sites. Winter trials had a well-mixed water column and no thermocline development. The absence of any thermocline creates a more homogenous medium for higher efficiency of tag transmissions and detections, which may have been responsible for the winter trial having the highest rates of detection in this study. Spring trials had a marginal 3°C thermocline develop from 20-30 m depth, with a further decrease of only 0.5°C until the bottom. Even if this slight thermocline did deter successful tag detections from the upper receiver, the lower receiver positioned below the thermocline would pick up these transmissions. Summer trials had a sharp thermocline, dropping from 30°C beginning around 25 m to 22°C at the bottom. Assuming tagged fish are residing at the bottom, tag transmissions would have had to penetrate a pronounced thermocline to reach either acoustic receiver for successful detection. Control transmitters at known locations can permit researchers to gauge the detection variability in the presence of changing environmental conditions but, unfortunately, these tags were not included in this study. However, given that several summer fish were detected for the entire tag life duration of 45 days and because fish classified under the unknown fate class were fairly evenly distributed among season, I am confident that potential losses in detection efficiency across seasons did not significantly alter the interpretation of my results, especially considering the short time scales (3 days) that were used in fate classifications. Nevertheless, researchers in future tagging studies must be aware of the variability in detection efficiency across different environmental landscapes and should deploy control transmitters (or sentinel tags) to account for this variability where possible (Kessel et al. 2013).

Across the majority of studies and species including this study, depth of capture appears to be the most consistent variable explaining release mortality in deep-water catch-and-release fisheries – increasing depth resulted in increasing discard mortality. This pattern was documented in Pacific Rockfish *Sebastes spp* (Hannah et al. 2008), West Australian Dhufish

Glaucosoma hebraicum (St John & Syers 2005), Painted Comber *Serranus scriba* (Alós 2008), Gag Grouper *Mycteroperca microlepis* (Burns et al. 2002, Rudershausen et al. 2007, Sauls 2014), and most pertinently Red Snapper where depth was the most important factor in determining release mortality (Campbell et al. 2013). Results from this study concur with these previous findings, as fish in the shallower (30 m) depth were over twice as likely to survive as at the deeper (50 m) depth. Survival during spring trials where two depths were compared was 85% at 30 m and 63% at 50 m. Both these estimates fall within the range of the SEDAR31-DW22 meta-analysis estimates (Campbell et al. 2012) but are nearer the lower boundary. This likely is attributed to the cooler spring water temperatures in which the depth comparison was performed. Increases in sea surface temperature generally resulted in increases in mortality (Gale et al. 2013). If this experiment were to be replicated in warmer summer months, I would expect to see slightly higher estimates of mortality at both depths but especially at the deeper 50 m depth, where the presence of the thermocline and large surface-bottom temperature differentials further compromises chances of survival.

The apparent correlation between mortality and depth is most probably because of the link between depth and the extent of barotrauma injuries caused by catastrophic decompression (Rummer 2007, Campbell et al. 2010, Pribyl et al. 2011). The severity of barotrauma symptoms witnessed typically increase with depth, as increased pressure changes directly result in higher volumetric expansion of internal gases. However, in some studies visible barotrauma symptoms from fish caught in deeper waters appeared reduced or absent (Brown et al. 2010, Campbell et al. 2013). Further examination revealed that this absence of visible barotrauma injuries can occur when the swim bladder ruptures from overexpansion of gases (Rummer 2007, Rogers et al. 2008, Roach et al. 2011, Kerwath et al. 2013, Campbell et al. 2013). This allows otherwise displaced internal organs (i.e., stomach or intestinal eversion) to remain inside the body cavity so that the fish upon surfacing may appear healthy and unafflicted by barotrauma injuries when in fact their survival chances are severely depressed. Furthermore, fish that have ruptured swim bladders may have neutral or negative buoyancy allowing them to easily re-submerge at the surface and disappear from sight, and be presumed to survive, when in fact they merely perished and sank to the bottom. Some caution should be taken when using fish condition indices as proxies for predicting post-release survival as the indices may have a tendency to underreport overall discard mortality because the visible extent of barotrauma symptoms present may not be indicative of ultimate fate.

This study was able to account for delayed mortality in addition to surface mortality through the use of ultrasonic acoustic telemetry. Previous researchers estimating delayed mortality of Red Snapper in the field relied on caging experiments, which have an inherent bias because they exclude predatory effects, prevent foraging, and restrict natural movement (Campbell et al. 2013). In such studies, separating the influence of caging effects from barotrauma affliction in estimating mortality is difficult. Delayed mortality estimates in caging studies ranged from 20 to 71% at depths from 20 to 50 m (Gitschlag & Renaud 1994, Render & Wilson 1994, Diamond & Campbell 2009). Using acoustic telemetry allowed me to estimate delayed mortality in fish that were unrestricted in movement and behavior. Comparatively, I found delayed mortality estimates ranging from 0 to 21% dependent upon season at discrete depths of 30 and 50 m. The smallest and largest estimates of delayed mortality were observed in the spring season, at the shallower and deeper depths, respectively. Estimates of survival in this study were higher than reported from caging studies, suggesting that the effect of caging itself seems to be an influential factor and substantially contributes to post-release mortality. The exclusion of predators should enhance survival, but this is seemingly less important than the need to move unrestricted, presumably to forage. Predator abundance is typically low and highly variable, so the benefits of caging are minimal when compared with the energetic requirements needed to survive. Using acoustic telemetry eliminates one bias associated with caging practices and allows fish to behave unhindered, thus, representing a more natural post-release scenario.

A primary challenge in using acoustic telemetry for estimating delayed mortality when compared with passive mark-recapture methods is a limitation of sample size. Acoustic telemetry instruments are costly and deployment of these technologies is both time consuming and logistically complex, especially in deep water environments. The inherent cost of these transmitters restricts use of large sample sizes that are possible to attain using anchor tags. Further complications are created by the detection limits of acoustic receivers and the variability in detection efficiency because of environmental fluctuation. Using a fish known to have high site fidelity such as Red Snapper can increase the likelihood of detection as they theoretically remain within range of receivers positioned on the structure. Lastly, many acoustic telemetry studies have noted a substantial portion of tagged fish have an immediate post-release emigration event likely in response to capture and handling stress (Schroepfer & Szedlmayer 2006, Lowe et al. 2009, Topping & Szedlmayer 2011a). This emigration event quickly moves fish outside the detection range with potentially few to zero acoustic transmissions being detected. Without this acoustic information, and if fish are never recaptured, the fate of these emigrants is never known. In the present study, I experienced 42 of 111 (38%) individuals recording too few acoustic detections to classify their fate with any confidence. These fish classified as unknown were omitted from inclusion in survival analysis, which drastically reduced the experimental sample size. The number of unknown fish was fairly consistent across seasons and release treatments with each group experiencing at least one unknown and the maximum being five. The removal of unknowns thus did not bias one group unfairly with a disproportionate sample size compared to others. Despite the low sample size, several patterns still emerged and future replication would better elucidate these results by minimizing confidence intervals. Nonetheless, the advantages of acoustic telemetry and the uniqueness of the data outweigh some of the more challenging aspects of this tracking method.

A unique aspect in integrating accelerometer and depth sensors into acoustic transmitters was the ability to detect exactly when delayed mortality was occurring. The total mortality estimate of 30% (surface + delayed) is comparable to previous estimates of discard mortality found at these depths in SEDAR33-21 (Campbell et al. 2013), though typically studies from this meta-analysis did not include estimates of delayed mortality. Of the eight fish that experienced delayed mortality in our trials, these fish persisted for three days before succumbing to delayed mortality. At this point in time, acceleration values became zero and depth reflected the site depth, illustrating that fish were not moving and were lying on the seafloor. Transmitters of several fish continued to transmit these data for days to weeks after mortality had occurred. Without sensor information these fish would in all likelihood have been classified as survivors that exhibited high site fidelity throughout the duration of the transmitter tag life, instead of being fish that perished three days following catch-and-release. The ability to differentiate mortality from survival is obviously of paramount importance in tagging studies that not only assess post-release mortality, but also when estimating site fidelity, residency time, and migration patterns. Acoustic tags that lack sensor data and only relay presence/absence information may be insufficient to answer questions addressing these topics. Based on my finding of delayed mortality occurring at three days, I recommend that any studies assessing post-release mortality should monitor fish for a minimum time period of three days to ensure that lingering effects of the catch-and-release process that may cause mortality are accurately documented.

Of central importance to effective fisheries management is the ability to accurately estimate population demographic parameters for stock assessments. For Red Snapper in the GOM a high level of uncertainty has surrounded estimates of discard mortality, which represents an important parameter due to the high volume of discards that occur in this fishery. Historically, managers have focused on immediate mortality but have not incorporated delayed mortality into population models. If delayed loss is not accounted for in stock assessment models, it is likely that total mortality will be underestimated. Until recently, researchers were challenged by inherent limitations in the methods involved with making these mortality estimates. For example, mark-and-recapture studies suffer from low recapture rates, tag loss, and inaccurate reporting, and caging studies are biased because they restrict natural movement and behavior (Campbell et al. 2012). Acoustic telemetry has advantages that can overcome some of these drawbacks. The present study enhances the understanding of delayed mortality and post-release behavior of Red Snapper and provides conclusive information documenting the fate of regulatory discards. Estimates of delayed post-release mortality from this study can be integrated into stock assessment models to reduce uncertainty over discard mortality estimates and ultimately improve estimates of Red Snapper population dynamics.

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CHAPTER III:

RECOVERY POTENTIAL AND POST-RELEASE BEHAVIOR OF RED SNAPPER DETECTED USING ACOUSTIC TELEMETRY

ABSTRACT

Because of intense regulations in the Gulf of Mexico Red Snapper fishery, catch-and-release has become increasingly prevalent during the last decade. Given such a high discard rate, determining the best-release practices for discarding fish is essential to maximize their survival. Additionally, methods have been sought to maximize survival immediately upon release, but there has been no evaluation on how different techniques may affect the behavior and activity of Red Snapper over longer time scales. To examine post-release behavior patterns and activity levels, Red Snapper were tagged across a variety of treatments with ultrasonic acoustic transmitters and acceleration and depth data were recorded for approximately 45 days. Red Snapper have diel acceleration and depth differences, and these behaviors were not altered by release method. Venting, non-venting, and rapid recompression release treatments did not differ in their outcome on long-term fitness or behavior for discarded Red Snapper when compared to the control group. Furthermore, fish released using different methods did not have reduced activity or behavior based on the distribution of accelerometer values. That various release treatments do not place an added risk of mortality on discarded Red Snapper is a critical and positive piece of information for managers making determinations on the best-release practices for minimizing discard mortality and promoting sustainable fisheries through catch-and-release regulations.

INTRODUCTION

The success of catch-and-release fishing as a management tool is predicated upon the assumption that discarded fish will survive (Cooke & Suski 2005, Arlinghaus et al. 2007). In shallow waters, catch-and-release survival tends to be high and anglers often witness discards actively swimming away by sight. In deeper waters, however, catch-and-release survival is typically much lower because of barotrauma-related injuries, and it is often difficult to visually determine if fish have survived once they have been discarded and re-submerge. Fish that suffer immediate mortality at the surface from buoyancy regulation problems or depredation can be easily spotted and accounted for, but fish that swim down and disappear have a more ambiguous fate, and their survival outcome is more difficult to classify. Fish capable of re-submerging may still suffer from lingering barotrauma effects and experience delayed mortality after catch-and-release in deep-water environments. What characteristics enable some fish to survive while causing others to succumb to delayed mortality and are these patterns caused by certain elements of the catch-and-release process?

In the Gulf of Mexico, Red Snapper (*Lutjanus campechanus*) fishery management has been hotly contested (Cowan et al. 2010), and there is widespread disagreement among fishing sectors, scientists, and managers on issues such as actual stock size, quota allocations, and fishing regulations. Over the last decade, the recreational sector has experienced drastic reductions in the length of its open fishing season due to repeated overharvest of the sectors' total allowable catch quota. During 2014, the recreational season was nine days, down from 46 days in 2012, and 75 days in 2009 (GMFMC 2014). Bag reductions and size limit increases have also accompanied seasonal restrictions and the combination of these regulations has been successful to the point where Red Snapper stocks are no longer undergoing overfishing, though they remain in an overfished state and are still rebuilding (SEDAR 2013). The successively shorter seasons incidentally reflects a healthier stock, as the average fish being caught is larger than in previous years. Unfortunately for recreational anglers, this means that the total allowable catch quota is reached faster and results in the fishery being closed sooner. From a management perspective, this means that there is a larger proportion of “regulatory discards,” or fish that must be released following capture because they are caught out-of-season, do not meet the minimum size limit, or the angler has reached their bag limit. Furthermore, with only a two fish bag limit, anglers often discard otherwise retainable fish to catch and keep larger ones. The increasing amount of regulatory discards occurring from shorter open seasons and high-grading practices places an added emphasis on effective release methods that ensure the highest chance of survival for fish that are discarded.

High levels of discard mortality associated with barotrauma in deep-water fishes such as Red Snapper represents a significant impediment to sustainable catch-and-release fishing (Rummer 2007). Various management strategies, such as venting and rapid recompression, have been adopted in an attempt to mitigate these losses. Venting, the process of puncturing the swim bladder with a hollow needle to allow the escape of excess gases built-up during ascent to the surface, has been the most widely applied technique for deep-dwelling fishes. However, this strategy has been heavily scrutinized (Wilde 2009) to the point where some managing agencies have recently rescinded any venting requirement prior to release (i.e., Red Snapper; GMFMC), although perceptions of the effectiveness of venting practices remain positive with the public (Scyphers et al. 2013) and recent laboratory experiments show very positive benefits of mitigating barotrauma using this and other methods (Drumhiller et al. 2014). An alternative technique that eliminates the need for puncturing the swim bladder is rapid recompression. This method holds the fish by a number of mechanisms (e.g. Shelton fish descender^{TM}, SeaQualizer^{TM}) on a weighted line and quickly descends the fish back to depth, thereby rapidly recompressing the swim bladder prior to release at or near the seafloor. Rapid recompression devices are still in the early scientific test phase but early results show that this method highly increases the chances of post-release survival (Jarvis & Lowe 2008, Rogers et al. 2011, Hannah et al. 2012, Pribyl et al. 2012). While these tools appear to enhance the chances of survival immediately following catch-and-release, the longer-term effects on fitness and behavior have not been investigated. There is substantial scientific evidence that indirect fitness-level consequences associated with catch-and-release fishing has a negative effect on long-term fitness by reducing growth (Siepker et al. 2007), reproductive output (Ostrand et al. 2004), and possibly incurring long-term discard mortality (Donaldson et al. 2008). Thus, determining release methods to minimize these negative consequences is essential for sustainable catch-and-release fishing and minimizing long-term discard mortality.

Traditional mark-recapture studies with passive tags have been the predominant method of assessing long-term survival and movement of Red Snapper in the Gulf of Mexico. While this method is advantageous for its simplicity, low cost, and capability of producing large sample sizes, the inherent drawback is that fish must be recaptured to obtain data. Mark and recapture studies for Red Snapper in the Gulf of Mexico have return rates ranging from approximately 2-34% (Beaumariage 1969, Fable 1980, Szedlmayer & Shipp 1994, Patterson et al. 2001, Diamond et al. 2007, Strelcheck et al. 2007). Using these recapture data, it is possible to estimate metrics such as mean and maximum days at liberty, distance traveled, and growth rates upon recovery of the fish, but most importantly, the fate of fish not returned is unknown. Recently, ultrasonic acoustic telemetry has provided the technology to monitor fish remotely and does not require recapture of the fish to recover data. Acoustic transmitters relay a unique identification code indicating presence/absence data to a stationary acoustic hydrophone receiver that stores the data, whereby it can be downloaded upon retrieval. From these daily and hourly acoustic returns, it is possible to examine movement patterns enabling estimations of site-fidelity, residency, and diel migrations. Acoustic telemetry methods have been highly successful for studies involving Red Snapper (Szedlmayer & Schroepfer 2005, Peabody & Wilson 2006, Westmeyer et al. 2007, Topping & Szedlmayer 2011a, b). Studies using presence/absence tags found differences in the number of detections between diel periods, showing that Red Snapper moved away from structures at night, presumably reflecting foraging activity (Szedlmayer & Schroepfer 2005, Peabody & Wilson 2006, Topping & Szedlmayer 2011b). Diet analysis from Red Snapper revealed significant diet shifts coincident with diel period (Ouzts & Szedlmayer 2003, McCawley et al. 2006).

Recent technological advances in acoustic telemetry have introduced tags with sensors that collect acceleration, depth, and temperature data in addition to traditional presence/absence information. These data allow even finer-scale resolution in movement studies and have made it additionally possible to examine aspects of behavior, physiology, and mortality (Donaldson et al. 2008). Tri-axial accelerometer sensors in particular have recently become an essential instrument in a wide range of fish physiology and behavioral studies in the wild that have included estimating energy expenditure and metabolic rates in Bonefish, *Albula vulpes*, (Murchie et al. 2011, Brownscombe et al. 2013), studying swimming behavior and activity in migrating Pacific Salmon, *Oncorhynchus sp.*, (Wilson et al. 2013, 2014), discriminating foraging behavior in Tigerfish, *Hydrocynus brevis*, (Baras et al. 2002); and in combination with depth sensors to examine diving behavior of Tiger Sharks, *Galeocerdo cuvier*, (Nakamura et al. 2011) and Great

Barracuda, *Sphyraena barracuda*, (O'Toole et al. 2010). Data loggers equipped with accelerometer sensors have been the preferred method of data collection because they have a large storage capacity and can be programmed with extremely short ping intervals (< 5 s) for studies requiring high temporal resolution. One drawback to data loggers, however, is they require recapture of the animal in order to recover associated data. For fish experiencing low recapture rates, the use of loggers may be impractical and costly. New technology has made it possible to equip acoustic transmitters with accelerometers, thereby avoiding the need to recover the animal to collect data. Recapture rates for Red Snapper in the western Gulf of Mexico are extremely low, ranging from 2 – 6% (Fable 1980, Diamond et al. 2007), so only with the advent of accelerometer transmitters has it been feasible to examine the post-release behavior of Red Snapper acoustically using this new technology.

The overall goal of this experiment was to analyze the post-release behavior of Red Snapper in the Gulf of Mexico using accelerometers and depth sensors. Specifically, I compared how different release methods (e.g., venting, rapid recompression, non-venting) affected long-term behavior of fish surviving the catch-and-release process and to determine if certain methods proved more beneficial for recovery. I also analyzed diel residency patterns in Red Snapper surrounding oil and gas platforms using novel accelerometer and depth sensor data to determine if diel vertical migrations or diel acceleration patterns emerged. Using accelerometer data, I constructed an ethogram to illustrate the allocation of energy expended by Red Snapper and determine if energy allocations differed among release treatments. Finally, using the combination of acceleration and depth data, I classified surviving Red Snapper into discrete character types based on their unique residency, activity, and behavioral attributes.

METHODS

Fish tagging

The northwestern Gulf of Mexico continental shelf contains predominantly soft, silty-clay benthic habitat with small areas of isolated natural hard-bottom substrate. The other major source of hard structure is provided by artificial reef habitats comprised primarily of oil and natural gas platforms, concrete culverts and other structures, and relict ships. Oil and gas platforms are popular fishing structures; thus, standing oil and gas platforms approximately 50 km east of Port Aransas, Texas were selected as study sites for these experiments. Sites MU-762-A and MU-759-A (approximately N27°45’, W96°35’) resided at 50 m water depth and sites MI-685-B and MI-685-C (approximately N27°55’, W96°35’) at 30 m water depth (Figure 3.1).

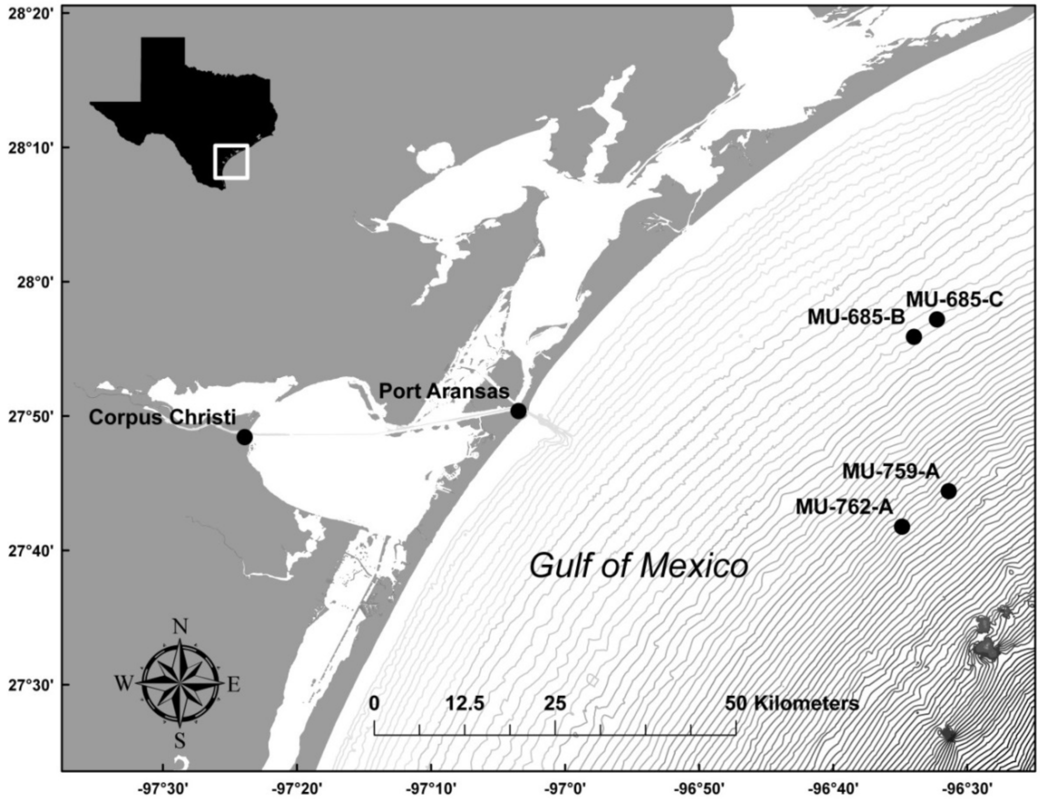

Figure 3.1.Study sites (standing oil/gas platforms) in the Gulf of Mexico off the South Texas coast where field tagging experiments occurred. Sites MU-685-B and MU-685-C reside at water depths of 30 m and sites MU-762-A and MU-759-A at 50 m.

Red Snapper were captured at each site using hook-and-line and were externally tagged with Vemco© V9AP ultrasonic coded acoustic transmitters (V9AP-2H, 46x9 mm, 69 kHz, random delay interval: 30-90 s, estimated battery life: 45 days) containing built-in acceleration and pressure (i.e. depth) sensors. To measure acceleration, the V9AP tags calculate a value (m s^{-2}) that represents the root mean square acceleration on three axes (X, Y, and Z) averaged over a fixed time interval (see Chapter II). Depth is calculated by an algorithm that coverts pressure sensors to a depth value. Because one goal of the study was to explore survival under a variety of release treatments, fish were rapidly (<3 min) tagged externally without anesthesia (IACUC AUP #02-11) to best replicate normal fishing and release practices and minimize artifacts associated with tagging related surgeries (i.e., venting and use of only survivors). Tagging procedures were validated through in-lab trials (Johnson et al. 2014). In these preliminary trials, tag presence did not impair fish behavior and tag retention using our external attachment method was 100% through 25 days. Tags were positioned below the anterior (3rd-6th) dorsal spines approximately 2-3 cm below the dorsal edge. Fish were punctured between pterygiophores below the anterior dorsal spines using a sterile stainless steel hollow surgical needle. Surgical grade suture monofilament was passed through one hollow needle, attached to the tag, and passed back through the second hollow needle and secured so that the orientation of the tag was parallel to the fish and on the opposite side as the secured monofilament. Fish were held in a tagging cradle with gills submerged in oxygenated water. An externally visible dart tag containing identification and reward information was also inserted into the posterior dorsal spine region.

Release treatments

Prior to tagging, fish were randomly assigned to one of four release treatments: (1) vented surface release; (2) nonvented surface release; (3) descended bottom release; and, (4) control (no barotrauma). Fish were released at the surface into an open-bottom 1.0 m^3 holding cage with mesh walls that protected fish from predation but enabled retrieval of fish (and transmitters) that experienced immediate mortality at the surface. During all trials the number of immediate surface mortalities post catch-and-release was recorded and incorporated into the analyses. Vented surface released fish were punctured in the abdomen posterior to the pectoral fin using a venting tool (Team Marine USA^{TM} pre-vent fish venting tool) to allow escape of excess gas built up in the swim bladder. Once all residual gas had been vented, these fish were tagged and released at the surface. Nonvented surface release fish were not vented prior to tagging and released at the surface. Descended bottom released fish were not vented prior to tagging but, instead of being released at the surface, were forced back to depth quickly using a weighted line with an inverted barbless hook (Shelton Fish Descender^{TM}) attached to the fish's jaw and released at the bottom. This setup is one of several rapid recompression tools that quickly return the fish to depth to counteract the effects of barotrauma through rapid gas recompression without venting. Control fish had no barotrauma prior to tagging and release. To achieve this, fish were captured at the study sites prior to experimental trials, transported to the Texas A&M AgriLife Research Mariculture Laboratory in Port Aransas, Texas, and held in 6400 L tanks for three weeks. Fish were treated for parasites using copper (II) sulfate and were fed three times weekly to satiation with a diet of squid and sardines. Fish recovered and began feeding quickly (typically within 24 h), and health and behavior of these fish were closely monitored. After a three-week holding period, fish were transported in oxygenated live wells to the study site where they were tagged and released along with fish assigned to the other release treatments in randomized order.

Experimental design

Three tagging trials occurred in different seasons: summer, winter, and spring. During each of these trials, water temperature, salinity, dissolved oxygen, and conductivity were measured using a Manta2 water quality multiprobe (Eureka Environmental Engineering). This unit was deployed to depth for each trial and recorded a data point at one second intervals. All drops were performed to a depth of 50 m at the same tagging site for each season: MU-762-A. Hourly sea surface temperatures for the duration of tagging trials (~ 45 days post tagging) were obtained from NOAA-NDBC station 42020 (N26°58’, W96°42’). Summer and winter trials were both performed at 50 m depth on site MU-762-A. Twenty fish were tagged and released on site using one of three release treatments: control, nonvented surface, or descended bottom release. However, because of repeated inability of nonvented fish to re-submerge during the summer trial and subsequent mortality, I was forced to modify the protocols and add a vented surface release treatment. Additionally, venting requirements were initiated in the fishery during the course of this study. Thus, the venting treat was not always included to represent a balanced design. Due to expense, tags were limited for this study that prevented each treatment during every season. Thus, for spring trials, where survivorship was expected to be high, I also incorporated a second depth (30 m) into the experimental design to test for depth differences at two sites for 30 m depth (MI-685-B and MI-685-C) and two sites at 50 m depth (MU-762-A and MU-759-A). At each depth, thirty-two fish were tagged among the two sites (*n* = 64) and all four release treatments were included. Two Vemco VR2W-69kHz acoustic monitoring receivers were attached to platform cross beams by SCUBA divers at each study site. Receivers were placed at depths of approximately 20 and 30 m for 50 m sites and at 15 and 25 m for 30 m sites.

Behavior profiles

VR2W receivers were retrieved from study sites after approximately 60 days and data were uploaded to Vemco VUE$^{©}$ software and then exported for analysis into R version 3.0.2 (R Development Core Team 2013). Acceleration and depth profiles for each fish were plotted over time using tag sensor data. Fine-scale movement and behavior of Red Snapper were analyzed in the surviving fish (n = 49). In some instances, tag drops were detected in survivors. These were characterized by substantial numbers of acceleration detections and vertical movements in depth for a period of several weeks before a sudden drop-off to zero acceleration and depth equal to the seafloor. This pattern was similar to the delayed mortality profile (Chapter II) with the exception that I know these fish have survived because they had previously been showing active and healthy acoustic profiles. Results from Chapter II studies showed that these fish crossed the critical time threshold of 72 hours, the point at which delayed mortality would occur.

Data analysis

Site fidelity and residency patterns of Red Snapper were examined on a daily scale using acoustic detection data and compared experimental release treatments (vented, non-vented, rapid recompression) against the control fish, which acted as a baseline for “normal” activity and behavior. Diel residency patterns were analyzed by pooling daylight hours and nighttime hours into diel period. Because our trials occurred over multiple seasons with different sunrise and sunset times, I averaged times to determine the closest approximation to represent diel period over all trials. The hours of 700-1900 were used for daylight hours, and 1900-700 for nighttime hours. A two-way fixed analysis of variance (ANOVA) was run to determine differences in diel period among release treatments and interactions between the fixed factors. Boxplots were used to show the distribution of hourly acceleration and depth values for control fish and an ANOVA was used to compare differences in values between diel periods. To examine the relationship between acceleration and depth, detection data was binned by hour. Hourly binning was necessary to ensure acceleration and depth values contained the same time stamp to allow for comparisons using a Pearson's correlation test. Acceleration and depth were plotted against time by release treatment. A LOESS model was fitted to points in each release treatment and resulting smoothing curves were qualitatively compared to reveal possible differences among release treatments in acceleration and depth data. Activity levels and behavior of Red Snapper was characterized by classifying the proportion of activity into four discrete levels: "rest", "low-activity", "roving", and "burst." Boundaries of these classifications were based on the quartile distribution of acceleration detections received for control fish. These boundaries were superimposed on the experimental release treatments (vented, non-vented, descend) and the proportion of detections in each activity level were used to generate an ethogram of behavior types for each release treatment. Statistical analyses were carried out in the statistical program R (R Development Core Team 2013) with significance tested at $\alpha = 0.05$.

RESULTS

Temperature data

Hydrographic variables were recorded during each of the three tagging days using a Manta2 water quality multiprobe. Temperature was plotted against depth to determine if thermoclines in the water column were present and if so, at what depths they ranged (Figure 3.2). During the winter, a thoroughly mixed water column at a constant 24°C was evident with no thermocline. Spring had a temperature range of 3.5°C (23.5°C at the surface to 20°C at the seafloor), with a thermocline beginning at a depth of 20 m. The summer profile had water temperatures ranging from 22-31°C with a steep thermocline beginning at 25 m depth and continuing to the seafloor. Sea surface temperatures for each season were recorded hourly from NOAA-NDBC station 42020 (N26°58’, W96°42’) and reported for a period of forty-five days after fish were tagged (Figure 3.3). Winter temperature declined over this time period and ranged from 23.7°C to 19.0°C and averaged 22.0°C ± 1.1 (mean ± SD). Spring temperature had an increasing trend ranging from 23.5°C to 30.7°C and averaged 26.8°C ± 1.5 (mean ± SD). Summer temperatures decreased ranging from 25.4°C to 28.9°C and averaged 27.1°C ± 0.7 (mean ± SD).

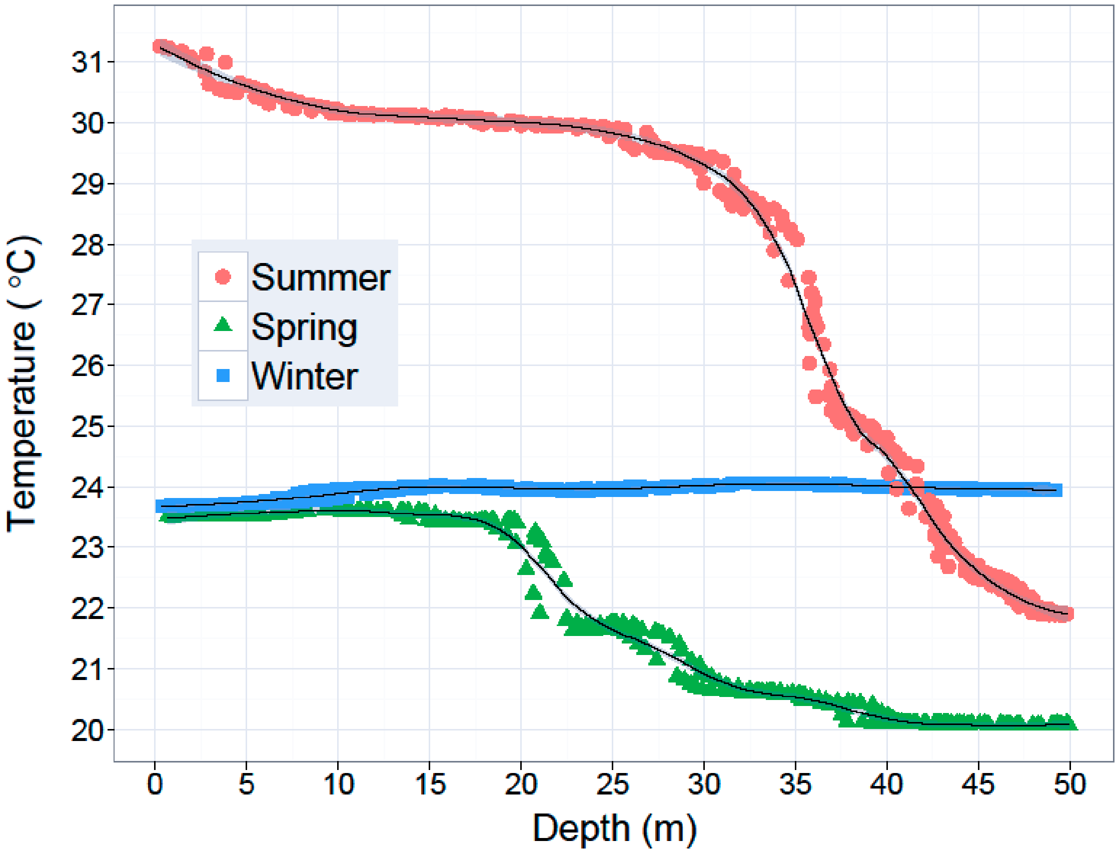

Figure 3.2. Temperature versus depth data collected using a Manta2 water quality multiprobe during three seasonal tagging trials at site MU-762-A (50 m). Black smoothing lines fitted to temperature data using loess model.

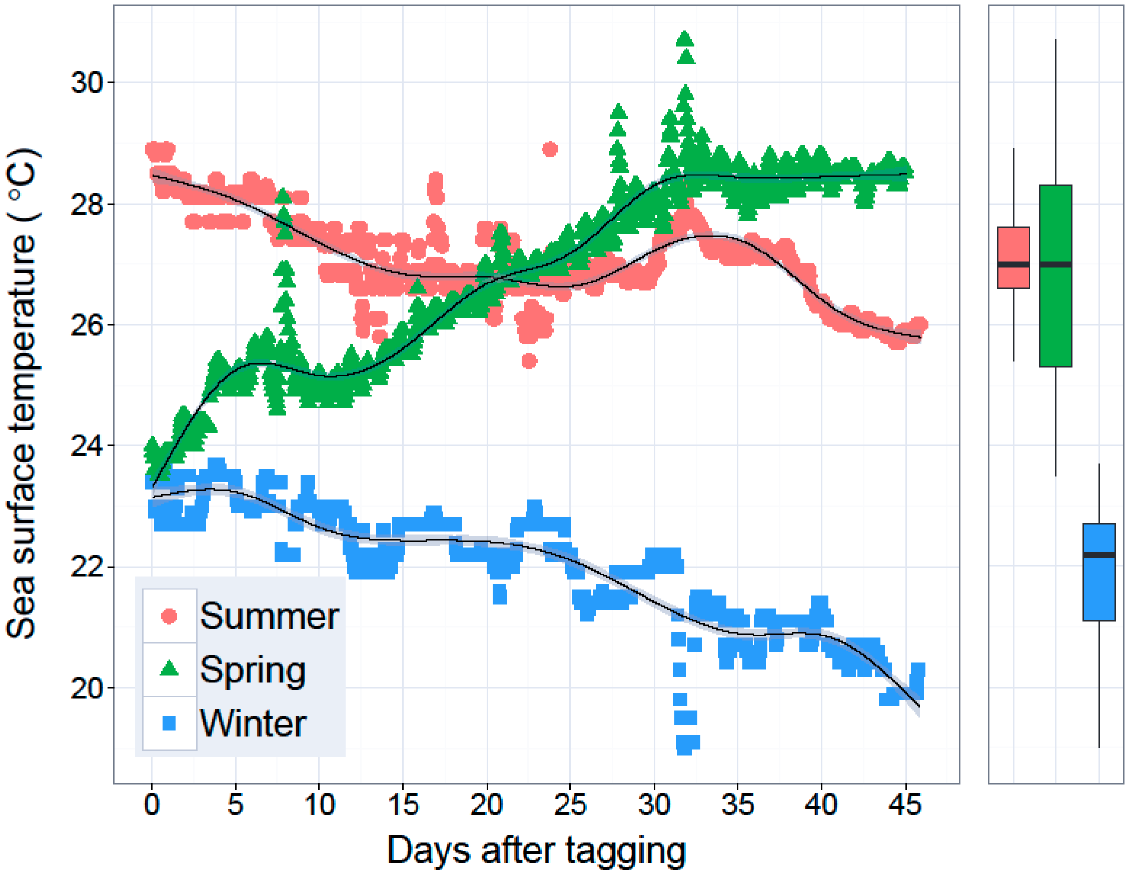

Figure 3.3. Sea surface temperatures (°C) during the 45 days fish were at liberty for three seasonal tagging trials. Data obtained from NOAA-NDBC buoy 42020 (N26°58’, W96°42’). Boxplots show distribution of temperature data for each season. Black smoothing lines fitted to temperature data using a loess model.

Fish tagging

A total of 111 Red Snapper were caught, tagged, and released. Using the acceleration and depth profiles of fish generated from sensor data, I determined that 49 fish survived and transmitted sufficient detections to retain for behavioral analyses. Total lengths of all surviving fish ranged from 321-651 mm TL (Figure 3.4) with a mean of 459 ± 12 mm (mean ± SE). No significant differences occurred in TL among release treatments (ANOVA, $F_{3,46} = 0.707$, $p = 0.553$). Because I was interested in examining mortality across all seasons for this chapter, all fish were combined by release treatment. Nine control, 15 descend, 17 nonvented, and eight vented fish survived and were used for further analysis in this study.

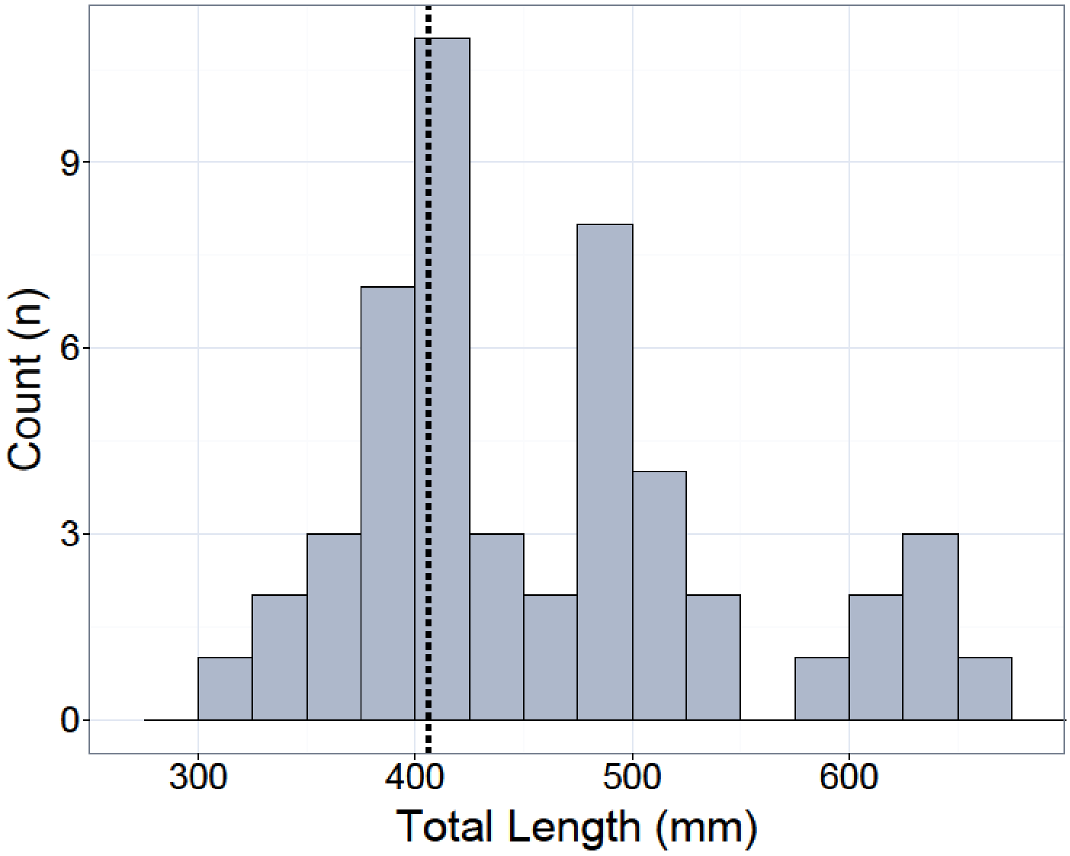

Figure 3.4. Distribution of total lengths (mm) for all Red Snapper survivors during tagging trials binned in 25 mm increments ($n = 49$). Dashed line represents the federal minimum size limit for Red Snapper in the recreational fishery (406 mm, 16 inches).

Site fidelity and residency

Red Snapper residency ranged from a minimum of three days to a maximum of 45 days, which corresponds to the estimated transmitter battery life (Figure 3.5). Mean residence time was 24 days (53% of possible detection days). This mean residence time represents a conservative estimate given that there was evidence that some fish experienced tag sheds (n = 6), and detections past this period were not counted in total residency estimates. Many fish experiencing tag sheds were fish that stayed continuously on site and likely remained there after tag shedding occurred. There was not a significant difference in mean residency times among release treatments (ANOVA, $F_{3,46} = 0.407$, $p = 0.749$). Twenty-four fish (49%) stayed on site continuously and registered at least one detection (typically many more) per day before emigrating from the site and not returning. Of these 24 continuously resident fish, four (Fish 8, 9, 10, and 36) remained on site every day for the entire 45-day monitoring period. Eleven fish were absent from the site for less than three days only. For the spring trial that involved multiple tagging sites, there was no site-to-site movement detected in any of the fish. Red Snapper exhibited exclusive fidelity to one site over the 45-day monitoring period.

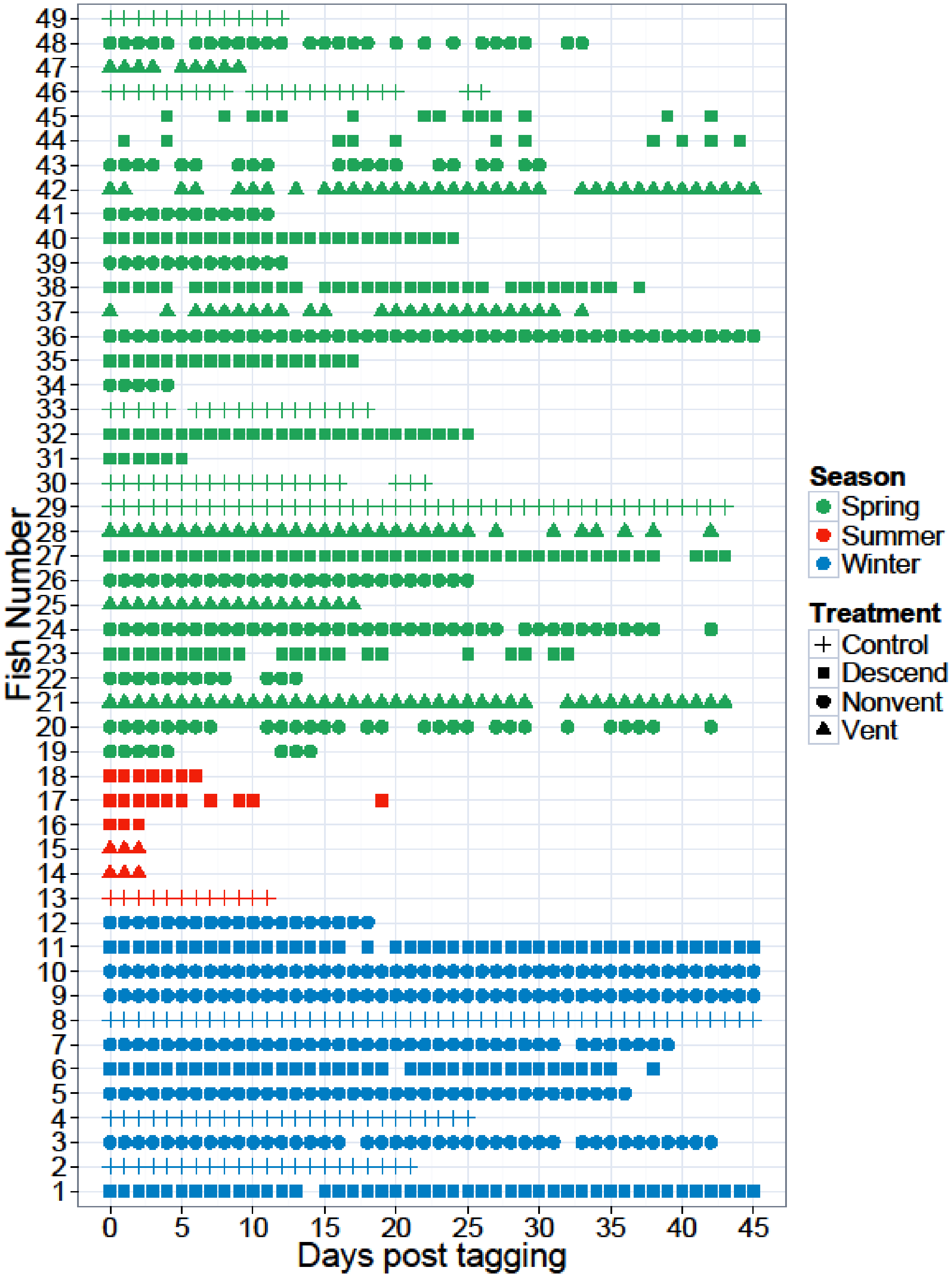

Figure 3.5. Abacus plot showing daily detections for each surviving fish (*n* = 49) for 45 days after tagging. Colors=seasons, shapes=release treatments. Each point represents a daily detection; multiple detections per day still register as one point.

Acceleration and depth sensors provided additional information to supplement traditional presence/absence data in examining residency patterns of Red Snapper. These sensor data made it possible to classify fish into four unique behavioral types (Figure 3.6). Residents remained on-site continuously and were highly active, registering multiple detections every hour and changing speeds and depths frequently. Fish that emigrated showed an initial continuous residency pattern with frequent detections per hour and acceleration and depth changes before leaving the array. Transient fish had patterns of temporary residency, remaining on-site and registering high levels of activity for a period of several days before moving off-site for a similar amount of time and then returning for one or more subsequent short-term residency periods. Tag sheds were detected in fish that would otherwise have likely been classified as residents. These fish had similar profiles as residents for several weeks until acceleration values suddenly dropped to zero, a pattern indicative of tag shedding.

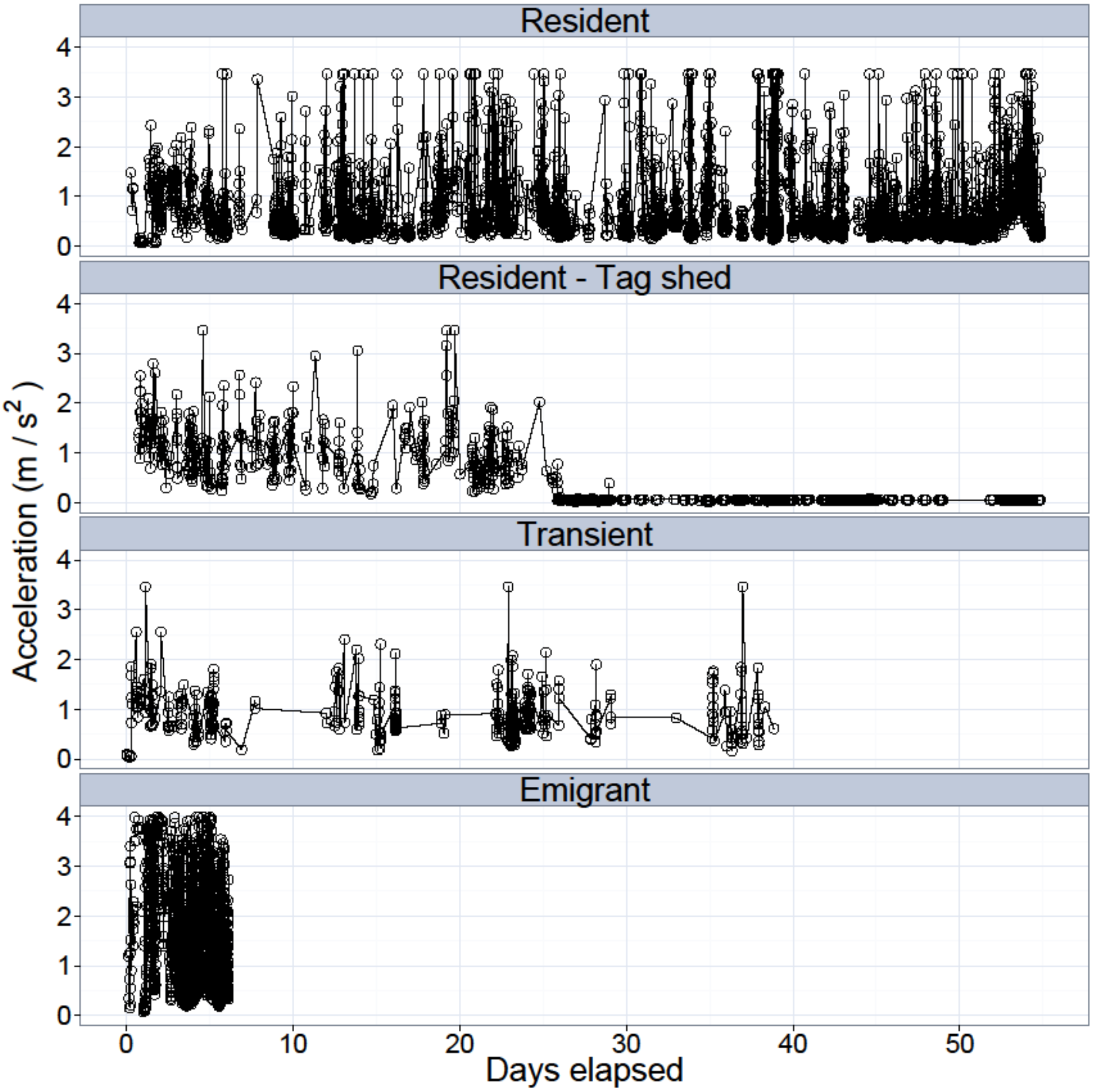

Figure 3.6. Acoustic profiles of four different behavior types elucidated by acceleration sensor data. (a) Resident, (b) Resident with tag shed, (c) Transient, and (d) Emigrant.

Diel movement patterns

Diel movement patterns of Red Snapper were determined by dividing detection data into hourly bins over a 24-hour period. Diel period was split into day and night time periods with 7:00 sunrise and 19:00 sunset times. There was a significant difference in the number of total detections (acceleration + depth) between diel period (ANOVA, $F_{1,94} = 138.95$, $p < 0.001$; Figure 3.7). To account for differences in the number of surviving fish per release treatment, detections per hour were scaled by dividing the total number of detections per hour by the number of fish in each release treatment. Using scaled data, there was also a significant difference in detections between diel period (ANOVA, $F_{1,94} = 116.84$, $p < 0.001$). During the day, there were 118.81 ± 5.85 (mean ± SE) detections per hour per fish compared to 43.33 ± 3.81 (mean ± SE) during the night. When looking at diel patterns in detections among release treatments, there was a significant interaction between release treatment and diel period (ANOVA, $F_{3,88} = 4.90$, $p < 0.01$). The test for main effects showed that diel period was a significant factor at each treatment level; there were significantly more detections received during the daytime than there were at night for each release treatment (ANOVA, $F_{1,88} = 267.69$, $p < 0.001$; Figure 3.8). Fish that survived the catch-and-release process had similar diel movement patterns over longer time periods regardless if they were vented, not vented, or rapidly recompressed. Given that the detection probability of a transmitter is a function of the proximity to a receiver, fish appear to have remained on-site within the platform structure during the day, while moving off-site during night hours.

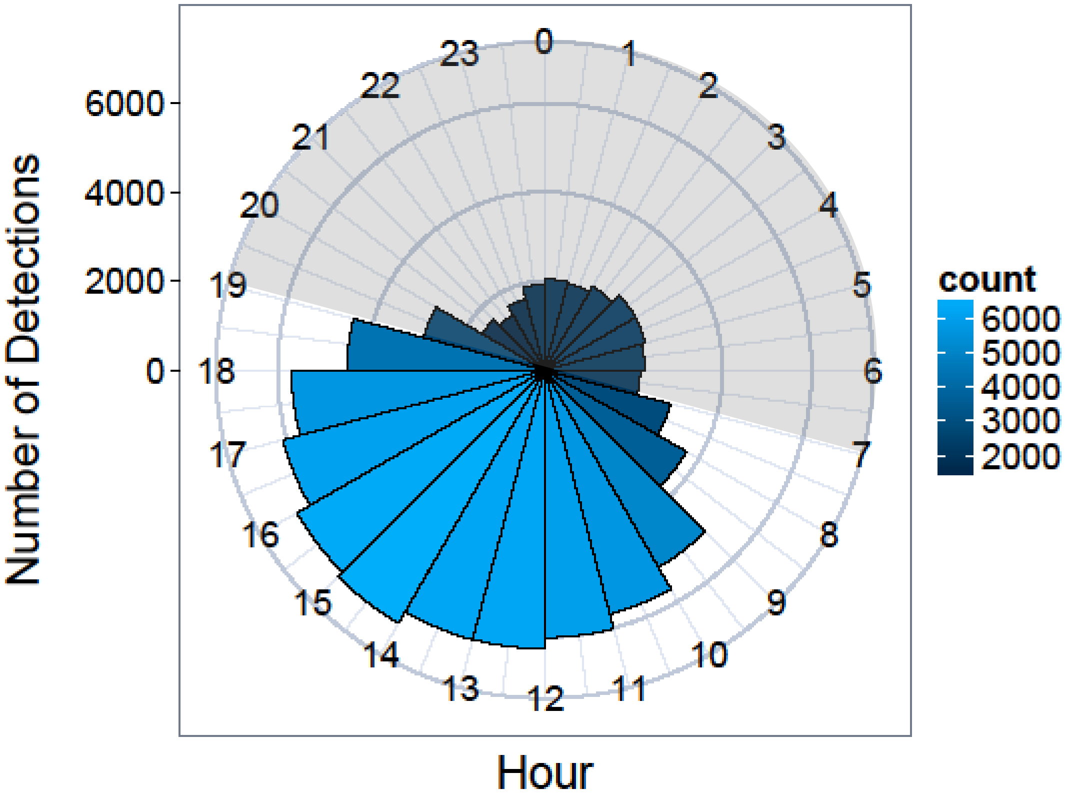

Figure 3.7. Polar histogram of the number of detections registered per hour (24-hour clock) for all fish. Mean nighttime hours considered to be between 1900 and 700 (shaded region).

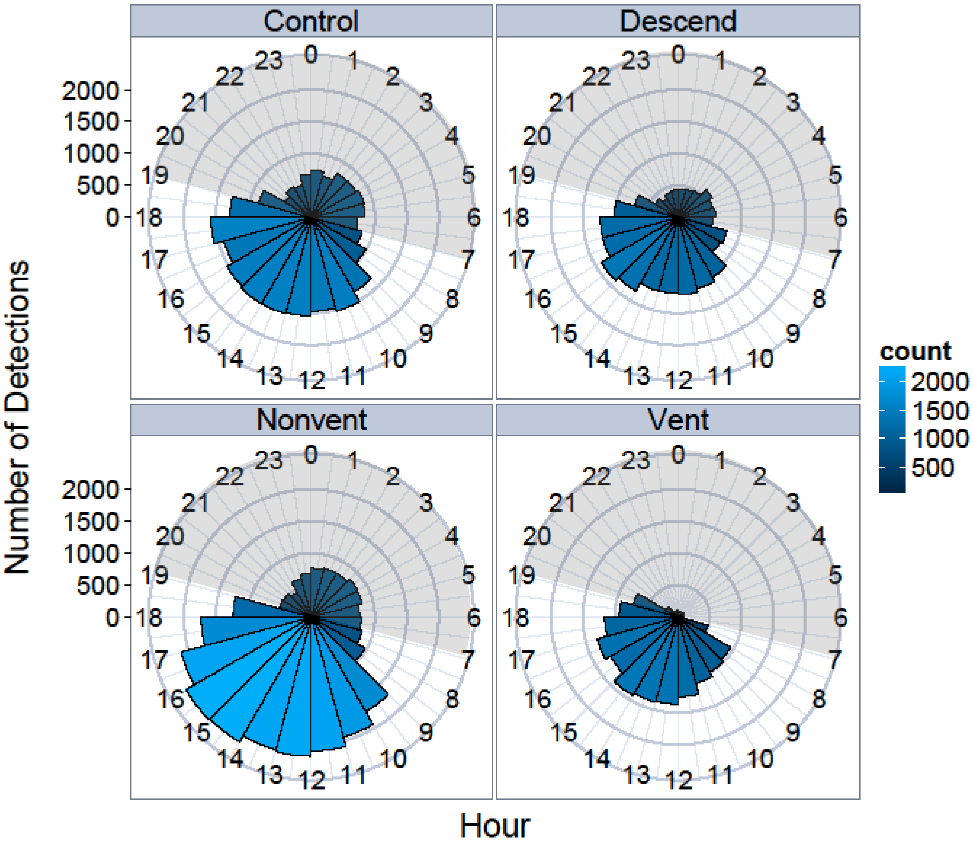

Figure 3.8. Polar histogram of the number of detections registered per hour (24-hour clock) per release treatment: control, descend, nonvent, or vent. Number of detections based on unscaled data. Mean nighttime hours considered to be between 1900 and 700 (shaded region).

Using acceleration and depth sensor data, I also compared diel activity and behavior of control fish after catch-and-release (Figure 3.9). Control fish had significantly higher acceleration at night compared to the day (ANOVA, $F_{1,12642} = 453.40$, $p < 0.001$). They also had vertical diel movement with a significant difference in depth between diel period (ANOVA, $F_{1,12505} = 1346$, $p < 0.001$). At night, Red Snapper resided an average of approximately 5.5 m higher in the water column than during the day. These fish also used a larger vertical range of the water column at night as indicated by the distribution ranges (Figure 3.9).

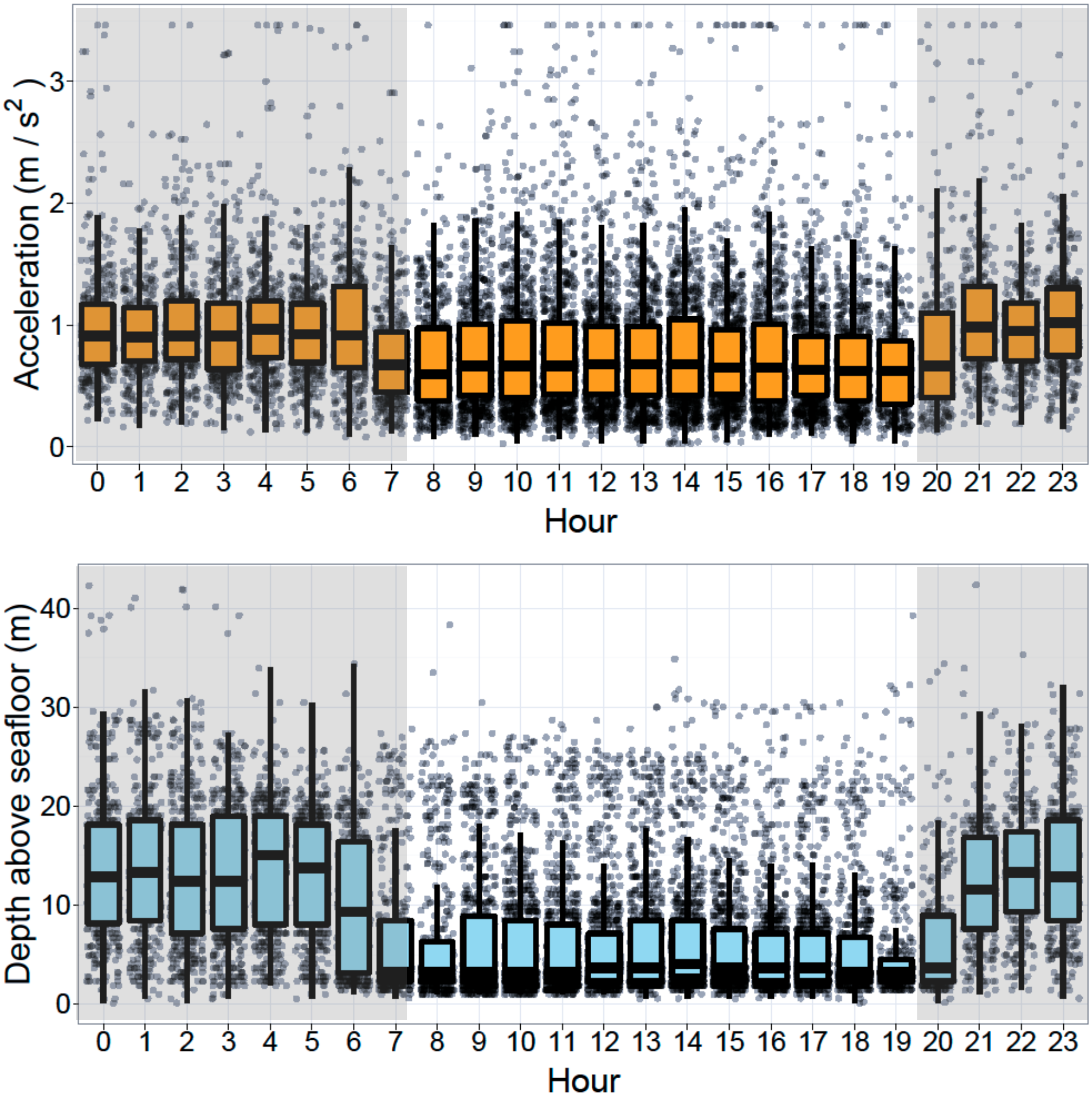

Figure 3.9. Distribution of acceleration (upper panel) and depth (lower panel) detection data for control fish over a 24-hour diel period. Mean nighttime hours considered to be between 1900 and 700 (shaded region). Points represent individual detections and were sorted into hourly bins.

Acceleration, depth, and release treatments

The relationship between acceleration and depth sensor data was analyzed to determine if any patterns emerged. Because there is a delay in the transmission timing of acceleration and depth sensors, acceleration and depth data were averaged into hourly bins for analysis. Acceleration was plotted against the depth above the seafloor for all fish by release treatment (Figure 3.10). A significant correlation between acceleration and depth was detected for Red Snapper across all release treatments (Pearson's $r = 0.329$, $p < 0.001$).

Acceleration values derived from sensor data were plotted over the 45-d monitoring period to examine noticeable differences between the release treatment groups. Data were fitted to a smoothing curve using a loess generalized additive model for each level of release treatment and these four curves were compared (Figure 3.11). All release treatments followed a similar pattern as the control fish in acceleration over 45 days, with mild fluctuations between mean acceleration values of 0.6 m/s^2 and 1.0 m/s^2. Similarly, depth was plotted over 45 days to examine changes in depth profiles due to release treatment and data were fitted to a smoothing curve using a loess generalized additive model (Figure 3.12). Within the first 10 days, subtle differences occurred in depth profiles between release treatments, with descended fish averaging shallower depths than the control fish and the vented treatment residing closer to the bottom than the control. Nonvented fish closely mirrored the control fish profile. After approximately 2 weeks, the three experimental treatment groups followed the control profile for the duration of the 45-day monitoring period.

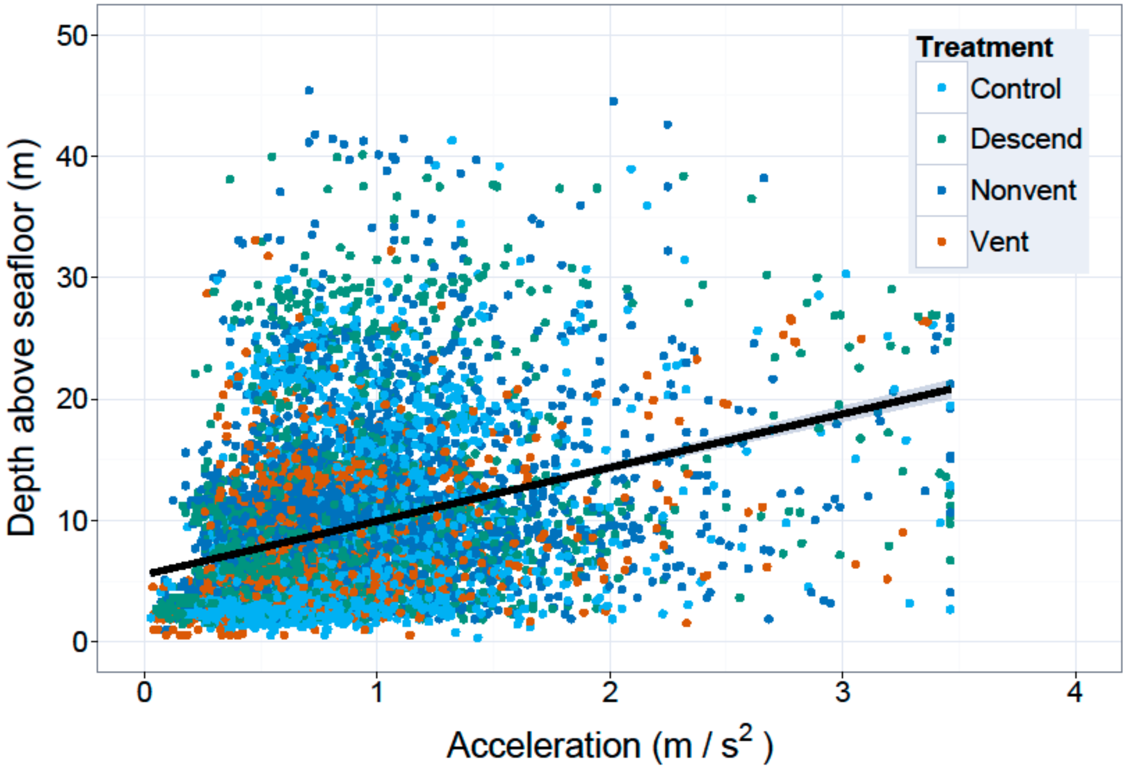

Figure 3.10. Correlation plot of values of acceleration against depth above the seafloor grouped by release treatment. Mean sensor value for acceleration and depth was calculated using hourly bins. Linear relationship between acceleration and depth above seafloor over all treatments is shown by the black line.

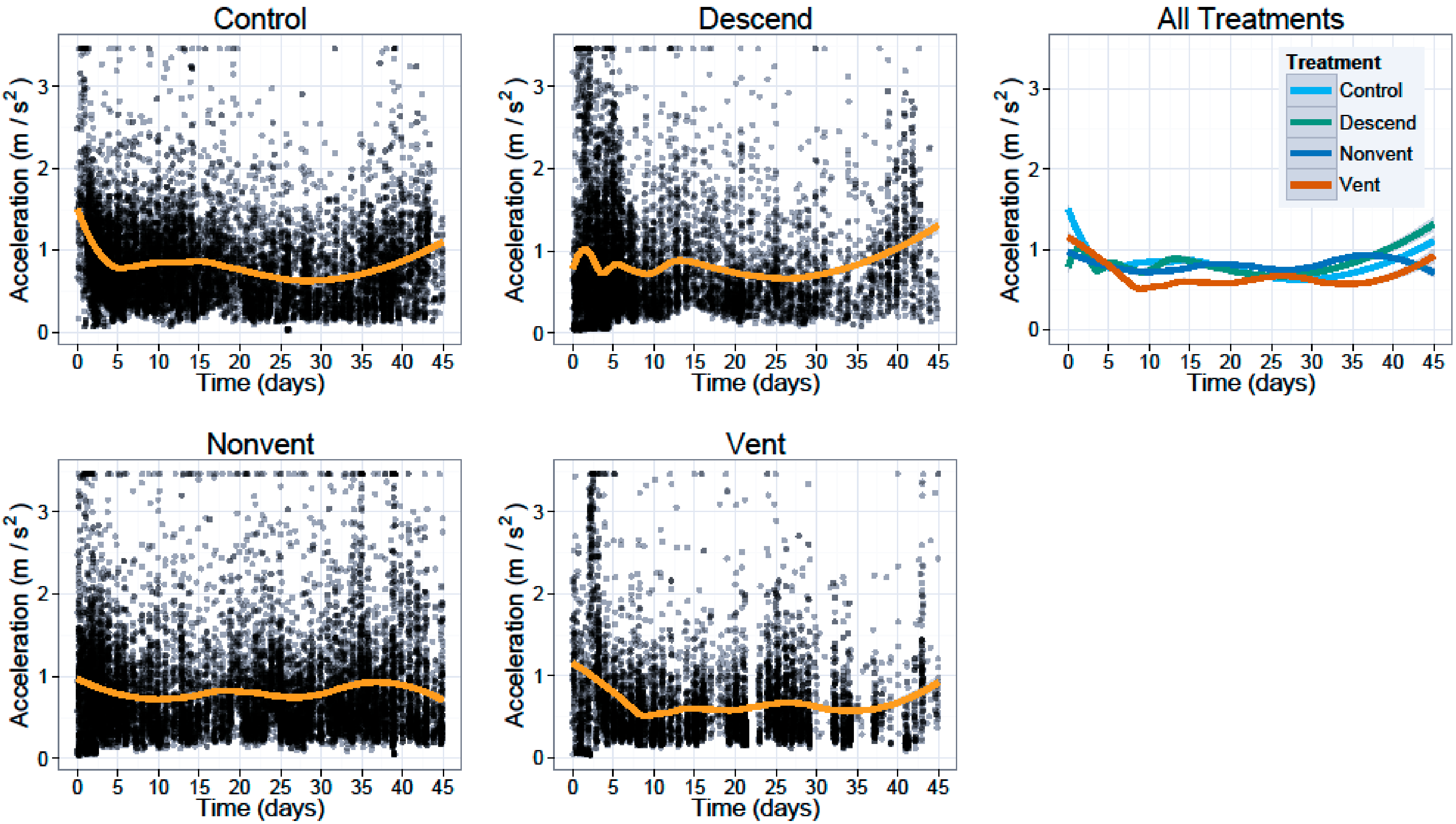

Figure 3.11. Acceleration (m/s^2) detection data of all fish by release treatment over the course of 45 days after tagging. Smoothing curves fitted with a loess generalized additive model (bandwidth, $\alpha = 0.5$). Far right panel is a comparison of the loess curves for all release treatments with points removed.

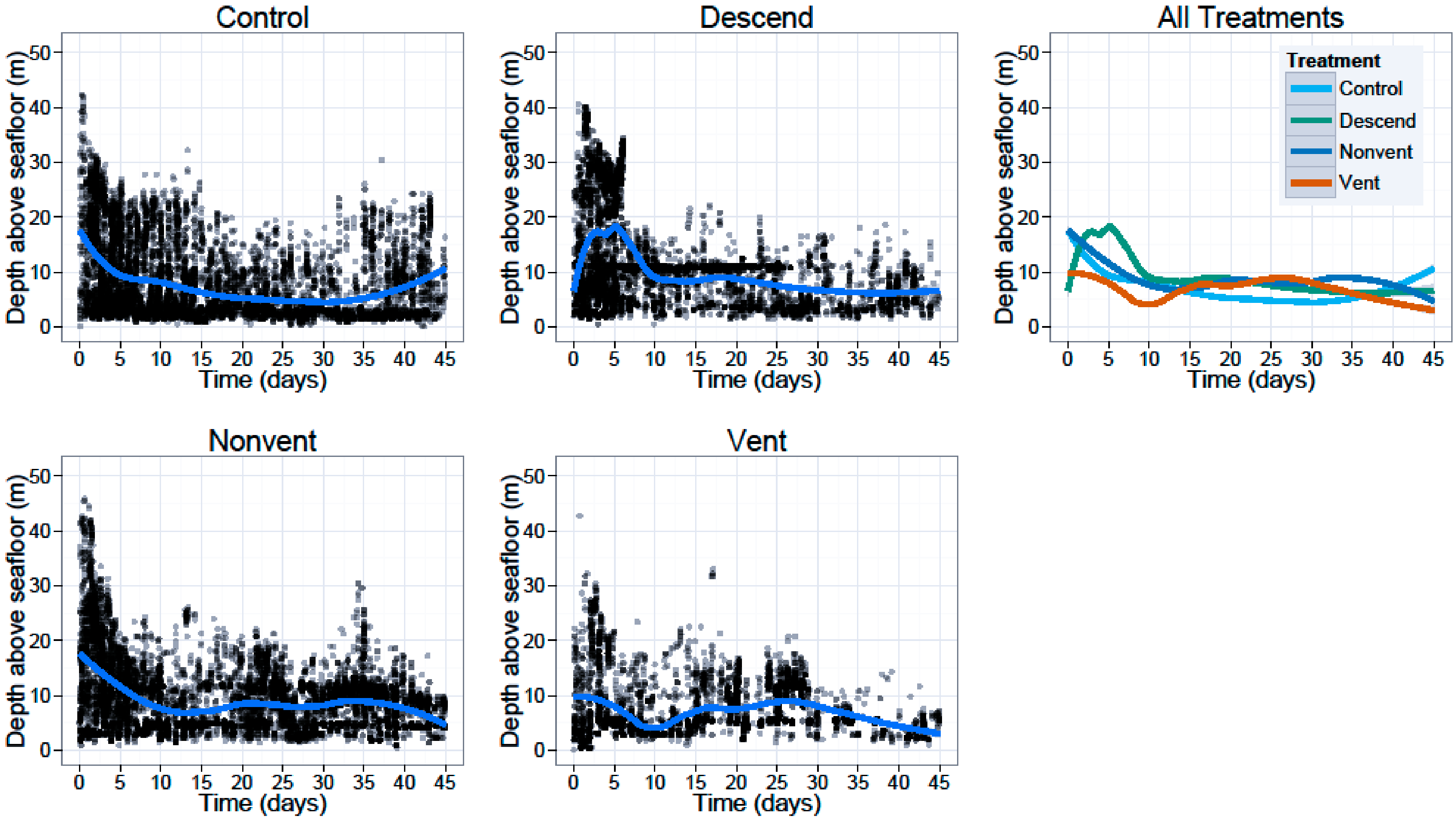

Figure 3.12. Depth (m above seafloor) detection data of all fish by release treatment over the course of 45 days after tagging. Smoothing curves fitted with a generalized additive model (bandwidth, *α* = 0.5). Far right panel is a comparison of the loess curves for all release treatments with points removed.

Behavior and activity ethograms

The behavior of tagged and released Red Snapper was characterized by classifying the proportion of activity into four discrete levels: “rest”, “low-activity”, “roving”, and “burst,” based on the distribution of acceleration detections received for control fish. Acceleration values were binned into 0.05 m/s^2 increments, and the count of acceleration detections per bin summarized in a histogram (Figure 3.13). The distribution of the control fish were as follows: Q_1 = 0.476, Q_2 (median) = 0.747, Q_3 = 1.073. Quartile values were rounded up to the nearest bin (0.5, 0.75, and 1.10, respectively). Fish less than Q_1 were classified as “resting,” fish within the interquartile range (IQR) were classified as “low-activity,” and fish higher than Q_3 but less than 3.45 were classified as “roving.” The fourth category “burst” represents the max-out value of the accelerometer sensor at 3.47 m/s^2. These fish are capable of much faster acceleration values; however, there is no way of knowing the actual value because of the maximum limitations of the sensor.

Once the boundaries of activity levels were quantified using the distribution of the control fish accelerometer detections, these values were superimposed on the three experimental release treatments (Figure 3.14). Using these boundaries and the distribution of acceleration detections for each release treatment, we constructed an ethogram that showed the percentage of time (as a proportion of total detections) that each fish spent performing each activity. The proportion of total acceleration detections was then compared among release treatments (Figure 3.15). Control fish spent approximately 27% of their time resting, 51% in low-activity mode, 21% roving, and less than 1% bursting. By contrast, descended fish spent a more balanced proportion of time resting (42%) and in low-activity (40%), with 17% roving, and less than 1% bursting. Nonvented fish spent 34% of their time resting, 46% in low-activity, 18% roving, and just over 1% bursting. Vented fish spent 39% of their time resting, 44% in low-activity, 16% roving, and less than 1% bursting. Although energy allocations varied somewhat by release treatment, no significant differences were detected. Across release treatment, fish spent the same proportion of time resting (ANOVA, $F_{3,45} = 1.605$, $p = 0.201$), in low-activity (ANOVA, $F_{3,45} = 2.212$, $p = 0.100$), roving (ANOVA, $F_{3,45} = 0.274$, $p = 0.844$), and bursting (ANOVA, $F_{3,45} = 0.635$, $p = 0.597$). The release treatments tested in this study do not differentially affect the activity levels of fish that have been discarded and survived.

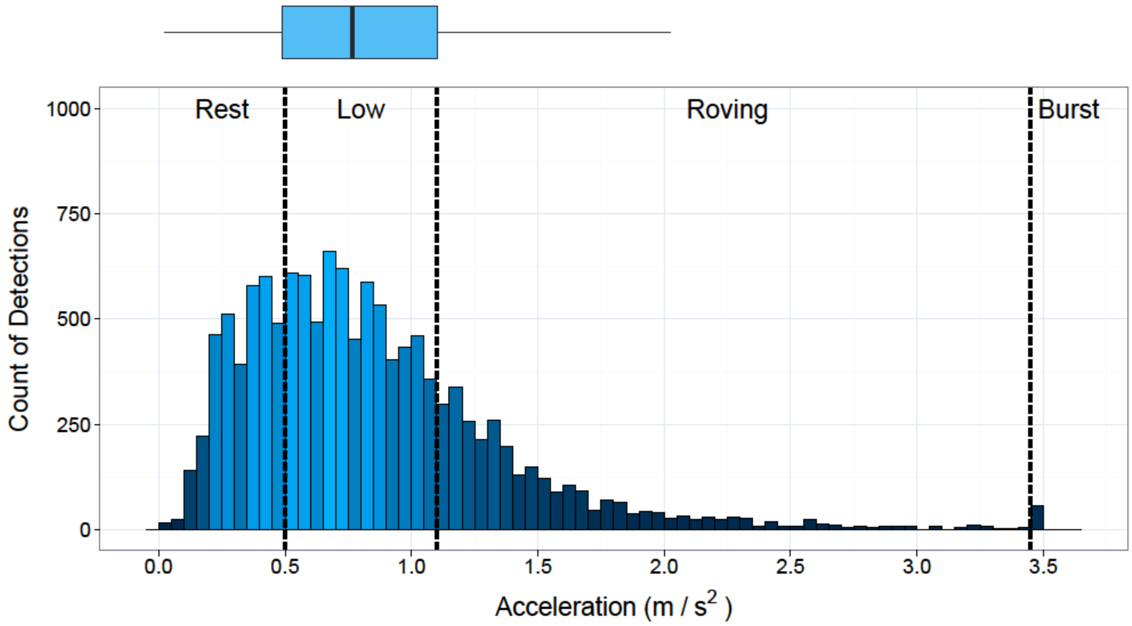

Figure 3.13. Histogram of the count of acceleration (m/s^2) detections for control fish (unscaled data). Four activity types determined using the distribution (represented by boxplot) of the control treatment: <Q_1 = “rest”, IQR = “low-activity”, >Q_3 = “roving”, and “burst” = 3.5 m/s^2 (the max-out value for the accelerometer sensor).

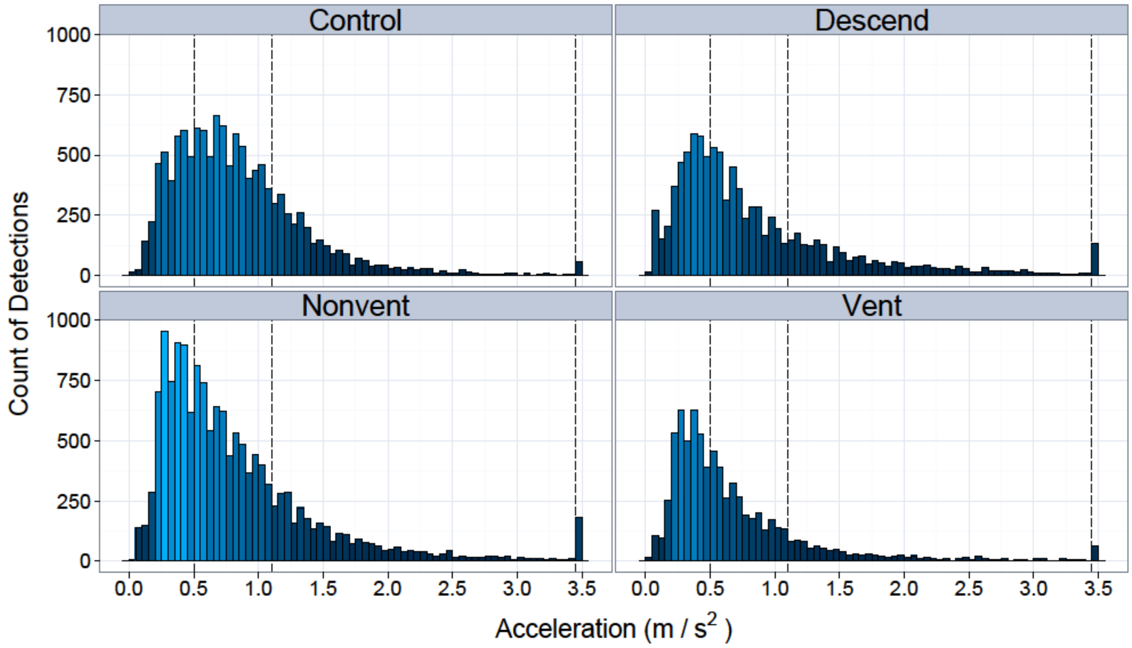

Figure 3.14. Histogram of the count of acceleration (m/s^2) detections per release treatment: control, descend, nonvent, or vent (unscaled data). The first two dashed lines represent the superimposed inter-quartile range (IQR) of the control fish used to specify the four activity types (“rest”, “low-activity”, “roving”, and “burst”). Spike at 3.5 m/s^2 in each panel represents the max-out value for the accelerometer sensor (i.e. “bursts”).

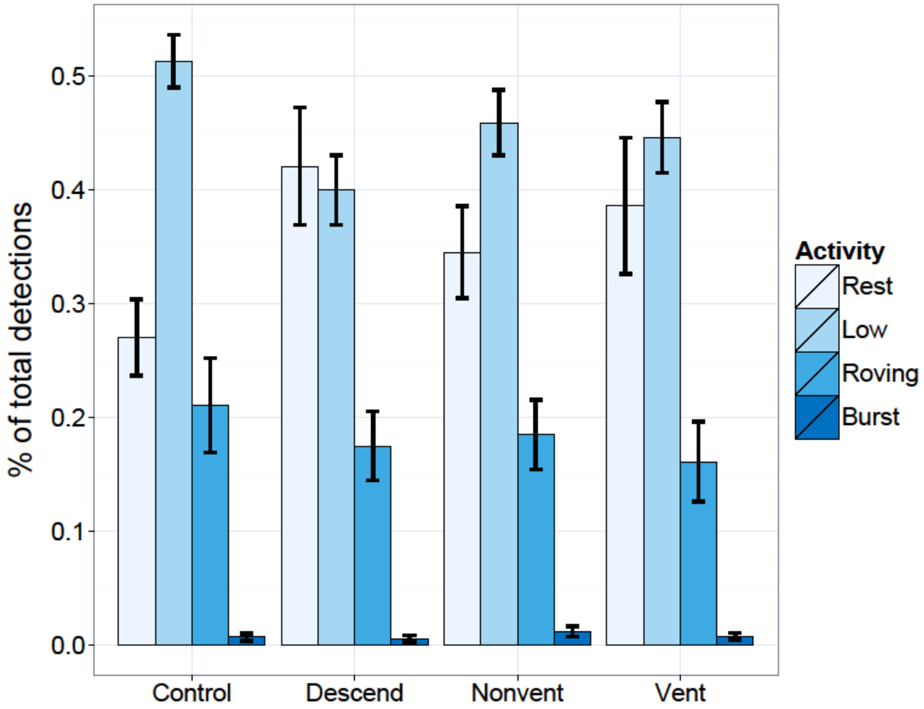

Figure 3.15. Ethogram showing the division in activity levels as a proportion of detections by release treatment (mean ± SE). Activity boundaries were quantified using the quartiles of the distribution of control fish.

DISCUSSION

This study is the first to examine post-release behavior and activity patterns of Red Snapper using acoustic transmitters equipped with accelerometer and depth sensors. Using this novel approach, I determined that Red Snapper display different acceleration and depth activity over diel time periods, and that acceleration and depth are correlated – fish higher in the water column typically had faster acceleration values than fish residing near the seafloor. I showed that venting, non-venting, and rapid recompression release treatments did not differ in their outcome on long-term fitness, behavior, or survival for discarded Red Snapper. Furthermore, fish released using different methods did not show reduced activity or behavior. That various release treatments do not place an added risk of mortality on discarded Red Snapper is a critical piece of information for managers making determinations on the best-release practices for minimizing discard mortality and promoting sustainable catch-and-release.

Fidelity and residency patterns in Red Snapper were similar to previous studies but the method of release did not alter this behavior. Red Snapper have high site fidelity to structured sites and this has been reported from both acoustic telemetry (Szedlmayer & Schroepfer 2005, Peabody & Wilson 2006, Westmeyer et al. 2007, Topping & Szedlmayer 2011a) and traditional mark-recapture tagging (Fable 1980, Szedlmayer & Shipp 1994, Watterson et al. 1998, Patterson et al. 2001). Though estimating long-term (i.e., 1 – 2 years or more) site fidelity was beyond the scope of this study, showing that release methods do not affect site preferences and residency patterns corroborates the findings of other studies, and increases the confidence of their estimates in the scenario that different studies have released Red Snapper using different methods. Because no differences in release treatments were observed in the study, site fidelity estimates among previous tagging studies can be considered comparable.

Accelerometer sensor data allowed me to detect the occurrence of tag shedding in the resident fish. Unique acoustic profiles generated from acceleration data revealed obvious tag shedding events and discerned these from profiles showing permanent residency. This resulted in more conservative estimates of residency as detections occurring after shedding events were not counted towards overall residency times. Without these acceleration data, differentiating highly resident fish behavior from a tag that has been shed was not possible. One assumption of telemetry data in estimating such behavioral parameters is that the probability of tag shedding is negligible (Pollock et al. 2004). Using transmitters equipped with accelerometer sensors enabled me to detect to the hour if and when a tag had been shed; thus, preventing any overestimations of residency times.

I detected diel residency patterns in Red Snapper during this study. Other researchers using presence/absence tags reported similar differences in the number of detections between diel periods, showing that Red Snapper moved away from structures at night, presumably reflecting foraging activity (Szedlmayer & Schroepfer 2005, Peabody & Wilson 2006, Topping & Szedlmayer 2011b). A significant difference in the number of detections per hour or diel period would seem indicative of residency patterns. However, environmental variables such as wind (Gjelland & Hedger 2013), temperature fluctuation (How & de Lestang 2012), the presence of thermoclines (Westmeyer et al. 2007, Mathies et al. 2013, Gjelland & Hedger 2013), and ambient biological noise (Payne et al. 2010, TinHan et al. 2014) can significantly influence acoustic detection efficiency, which may be misleading in making inferences about the movement of an organism based solely on number of detections alone. In one extreme case, data corrected for environmental influencing factors had the opposite result as uncorrected data (Payne et al. 2010), illustrating the importance of using reference tags where possible to account for variability in detection efficiencies driven by environmental fluctuations (Kessel et al. 2013). In the absence of reference tags, sensor data, as used in this study, also provide informative data with regard to movement and behavior. By using data obtained from acceleration and depth sensors, I can analyze actual speed (Murchie et al. 2011) and vertical movements (Afonso et al. 2012) over diel time periods. Ultimately and for future studies, reference tags in combination with sensor data would provide the best information on detection range, efficiency, and variability, but I was able to gain useful information in their absence from acceleration and depth sensors.

The use of accelerometer and depth sensors in my study provided novel and supplementary information in assessing diel movement patterns. During the night, Red Snapper had increased activity and also resided higher in the water column compared to daylight hours as indicated by accelerometer and depth sensor data. This finding coupled with the diel differences in detection frequency also observed suggests that Red Snapper seek refuge within the protection of structured habitats near the seafloor during the day and exhibit very little movement from these refuges. At night, fish leave sheltered habitats, move off-structure and off the seafloor, where they are more active and use a wider range of the water column. The primary diet of Red Snapper in this size class is comprised of fish (Ouzts & Szedlmayer 2003, McCawley & Cowan 2007, Wells et al. 2008). Thus, this active, mid-water behavior is likely representative of piscivorous foraging behavior and suggests that Red Snapper prefer fish as their primary food source during nocturnal feeding events, a pattern corroborated by aforementioned diet analysis studies. The positive correlation between increasing acceleration and shallower depth also supports this feeding preference, as more activity is undoubtedly required foraging for motile fish compared to sedentary benthic invertebrates.

No major behavioral differences were observed overall among release treatments. Fish rapidly recompressed using a descender hook, and either non-vented or vented and released at the surface, all exhibited similar acceleration and depth preferences over the 45 days fish transmitted data, though a couple minor deviations from the normal profile were observed. First, depth of fish released using the descend treatment had deeper initial start depths than other release treatments because of these fish being released on the bottom. The other three release treatments, including controls, were released at the surface and required fish to swim back to depth, which typically happened rapidly. The particular rapid recompression tool we used (Shelton Fish Descender^{TM}) requires the fish to be released on the bottom as the slack provided by hitting the seafloor enables the fish to release. More advanced devices, such as the SeaQualizer^{TM}, offer a pre-specified depth where the fish will be released, which can accommodate mid-water releases if returning the fish all the way to the bottom is not necessary or feasible. Second, the vented fish released using this method had marginally deeper average depth for the initial 12 days post-release, approximately. This time period may coincide with the estimated time it takes swim bladders to heal. Rummer (2007) stated that swim bladders in Red Snapper take on average 14 days to heal; however, Burns (2009) found sufficient healing in swim bladders so as to be functional within 2 – 4 days after puncturing using hyperbaric chamber experimentation. Reductions in vertical migrations have been linked to swim bladder rupture (Strand et al. 2005, Nichol & Chilton 2006), and it is possible that even the deliberate “venting” of the swim bladder may be sufficient impairment to compromise proper buoyancy regulation and minimize the vertical range of discarded fish. This may explain why fish that were vented showed depths closer to the seafloor initially.

I classified the activity levels of Red Snapper into discrete groups using the accelerometer sensor data. Overall, approximately half of the detections registered acceleration values corresponding to low activity (i.e. between 0.48 and 1.07 m/s^2). These values are comparable with the other studies using the same transmitter technologies (VEMCO© accelerometer acoustic transmitters). Murchie et al. (2011) determined that Bonefish (*Albula vulpes*) also spend the largest percentage of their activity in a "low-activity" mode (range: 0.23-0.78 m/s^2), and O'Toole et al. (2010) found the same low-activity behavior (range: 0.10-0.73 m/s^2) was also most prominent for Great Barracuda (*Sphyraena barracuda*). While I classified "bursting" movements of Red Snapper at 3.47 m/s^2, the sensor limitations precluded me from capturing the true and much quicker acceleration values that these fish are capable of displaying. Another technological drawback is that these sensors are programmed to average acceleration over a fixed period of time. Quick and unsustained bursts may go undetected as these values may not influence the average value significantly enough to register a value indicative of a burst. Thus, we likely underestimate the number of burst behaviors these fish really are showing. Nonetheless, accelerometers used in this study provide novel and useful information on energy expenditure and activity levels of Red Snapper and has immense potential for future physiological and behavioral studies.

While the method of release did not differentially affect the long-term behavior or activity of discarded Red Snapper, not all release treatments are equal in promoting survival. This is an important caveat. I focused on the long-term behavioral patterns in individuals pre-determined to have survived the catch-and-release process and may not be an accurate representation of the entire population. Certain release treatments are more beneficial in promoting survival of discarded fish more immediately after the catch-and-release process. In

Chapter II, I showed positive effects of venting and rapid recompression for reducing both immediate and delayed (< 3 days) discard mortality. With results from this study finding negligible effects of release treatment on survival in the long-term, managers should place increased weight on release methods that benefit survival in immediate, short-time scales and these should be prioritized as best-release practices for catch-and-release fisheries.

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CHAPTER IV:

HIDING IN PLAIN SIGHT: TRACKING THE POTENTIAL SPAWNING STOCK OF RED SNAPPER IN THE GULF OF MEXICO

ABSTRACT

Red Snapper (*Lutjanus campechanus*) in the Gulf of Mexico have been classified as overfished and undergoing overfishing for decades but have recently began strong recovery as a result of stringent management regulations. Despite recent historically low stock sizes, current recruitment has been much higher than predicted. One hypothesis to explain this paradox is the existence of a locally recruiting source population of large, highly fecund “sow” Red Snapper not targeted by either fishery or fishery-independent surveys that is responsible for maintaining high recruitment. These sow Red Snapper are relatively unfished because they may be using different habitats that release them from fishing pressure associated with commonly known structures where fishermen concentrate their effort. Using acoustic telemetry and catch-per-unit-effort data, my objectives were to: (1) test the hypothesis that large adult snapper have found spatial refuge from fishing by selecting different habitats than small adult snapper; and (2), investigate large-scale movement and small-scale habitat use patterns of sow Red Snapper. Sow Red Snapper tagged and tracked using mobile acoustic telemetry had 79% (11 of 14) relocation at initial tag sites after three months and 36% (5 of 14) after one year. Within the stationary acoustic array, sow snapper tagged on one platform had similar long-term habitat use patterns as small Red Snapper reported in the literature, residing at depths near the seafloor and within close proximity to structure. Catch-per-unit-effort at three popular surface platforms and three unknown sites revealed comparative catch rates and total lengths. However, there was a significantly higher abundance and mean size of fish before the recreational fishing season started compared to after it closed suggesting that localized depletion of a site can occur due to fishing pressure. Sow Red Snapper appear to have high site-fidelity, use shared habitats, and have similar movement patterns as small adult Red Snapper. The rapid recovery of Red Snapper stocks recently suggests that managers may have underestimated the spawning stock biomass or productivity of this stock, or potentially both. The site fidelity characteristics of sow Red Snapper and use of small and typically unknown habitat features support our hypotheses that a portion of the spawning stock of sow Red Snapper may have been overlooked and that the high recruitment observed in the stock may be originating from these non-targeted sources.

INTRODUCTION

Red Snapper (*Lutjanus campechanus*) is the most economically important reef fish species in the Gulf of Mexico (GOM). Management of the Red Snapper fisheries in the GOM is a complex and controversial issue (Cowan et al. 2010), particularly because Red Snapper have been classified as overfished since 1988 (Goodyear 1988) and were only recently removed from the overfishing category (Cowan 2011). The stock-recruit relationship of Red Snapper in the GOM has been especially problematic to describe for two reasons. First, the Red Snapper stock has been at very low levels since data collection and management efforts began in 1984 (Hood et al. 2007), so there are no medium or high stock sizes to indicate what recruitment would be at higher stock sizes. Second, recruitment levels seem to be much higher than historical output levels, although the stock size is estimated to be much lower than it was historically (SEDAR 2009, Shipp & Bortone 2009). This paradox of low stock biomass characterized by high recruitment is very puzzling because in addition to a reduction in the number of fish in the population, directed fishing also causes a reduction in the average size and age of individuals in the population (Nieland, Wilson, et al. 2007). Smaller female Red Snapper produce a fraction of the eggs that large, older individuals produce (Fitzhugh et al. 2004), so theoretically, a heavily fished population should show much lowered recruitment compared to an unfished stock even if stock sizes are equal. In Red Snapper, however, this does not appear to be the case. The spawning stock has remained at almost the same low level since 1984 and purportedly consists of fewer large individuals, but recruitment has varied almost 20-fold in the last 20 years (SEDAR 2013). The high levels of recruitment compared to historic levels seen in Red Snapper also means that future recruitment levels are difficult to predict, increasing the uncertainty in setting appropriate harvest quotas.

There are several hypotheses as to why recent recruitment levels been high, despite low spawner biomass. Potentially, the construction of large numbers of oil and gas platforms in the GOM over the past several decades has provided additional artificial reef habitat able to support increased recruitment of Red Snapper (Shipp & Bortone 2009). Increasing artificial reef habitat may have relieved the “bottleneck” (Osenberg et al. 2002) that previously prevented Red Snapper recruitment from increasing to current levels by effectively raising the carrying capacity of this environment (Shipp & Bortone 2009). Another possibility is the occurrence of a secondary pulse of recruitment originating from the Campeche Banks in the southern GOM, where Red Snapper have an extended spawning season (Brulé et al. 2010) compared with northern GOM stocks (Collins et al. 1996). However, this seems unlikely because of the extended distance of larval transport needed to occur within the estimated 22 – 28 days of the Red Snapper’s planktonic stage (Johnson et al. 2013). While some larvae may succeed in crossing the GOM and maintain gene flow, the limited amount is likely insufficient to account for the magnitude of recruitment being reported (Johnson et al. 2013). Finally, the assessment process may have underestimated the productivity of the stock.

In addition to these possible explanations, there may be a cryptic source of spawning stock biomass in the western GOM not accounted for in stock assessments that is responsible for delivering high recruitment to the fishery (i.e., the “Mother Lode” hypothesis). Large female (“sow”) Red Snapper (> 8 years old, > 700 mm TL) may be using different habitats than young adult (2-6 years old) Red Snapper, and these habitat preferences move them away from structures where commercial and recreational fishing pressure is concentrated. Bottom long-line surveys in offshore waters often capture large Red Snapper ranging up to 903 mm TL (Mitchell et al. 2004). These surveys also reported higher catch-per-unit-effort, larger maximum size (median, 755 mm TL), and older age (median, 11 years) in the western GOM compared with the eastern GOM (Mitchell et al. 2004). Anecdotal information from recreational fishing captains also suggests that sow snapper use different habitats than small adult snapper and are more prevalent off-structure over low relief areas. However, with the exception of the aforementioned study, there is a lack of information in the scientific literature detailing the habitat preferences, site fidelity, and movement patterns of these larger sow snappers in the western GOM. This information is critical given the reproductive potential of these sow snappers – one age eight female Red Snapper can produce nearly one million eggs per spawning event and over 25 million eggs over a single spawning season (Collins et al. 1996), which is the spawning potential equivalent to approximately 212 newly reproductively active (age 2) Red Snapper. With such high fecundity, the high recruitment levels in the fishery may be produced in part from this cryptic spawning stock biomass (i.e., “mother lode”) of large sow snapper residing at off-structure sites.

Many studies have documented the affinity of young adult Red Snapper for oil and gas platforms in the GOM (Gitschlag et al. 2003, Nieland & Wilson 2003, Peabody & Wilson 2006, Westmeyer et al. 2007, Gallaway et al. 2009, Shipp & Bortone 2009). Site residency and movement patterns of Red Snapper on these artificial reef habitats have been studied using both traditional mark-and-recapture and ultrasonic acoustic telemetry methods but results are somewhat contradictory (SEDAR 2012), with some researchers reporting long distance emigration events and short residency times (Patterson et al. 2001, Patterson & Cowan 2003, Westmeyer et al. 2007) and other researchers reporting high site fidelity and extended residency times (Szedlmayer 1997, Szedlmayer & Schroepfer 2005, Diamond et al. 2007, Strelcheck et al. 2007, Topping & Szedlmayer 2011a). Based on these conclusions, fishery managers suggest that Red Snapper likely have high site fidelity and residency patterns on short time scales of 1 – 2 years before emigrating and having increased movements over longer time scales (SEDAR 2012) that is occasionally driven by extreme climatic events (Watterson et al. 1998, Patterson et al. 2001, Topping & Szedlmayer 2011a).

Only one study has addressed habitat use and movement patterns of large sow Red Snapper in the western GOM (Mitchell et al. 2004), and no one has used ultrasonic acoustic telemetry methods in this region. In the eastern Gulf, Szedlmayer & Schroepfer (2005) acoustically tagged 54 fish with a mean size of 589 ± 14 mm (mean ± SE), which included nine fish characterized as sow Red Snapper (> 700 mm). All fish were tagged on artificial reef structure and exhibited residency times of 218 ± 28 d (mean ± SE). Topping & Szedlmayer (2011) have acoustically tracked the largest Red Snapper to date: 639 ± 81 (mean ± SD), and ranging up to 860 mm TL. These fish had much longer residence times at 542 d (median residence time) and included one natural reef along with five artificial reef habitats. Thus, the lack of information regarding sow movement patterns in the western GOM necessitates further study as these fish may be responsible for maintaining high recruitment levels for the fishery. The overall goal of this study was to test the hypothesis that older, larger sow Red Snapper in the western GOM have found spatial refuge from fishing by using different habitats than smaller adult Red Snapper. Furthermore, I hypothesize that this cryptic spawning stock is responsible for keeping local recruitment levels in the western GOM high and may possibly be acting as a source population for the eastern GOM, where recruitment levels are much lower (Saillant et al. 2010, Cowan 2011). Specifically, I test this hypothesis by using a combination of acoustic telemetry and catch-per-unit-effort trials. I then compared these movement and habitat use patterns of sow Red Snapper in the western GOM with smaller adult Red Snapper from previously published studies.

METHODS

Fish tagging

Acoustic telemetry was used to track sow Red Snappers to determine if they are using different habitats than smaller, younger adult Red Snapper. Large sow Red Snapper (> 700 mm TL) were captured using hook-and-line sampling using 5/0 circle hooks baited with squid (*Loligo sp*.), Gulf Menhaden (*Brevoortia patronus*), or scad (*Trachurus sp.*) at six sites during March and April 2010 (Figure 4.1). The six sampling sites represented three well-known, high-profile offshore oil and gas platforms and three relatively unknown, low profile sites expected to experience reduced fishing pressure. Sites ranged in depth from 38.0 – 46.9 m, were classified as either large or small habitat sizes, and included four artificial habitats and two natural habitats (Table 4.1). Fourteen fish were tagged internally with Vemco© V16TP-4x ultrasonic acoustic transmitters equipped with temperature and pressure (i.e., depth) sensors. Ten fish were tagged in March and an additional four fish were tagged in April at sampling sites (Table 4.2). Sensors were programmed to transmit at 69 kHz frequency at random intervals between 15 – 45 s. The range of temperature sensors was -5 to 35°C and the maximum sensor depth was 204 m. These specifications resulted in an estimated battery life of 440 days. Tags were surgically implanted in fish internally by making a small incision in the peritoneal cavity, inserting the V16TP-4x tag, and suturing the incision closed using braided suture (Ethicon® Vicryl 3-0 absorbable). Red Snapper survive this tagging process successfully and incisions heal within 7 – 10 days (Johnson et al. 2014). Fish were additionally dorsally tagged with a vinyl passive recovery tag containing a unique identification number and return and reward information should the fish be caught by recreational anglers during the trials. Prior to release, fish were held briefly on deck and monitored in a holding tank to ensure survival through the tagging process. Fish were released at depth using a weighted descender hook to rapidly re-submerge fish to the bottom. To monitor fish survival and behavior post release, a Vemco VR2W receiver tied to the boat at 10 m depth recorded acoustic detections of fish released during tagging operations. Further relocations were accomplished using both mobile and stationary tracking techniques.

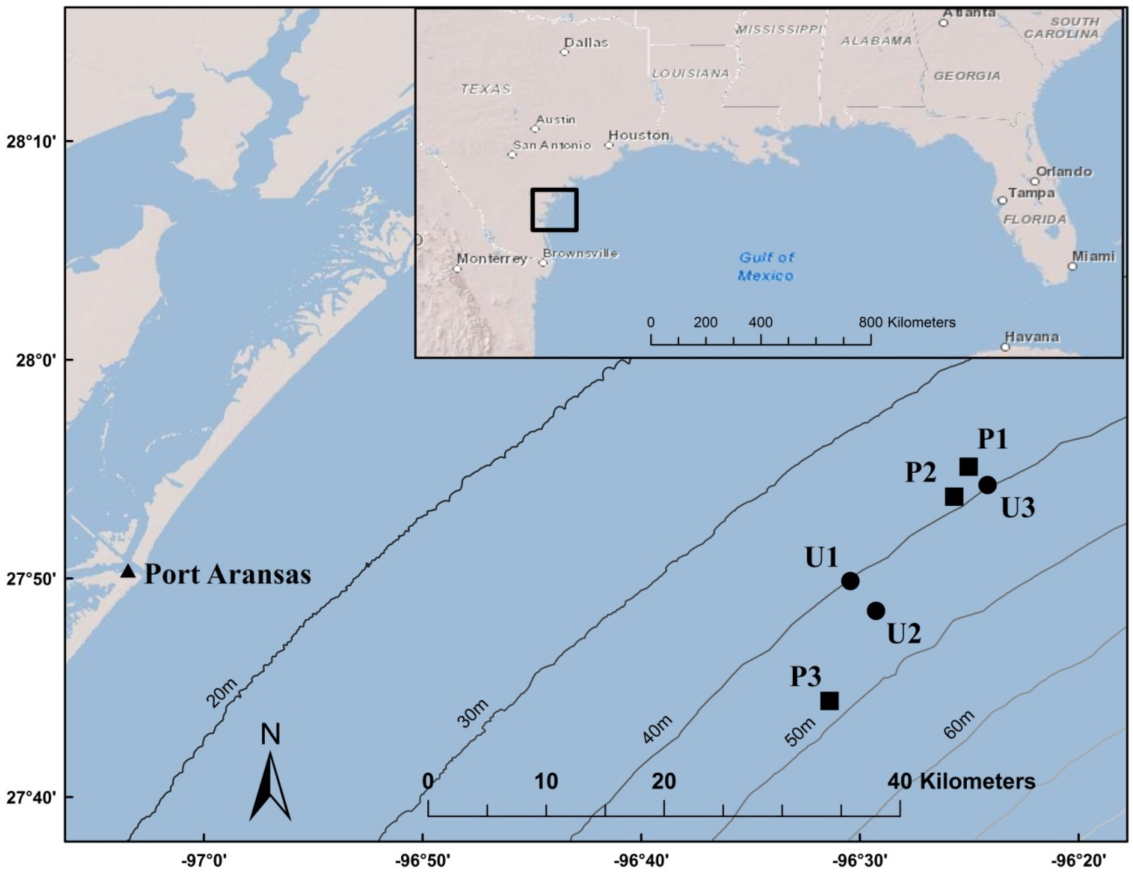


Figure 4.1. Study sites. Key: Platform, visible at the surface (■); Underwater, not visible at the surface (●). Contour lines paralleling the shore represent depth (m) in 10 m increments.

Table 4.1. Site descriptions for sow tagging studies. Key: (P) platform, visible at the surface; (U) underwater, not visible at the surface; Name: identity or name of site; Distance to port: distance to Port Aransas, the nearest port from sites.

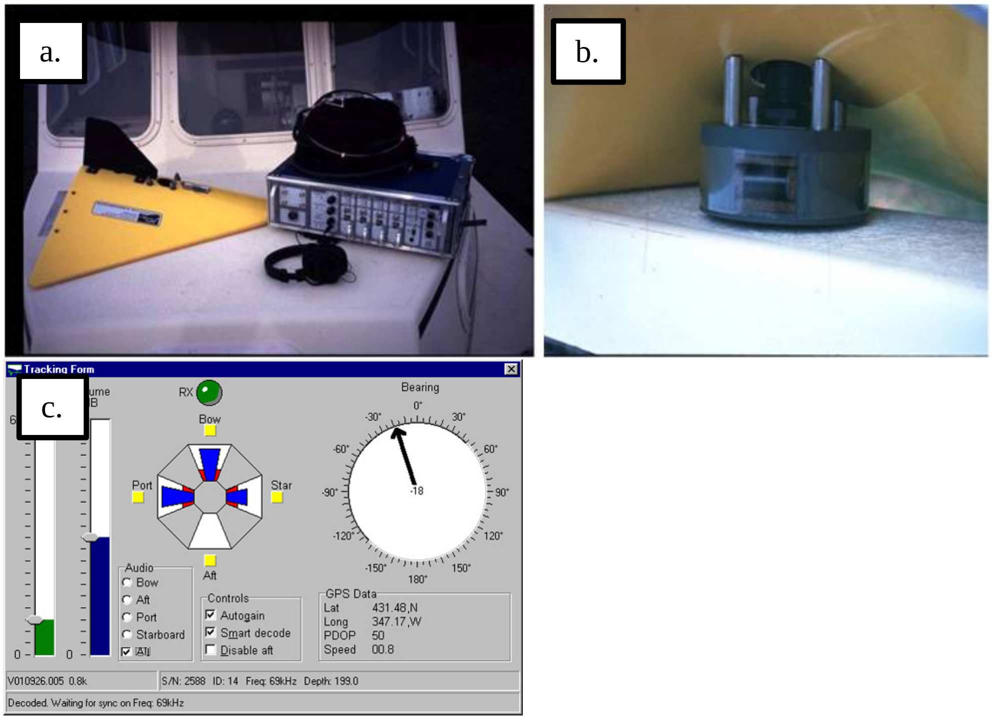
Site	Name	Latitude	Longitude	Distance to port (km)	Depth (m)	Visibility	Structure type	Site size
P1	MI-683-A	N27°55.115	W96°25.023	63.7	38.0	Visible	Artificial	Small
P2	MI-703-A	N27°53.751	W96°25.681	62.3	39.0	Visible	Artificial	Large
P3	MU-759-A	N27°44.406	W96°31.383	53.8	46.9	Visible	Artificial	Large
U1	MI-712-A	N27°49.886	W96°30.431	54.3	39.6	Not visible	Artificial	Large
U2	Great reef	N27°48.520	W96°29.264	56.3	43.6	Not visible	Natural	Small
U3	Secret spot	N27°54.274	W96°24.160	65.2	40.2	Not visible	Natural	Small

Table 4.2. Profiles and tagging characteristics for sow snapper tagged in 2010 (*n* = 14). Fish were tagged over two days at six different sites. Name: identity or name of site; TL: maximum total length (mm) of fish tagged; Deck time: time taken to unhook fish, tag with internal acoustic transmitter and external passive identity tag, and monitor in holding tank prior to release; Vemco tag serial #: unique acoustic telemetry identity code for each fish; Detections: number of acoustic detections registered from mobile VR28 and stationary VR2W acoustic receivers; Last detected: day of last registered acoustic detection; Days at large: number of days elapsed between tag date and last detected date.

Fish #	**Tag date**	**Site**	**Name**	**TL (mm)**	**Deck time**	**Vemco serial #**	**Detections**	**Last detected**	**Days at large**
1	18-Mar-2010	U3	Secret spot	726	5:01	1076266	156	1-Apr-2011	379
2	21-Apr-2010	U2	Great reef	694	4:45	1076255	11	14-Sep-2010	146
3	18-Mar-2010	U2	Great reef	673	5:27	1076259	12	16-Jun-2010	90
4	18-Mar-2010	U2	Great reef	685	3:53	1076262	8	16-Jun-2010	90
5	18-Mar-2010	U1	MI-712-A	715	2:52	1076258	40943	1-Apr-2011	379
6	18-Mar-2010	U1	MI-712-A	692	5:08	1076260	23352	1-Apr-2011	379
7	18-Mar-2010	U1	MI-712-A	742	4:30	1076261	4	16-Jun-2010	90
8	21-Apr-2010	P3	MU-759-A	742	4:43	1076253	1	21-Apr-2010	< 1
9	21-Apr-2010	P3	MU-759-A	694	4:15	1076254	5	1-Apr-2011	345
10	21-Apr-2010	P3	MU-759-A	739	3:43	1076257	1	21-Apr-2010	< 1
11	18-Mar-2010	P2	MI-703-A	721	5:08	1076263	259	1-Apr-2011	379
12	18-Mar-2010	P2	MI-703-A	772	4:30	1076264	7340	1-Apr-2011	379
13	18-Mar-2010	P2	MI-703-A	772	4:34	1076265	20	11-Aug-2010	146
14	18-Mar-2010	P1	MI-683-A	710	4:16	1076267	18	2-Sep-2010	168

Mobile Tracking

Five mobile tracking relocation trips to each of the six locations where sow Red Snapper were initially tagged (April, June, August, and September 2010, and April 2011) were made during the following year to the six locations. Additionally, the six sites chosen for this experiment are in close proximity of one another so if movement does exist there is a strong likelihood that individuals will be found at an adjacent site given their affinity for structure. Relocation was attempted using the Vemco© VR28 towable hydrophone and tracking system (Figure 4.2) for trips in June, August, and September 2010. The hydrophone was towed around each site at a speed of 2 – 3 knots until all fish initially tagged at the site had been detected or two hours had elapsed. Searching time was limited to two hours per site to maximize the number of sites visited during each offshore relocation trip due to time constraints. A handheld GPS unit connected to the VR28 tracking system recorded boat GPS coordinates at 30 s intervals. Detections and tag-transmitted sensor data were recorded on a laptop in real-time and stored in a data file. For relocation trips made in April 2010 and April 2011, the VR28 was not available. Instead, two Vemco VR2W acoustic receivers were dropped on a line with an anchor weight and buoy to supplement collection of relocation data we gathered using the VR28 mobile tracking system on other trips. Receivers were placed on the line to record data at 5 and 15 m above the seafloor. Data obtained through VR2W collection included tag sensor information but not GPS coordinates. Data recorded on VR2W acoustic receivers and the VR28 tracking system was downloaded using Vemco VUE© software and exported to ArcGIS (ESRI 2013) and R (R Development Core Team 2013) applications for data analysis.



GPS Data
Lat 431.48,N
Long 347.17,W
PDOP 50
Speed 00.8

V010926.005 0.8k

S/N: 2588 ID: 14 Freq: 69kHz Depth: 199.0

Decoded. Waiting for sync on Freq: 69kHz

Figure 4.2. (a) Vemco VR28 towable hydrophone platform and tracking system, (b) omni-directional hydrophone, (c) tracking system interface screenshot.

Stationary Tracking

To supplement VR28 relocation data and also gain better insight into finer-scale movement patterns and short-term residency habits of sow Red Snapper, I deployed a stationary acoustic array of VR2W receivers at two sites over a continuous two-month period of time. At one platform site (P2) and one underwater site (U1) two VR2W acoustic receivers were placed at 20 m and 30 m depth by scuba to passively record data continuously during the months of August through October. The array at site U1 was deployed on August 6th and retrieved September 16th (40 days). The array at site P2 was deployed on August 11th and retrieved October 8th (57 days). Fish monitored included the three fish tagged at site P2 and three fish tagged at U1 and any additional fish initially tagged at other sites that moved onto these sites containing the stationary acoustic array. After the sampling period had ended, receivers were retrieved by scuba and data downloaded using VUE software and exported for data analysis.

Catch-per-unit-effort

Red Snapper were sampled using hook-and-line at the six sites where fish were tagged to measure differences in abundance and size among different sites. Four equally experienced anglers each fished single hook, bottom hook and line gear for three separate 10-min intervals. Two anglers were randomly assigned small hooks (6/0 Eagle's Claw circle) baited with cut squid (*Loligo sp*.) or cut Spanish Sardine (*Sardinella aurita*). The other two anglers used "sow tackle" that consisted of larger (7/0 Owner circle) hooks and whole sardines or halved Atlantic Mackerel (*Scomber scombrus*) for bait. All anglers sampled directly off the bottom. Three sites were surface oil and gas platforms (P1, P2, P3) – highly visible and well-known sites that are frequently targeted by recreational fishermen. Three other sites were not visible from the surface and consisted of one cut-off oil and gas platform (U1) and two natural bottom sites (U2, U3) that were not well-known within the recreational fishing community. Fish captured were identified, measured for total length (mm), and released. Four trips were made in total in 2011 during the months of April, May, August, and September. Two trips were made before the recreational Red Snapper season opened in federal waters June 1st and two trips were made after the Red Snapper season closed July 18th to assess impacts of fishing pressure. Differences in catch-per-unit-effort (CPUE) and total length were tested using a two-way analysis of variance with Bonferroni correction to account for multiple tests (ANOVA, $\alpha' = \alpha/5 = 0.01$). Multiple regression (Venables & Ripley 2002) and model dredging (Barton 2013) techniques were used to determine the most influential variables in modeling catch and total length for CPUE trials.

RESULTS

Tagging

I used acoustic telemetry to monitor Red Snapper movement and behavior in the western Gulf of Mexico. Sow Red Snapper (*n* = 14) were tagged at six locations with Vemco© V16TP-4x ultrasonic acoustic transmitters equipped with temperature and pressure (i.e., depth) sensors. Mean site depth of the six sites was 41.2 ± 3.4 m (± SD). Ten fish were tagged March 2010 at five of six sites: one fish was tagged at site P1, three fish at site P2, three fish at site U1, two fish at site U2, and one fish at site U3 (Table 4.2). The final four fish were tagged April 2010: one additional fish at site U2, and three fish at site P3. All Red Snapper tagged had been hooked in the side of the mouth, thereby minimizing potential mortality resulting from deep or foul hooking. Total length (TL) of fish tagged was 719.8 ± 31.0 mm (mean ± SD) and ranged from 673 – 772 mm. On deck time during tagging procedures was 4:28 ± 40 s (mean ± SD). All fish were monitored in the holding tank and all showed active and alert responses prior to release. Fish were released at the bottom using a Shelton Fish Descender^{TM}, an inverted barbless hook on a weighted line that attaches to the fish's jaw to rapidly descend the fish to the seafloor. This method has been shown to alleviate the effects of barotrauma and increase survival in discarded fish.

Mobile Tracking

To identify long-term habitat use and site fidelity patterns, five relocation trips using the VR28 mobile tracking hydrophone were made over one year to the six sites where sow Red Snapper were acoustically tagged and released. A handheld GPS unit linked to the VR28 recorded GPS coordinates corresponding to boat position at 30 s intervals, enabling a boat track to be generated using GIS. Registered acoustic detections were overlaid on top of the boat track in GIS to visualize boat position when fish were detected using the VR28 for relocation trips in June, August, and September 2010. During the June 2010 relocation trip, eighteen detections representing two individuals (Fish 11 and 13) were registered at site P2 and nineteen detections representing four individuals (Fish 4, 5, 6, and 7) were registered at site U1 (Figure 4.3). Two fish relocated at site P2 were both initially tagged on that same site in March 2010. The one remaining fish also tagged on this site was not detected during this trip. On site U1, all three fish initially tagged there in March 2010 were relocated on that same site. One additional fish, initially tagged at site U2, had moved and was successfully relocated at site U1. Tracking distance varied considerably: the distance to the site from the boat when acoustic detections occurred using the VR28 was 81 ± 69 m (mean ± SD) and ranged from 17 – 443 m (*n* = 203).

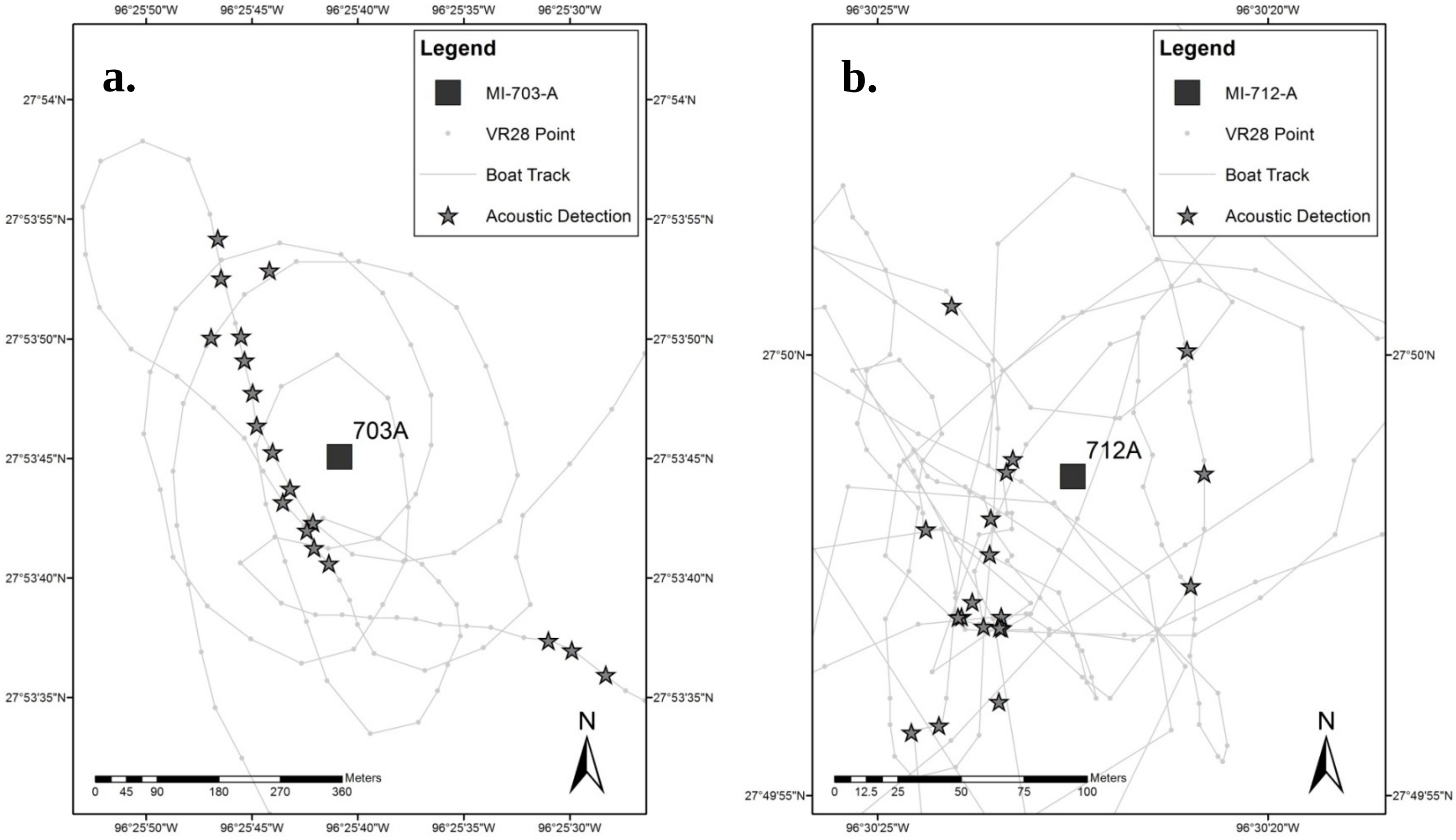


Figure 4.3. Boat track and registered acoustic detections from VR28 towable hydrophone at: (a) site P2 (MI-703-A) and (b) site U1 (MI-712-A), from June relocation trip. VR28 points represent boat GPS position at 30 s intervals and connecting lines illustrate boat path. Stars show acoustic detections of tagged Red Snapper. Note differences in scale between two panels.

Over all five trips, tagged Red Snapper were successfully relocated 33 times out of a possible 60 (55%) relocation events (Figure 4.4). In April 2010, all six sites were visited and 9 of 10 (90%) tagged Red Snapper were successfully relocated (four additional fish were tagged on this trip). All relocated fish were found on the site where they were initially tagged (i.e., no site-to-site movement). In June, all six sites were visited and 9 of 14 (64%) fish were relocated. One fish moved sites: fish 4 moved 3.3 km from its initial tag site U2 to site U1. In August, only 4 of 6 sites were visited, as the focal point of this trip was to deploy the stationary VR2W acoustic array on sites P2 and U1. I chose to deploy the stationary arrays, after determining how site-attached the fish were to the original tagging location. This stationary array also allowed me to assess fine-scale habitat use patterns. Relocation efforts were made for these two sites and two nearby sites (P1 and U3), with 2 of 8 (25%) fish successfully relocated. Time constraints prevented visiting sites P3 and U2, where six additional fish were tagged between the two sites. One fish was relocated at site P2 and the other at site U1, with both fish exhibiting no movement from their initial respective tagging site. In September, all six sites were visited and 7 of 14 (50%) fish were relocated. No site-to-site movement in relocated fish was observed. All three fish tagged on site P2 were relocated there, 2 of 3 fish were relocated on site U1, and one fish each was relocated on sites U2 (of three) and U3 (of one). In April 2011, over one year after initial tagging began, all 6 of 6 sites were visited and 6 of 14 (43%) fish were relocated. These fish had spent up to 379 days at large since they were initially tagged and released. One of six relocated fish (fish 12) was detected at a site P2 that is 2.7 km from the initial tagging site P1. The 5 of 6 (83%) other fish were found at their initial respective tagging sites. Over all mobile tracking efforts, 5 of 14 (36%) fish exhibited site-to-site movement and were relocated at a different site from where they were initially tagged and had traveled 8.51 ± 5.12 km (mean ± SD) and ranged from a minimum distance traveled of 2.74 km to a maximum of 13.14 km.

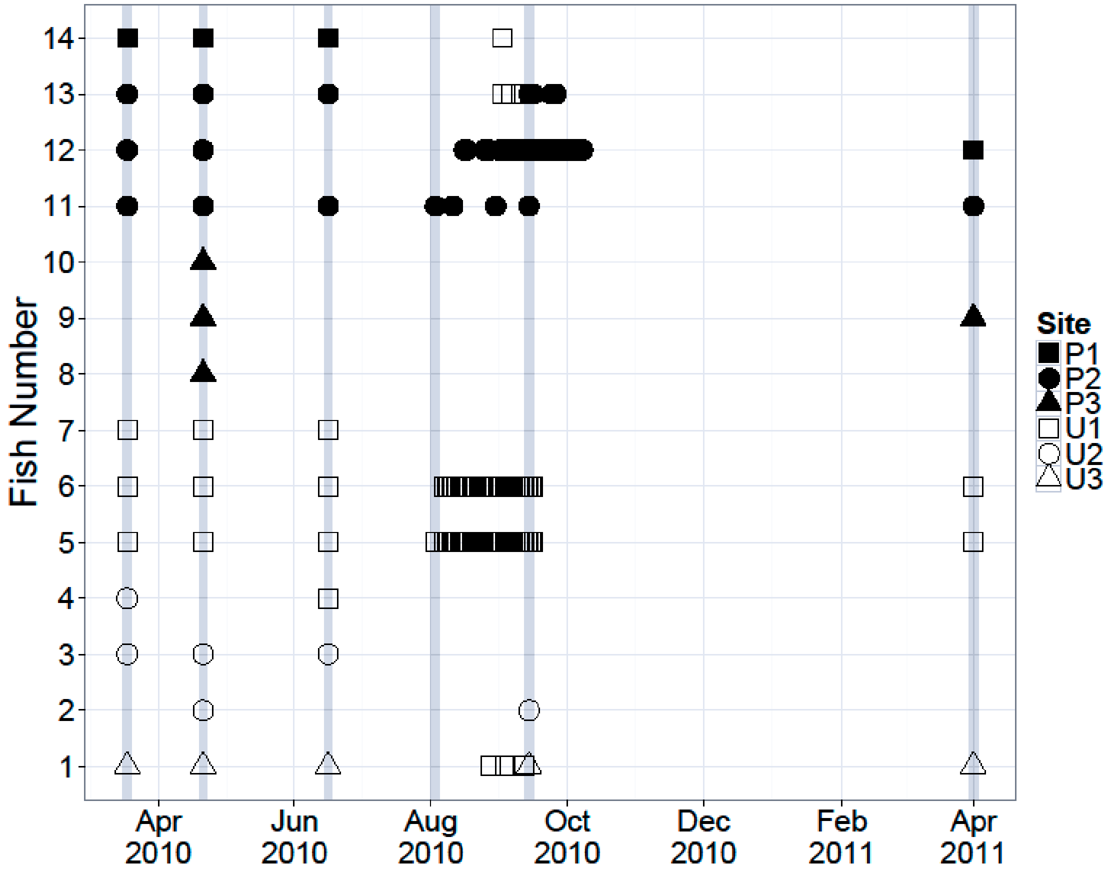


Figure 4.4. Daily acoustic detections of tagged sow Red Snapper. The y-axis shows the unique identification number that represents each tagged fish. The x-axis shows the dates from when fish were first tagged (March 2010) through the final relocation trip (April 2011). Four fish (2, 8, 9, and 10) were tagged in April and all others were tagged in March. Vertical gray bars represent dates when relocation trips with the VR28 towable hydrophone were made. Continuous coverage from August to October was provided by stationary VR2W acoustic receivers. Symbols represent one of six tagging sites, with filled shapes reflecting platform sites, and open shapes reflecting underwater sites. A change in symbol along a row indicates site-to-site movement of that particular fish.

Stationary Tracking

To examine short-term residency, behavior, and habitat use patterns of sow Red Snapper, acoustically tagged fish were tracked using a stationary VR2W acoustic receiver array that was deployed in August to October on two sites: P2 and U1. Two VR2W acoustic receivers were deployed at each site at far opposite ends of the structure to passively record acoustic detections of tagged fish. Stationary tracking between the two sites detected 7 of 14 (50%) tagged fish (Figure 4.5). Two of three fish tagged at site U1 (Fish 5 and 6) were detected and registered a combined total of 64,295 detections during deployment of the array on site from August 6th – September 16th (40 days). Fish 5 registered 40,943 detections over 40 days (Figure 4.6). This fish remained within the array continuously, registering one hundred or more detections each day hydrophones were deployed. The point at which detections cease corresponded with the date the VR2W hydrophones were retrieved by scuba divers on September 16th. Fish 6 registered 23,352 detections over 37 days and continuously remained on site U1 for all but one period of three consecutive days (Figure 4.7). All three fish tagged at site P2 were detected while the stationary array was deployed on site from August 11th – October 8th (57 days). Fish 12 registered 7,340 detections over 36 days and showed nine immigration events into the array that varied in duration from 1 – 7 days (Figure 4.8). Fish 11 registered 259 detections over 4 days but did not remain on site for longer than a 24 hour period before emigrating from the array. Fish 2 registered 17 detections over 7 days and, interestingly, spent three of those days on site U1 before moving to site P2, where it was detected on four different, nonconsecutive days.

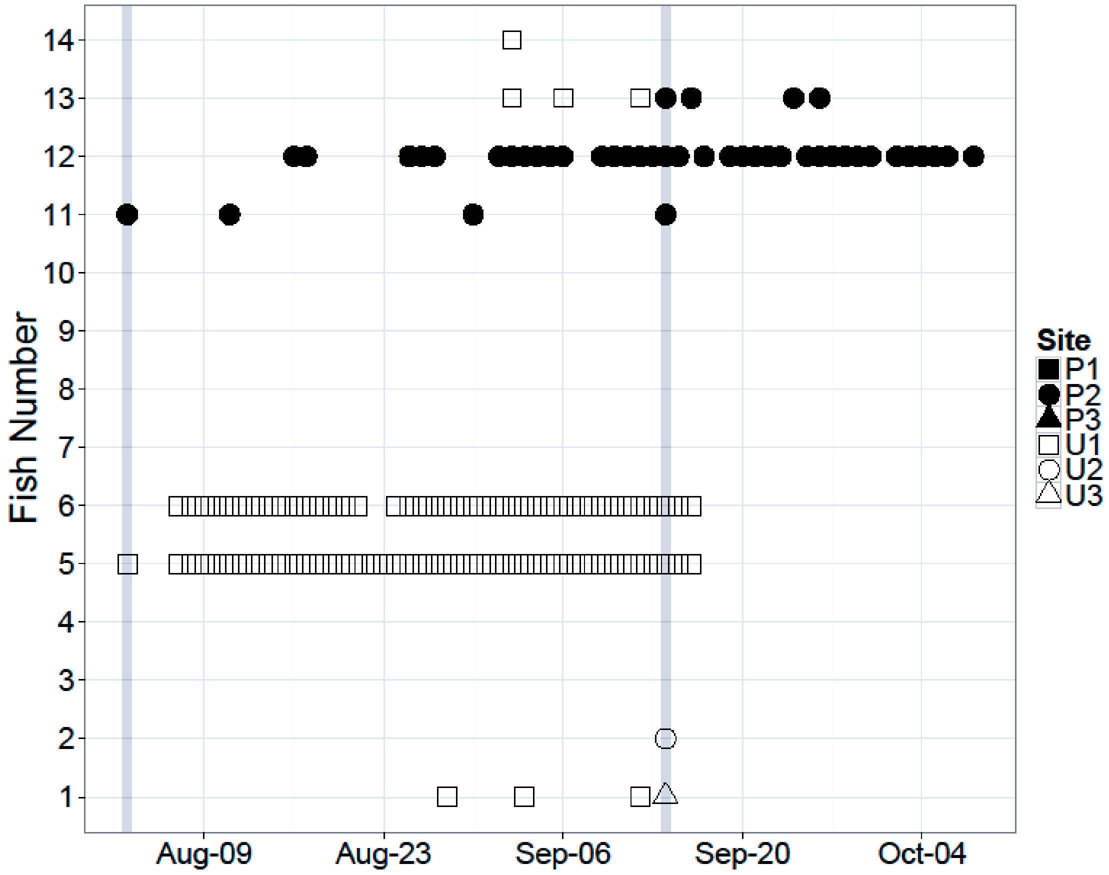


Figure 4.5. Daily acoustic detections of tagged sow Red Snapper zoomed-in during stationary acoustic array deployment. The y-axis shows the unique identification number that represents each tagged fish. The x-axis shows the dates when the stationary VR2W acoustic array was deployed on sites P2 and U1 and maintained continuous acoustic coverage on these two sites. Vertical gray bars represent dates when relocation trips with the VR28 towable hydrophone were made. Symbols represent one of six tagging sites, with filled shapes reflecting platform sites, and open shapes reflecting underwater sites. A change in symbol along a row indicates site-to-site movement of that particular fish.

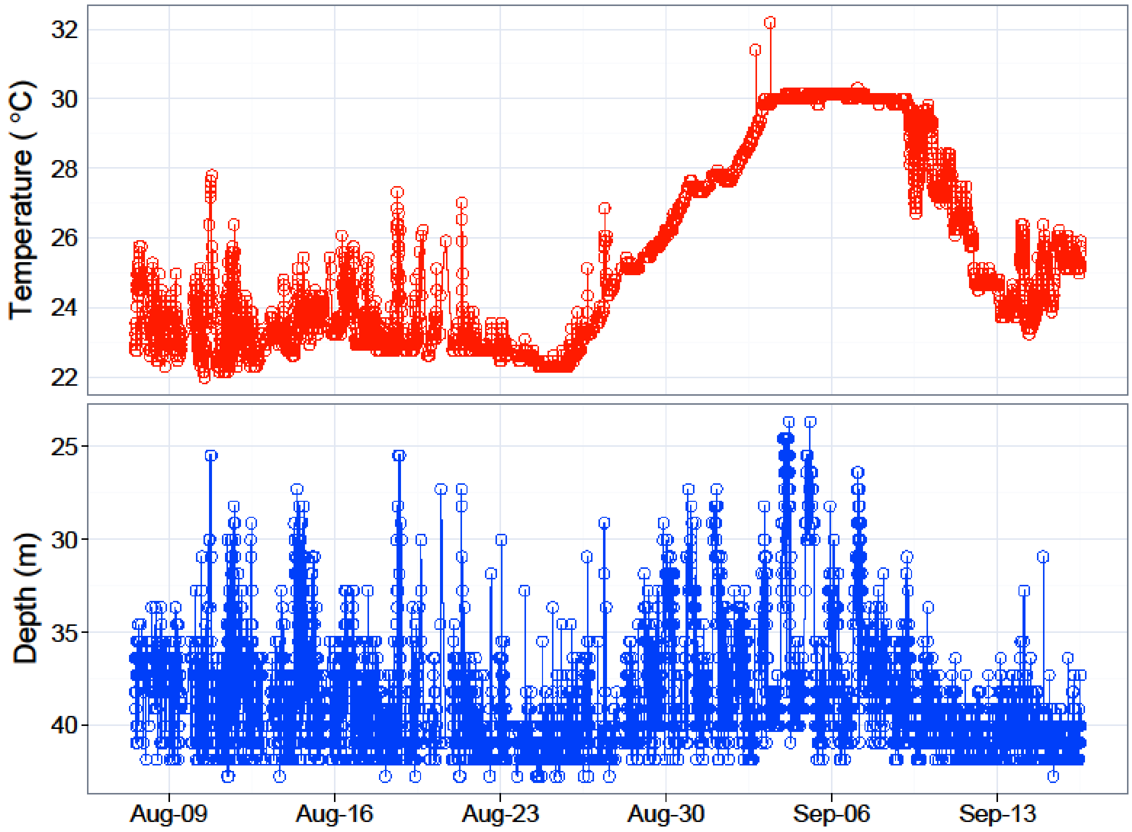


Figure 4.6. Fish 5 acoustic telemetry profiles from acceleration and depth sensor data detected using the stationary VR2W array deployed from August 6 to September 16 on site U1. Open points represent acoustic detection events and are connected by straight lines.

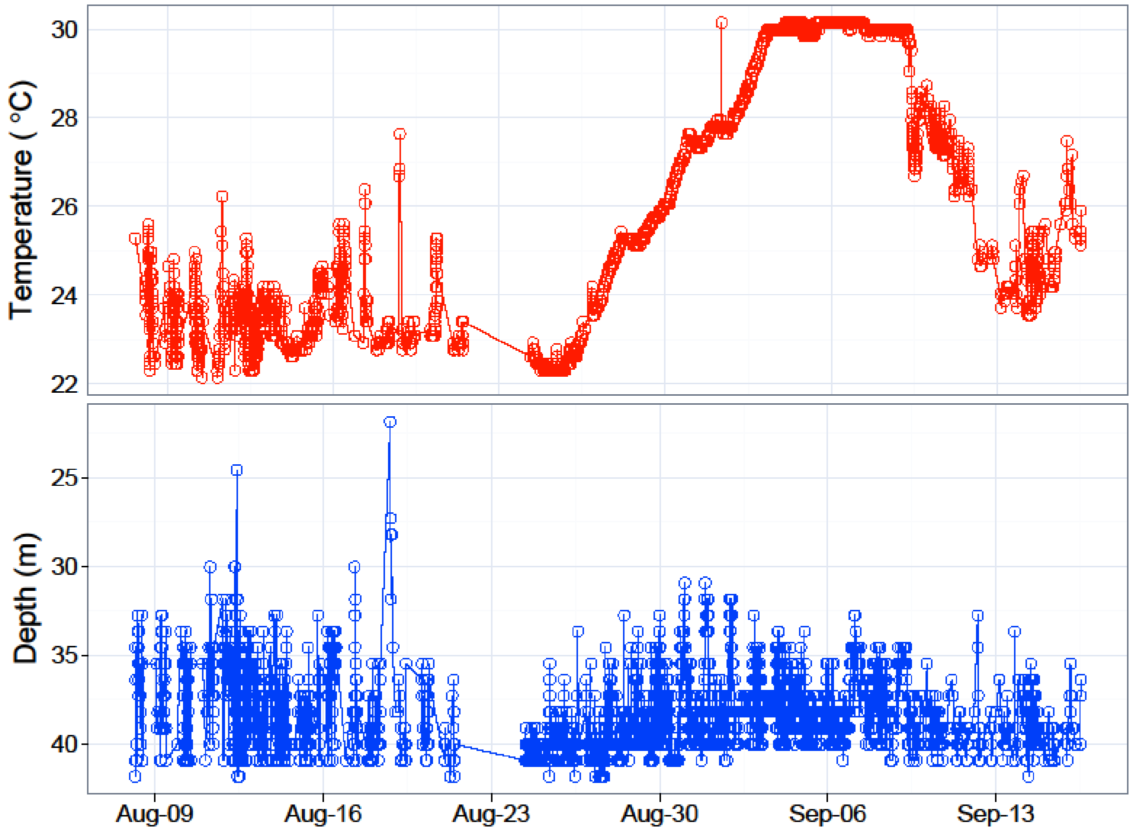


Figure 4.7. Fish 6 acoustic telemetry profiles from acceleration and depth sensor data detected using the stationary VR2W array deployed from August 6 to September 16 on site U1. Open points represent acoustic detection events and are connected by straight lines.

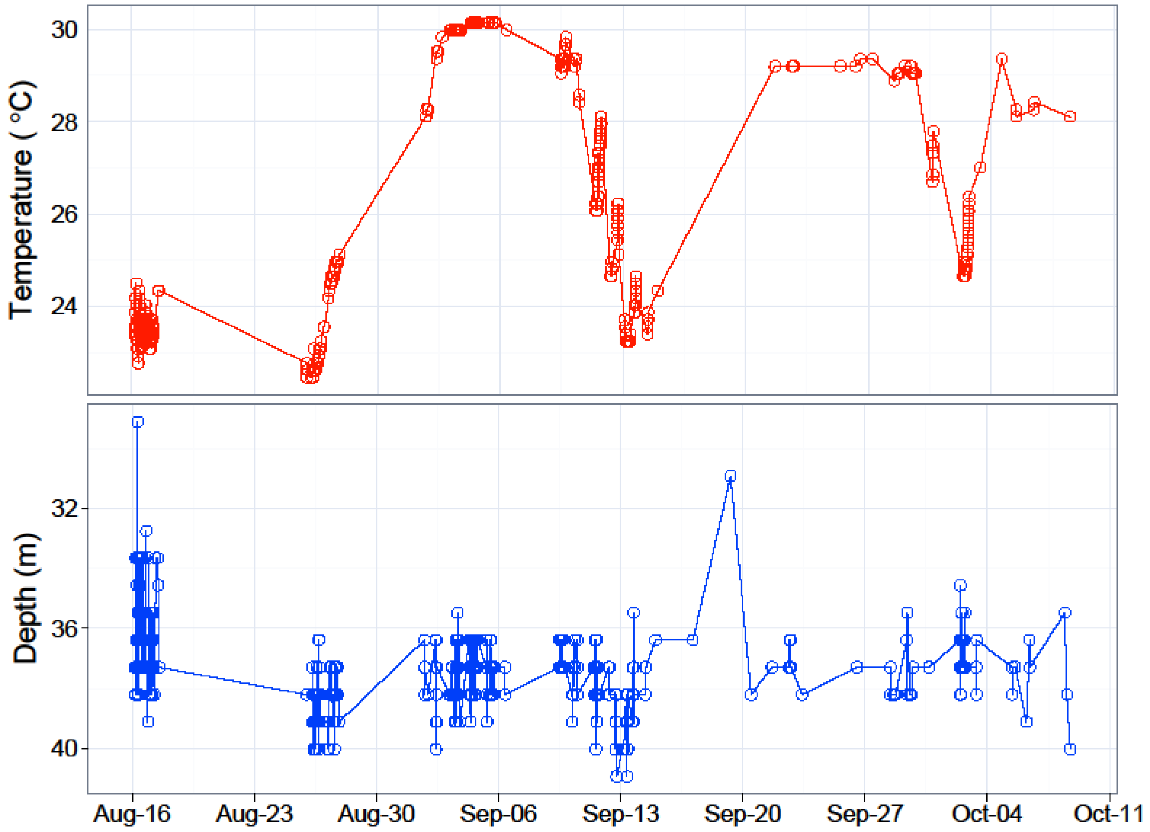


Figure 4.8. Fish 12 acoustic telemetry profiles from acceleration and depth sensor data detected using the stationary VR2W array deployed from August 11 to October 8 on site P2. Open points represent acoustic detection events and are connected by straight lines.

Temperature and depth sensors built into the acoustic transmitters attached to fish recorded sensor data for three individuals: fish 5, 6, and 12. All three fish tended to reside within 10 m of the seafloor for the majority of time (Figure 4.9). Mean depth for fish 5 was 39.2 ± 2.7 m (mean ± SD) and ranged from 23.7 – 42.8 m. Temperature ranged from 22.0 – 32.1°C with a mean of 25.2 ± 2.6°C (mean ± SD). Mean depth for fish 6 was 38.7 ± 1.8 m (mean ± SD) and ranged from 21.8 – 41.8 m. Temperature ranged from 22.1 – 30.2°C with a mean of 26.3 ± 2.7°C (mean ± SD). Mean depth for fish 12 was 37.4 ± 1.2 m (mean ± SD) and ranged from 29.1 – 40.9 m. Temperature ranged from 22.5 – 30.2°C with a mean of 26.3 ± 2.9°C (mean ± SD). In all three fish, temperature drastically increased on August 26th from 23°C to 30°C where it sustained for approximately one week before decreasing back to 24°C. During this period, there was no drastic increase in the depth profiles of fish.

To determine if sow fish had diel patterns, I compared the number of detections received during the day (7:00 – 19:00) and night (19:00 – 7:00) while the stationary arrays were deployed. An increased number of detections were received during the day when compared with night (Figure 4.10), suggesting that fish resided closer or within the structure during the daytime and moved off structure at night. Though the overall number of detections was different among the three fish, this diel pattern was evident in all fish monitored using the stationary tracking array.

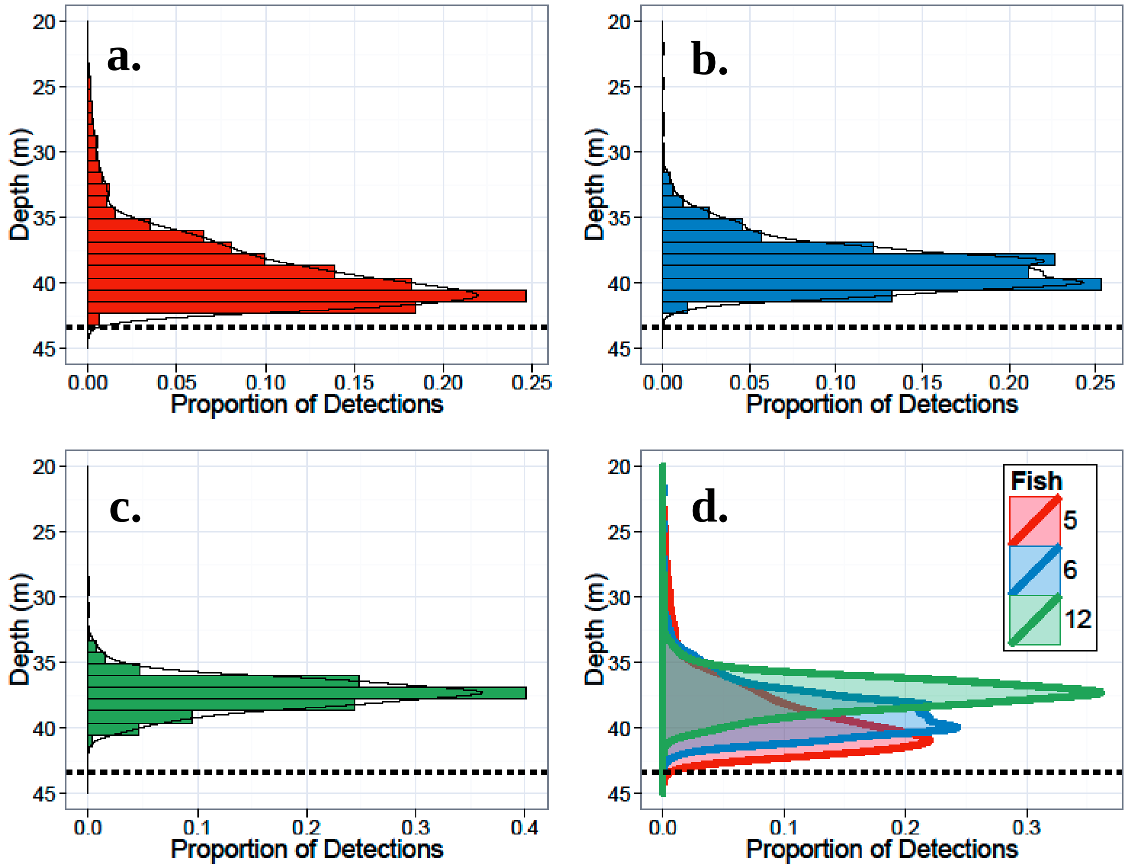


Figure 4.9. Histogram of proportion of detections by depth derived from sensor data for sow fish: (a) fish 5, (b) fish 6, and (c) fish 12, binned in 0.9 m increments (equivalent to depth sensor precision). Dashed line represents the seafloor depth at the site. (d) Density curves of all three fish fitted together in one panel for comparison.

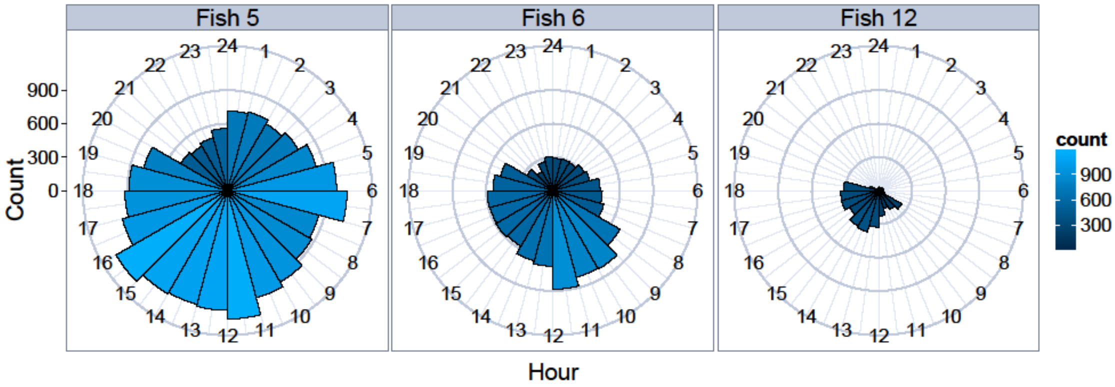


Figure 4.10. Clock plot histogram showing the count of detections received per hour for sow fish 5, 6, and 12 detected during deployment of the stationary receiver array.

Catch-per-unit-effort and size differences

Four fishing trips were made to compare catch-per-unit-effort (CPUE) and total length (mm) of Red Snapper among the six sites to determine if sow Red Snapper were using different habitats than smaller adult Red Snapper. Two trips occurred before the start of the recreational Red Snapper season that opened June 1 and two trips followed the closing of the season July 18 in 2011. This allowed me to assess the impact of fishing pressure on CPUE and size. Catch-per-unit-effort was calculated as the catch per site, per sampling trip, divided by hook size (two), divided by the number of time intervals (three). Catch-per-unit-effort of Red Snapper was significantly higher before the recreational fishing season than after (Figure 4.11a; Student's t = 3.647, df = 109.125, $p < 0.001$, $n = 365$). Before the season opened, CPUE was 3.139 ± 0.295 (mean ± SE) and after the season closed, CPUE was 1.917 ± 0.159 (mean ± SE). The total length of Red Snapper was also significantly longer before the season then after (Figure 4.11b; Student's t = 5.459, df = 211.489, $p < 0.001$, $n = 348$). Before the season, TL of Red Snapper was 546.8 ± 6.2 (mean ± SE) and after the season ended, TL was 488.0 ± 8.5 (mean ± SE). These data show both size and abundance of Red Snapper could be reduced through targeted, localized fishing.

Multiple regression and model dredging techniques revealed five additional variables as influential in the model: site, visibility (whether the structure was visible from the surface or underwater), structure type (artificial or natural), habitat size (large or small), and bait size (large or small). Two-way ANOVAs ($\alpha = 0.05$) were performed to determine the significance of several variables on CPUE (Figure 4.12; Table 4.3). Each influential variable was run as a fixed factor with season as the second fixed factor along with the interaction. Against all variables in each two-way ANOVA, season was significant ($p < 0.001$): catch-per-unit-effort was higher before the recreational fishing season began than after it closed. Site was significant ($p < 0.001$) as was the *site x season* interaction ($p < 0.001$), likely caused by sites P1 and P2, where CPUE was actually higher after the season than before. Visibility was significant ($p < 0.01$) with the *visibility x season* interaction significant ($p < 0.05$): non-visible sites yielded higher CPUE than visible sites. Structure type was not significant ($p = 0.561$) revealing that there was no difference in CPUE between artificial and natural habitat types. Habitat size was not significant ($p = 0.455$) showing that there was no difference in CPUE between large and small size habitats. Lastly, bait size was not significant ($p = 0.187$) demonstrating that there was no difference in CPUE between using large baits on larger hooks versus small baits on smaller hooks.

The same two-way ANOVA model that was used for CPUE was also applied for TL (Figure 4.13; Table 4.3) using the same five variables (site, visibility, structure type, habitat size, and bait size) as fixed factors and season as the second fixed factor along with the interaction. Similarly, season was a significant factor in all two-way ANOVAs with each variable ($p < 0.001$): Red Snapper TL was significantly larger before the fishing season than after. No interactions between season and any of the five variables were significant (Table 4.3). Main effects of three of the five variables tested showed significant differences. Site was highly significant ($p < 0.001$) indicating that fish TL differs between sites. Habitat size was significant ($p < 0.001$) with smaller habitat sizes showing larger mean TL than large habitat sizes. Lastly, bait size was significant ($p < 0.01$) with larger baits catching larger fish than smaller baits. Visibility was not significant ($p = 0.064$) but exhibited a trend that visible sites yielded slightly larger fish than not visible (i.e., underwater) sites. Structure type was also not significant ($p = 0.080$) indicating that fish of similar TL inhabit artificial and natural habitats equally.

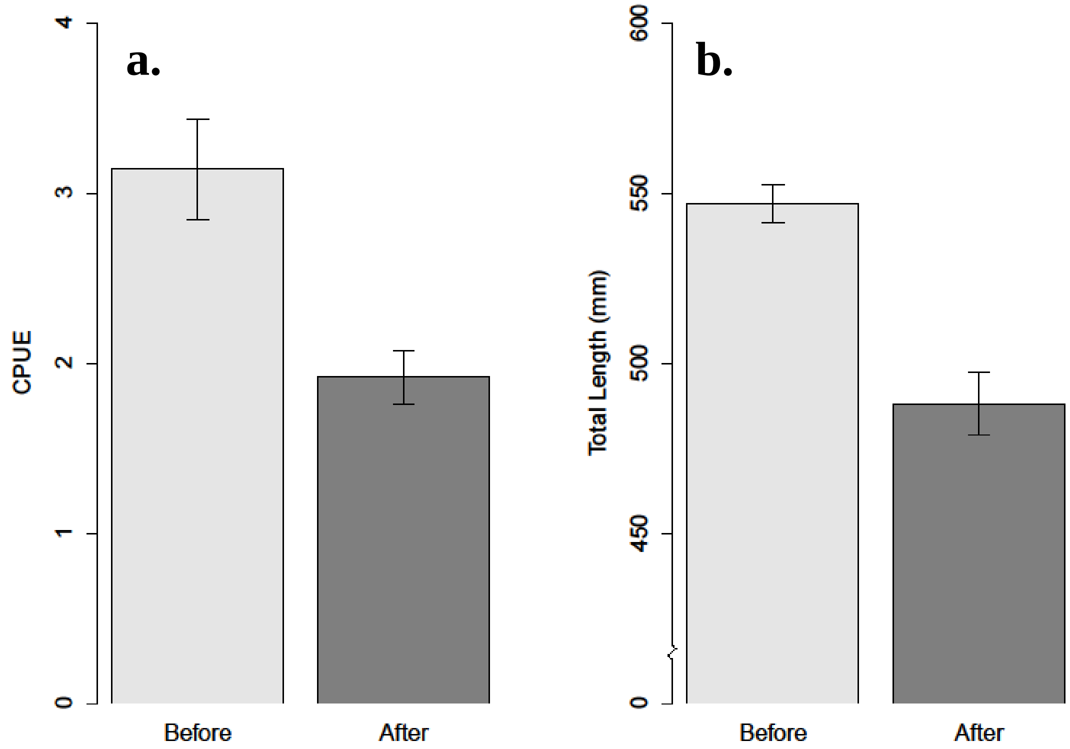


Figure 4.11. (a) Mean (± SE) catch-per-unit-effort (CPUE) and (b) total length (mm) of Red Snapper caught before and after the recreational Red Snapper season (*n* = 365). Catch-per-unit-effort was calculated as the catch per site, per sampling trip, divided by hook size (two), divided by the number of time intervals (three).

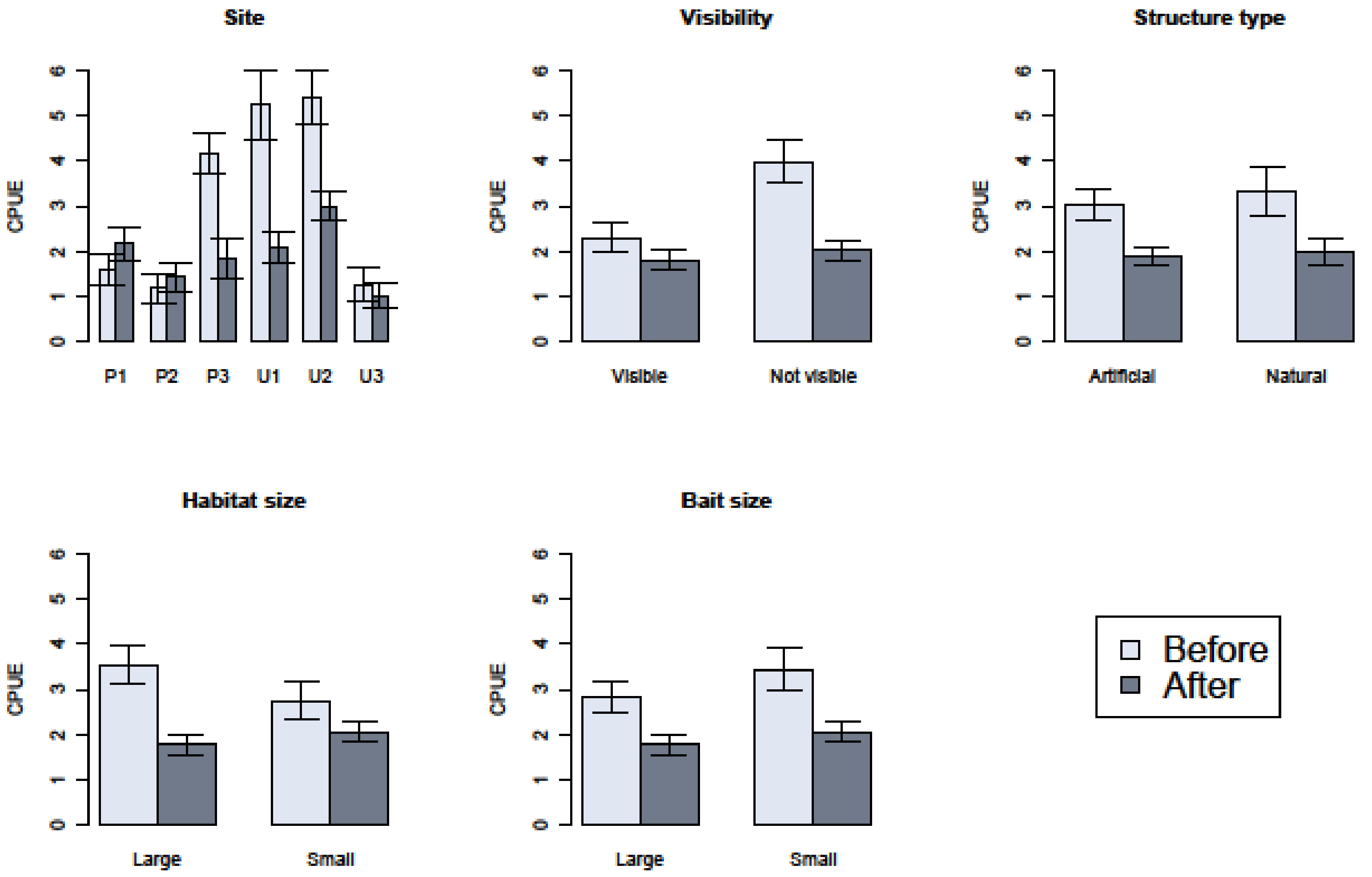


Figure 4.12. Mean (± SE) catch-per-unit-effort (CPUE) of Red Snapper caught before and after the recreational Red Snapper season across site variables. Catch-per-unit-effort was calculated as the catch per site, per sampling trip, divided by hook size (two), divided by the number of time intervals (three). Significant differences were tested using a two-way ANOVA with site variable and season as fixed factors along with the interaction (see Table 4.3 for significance).

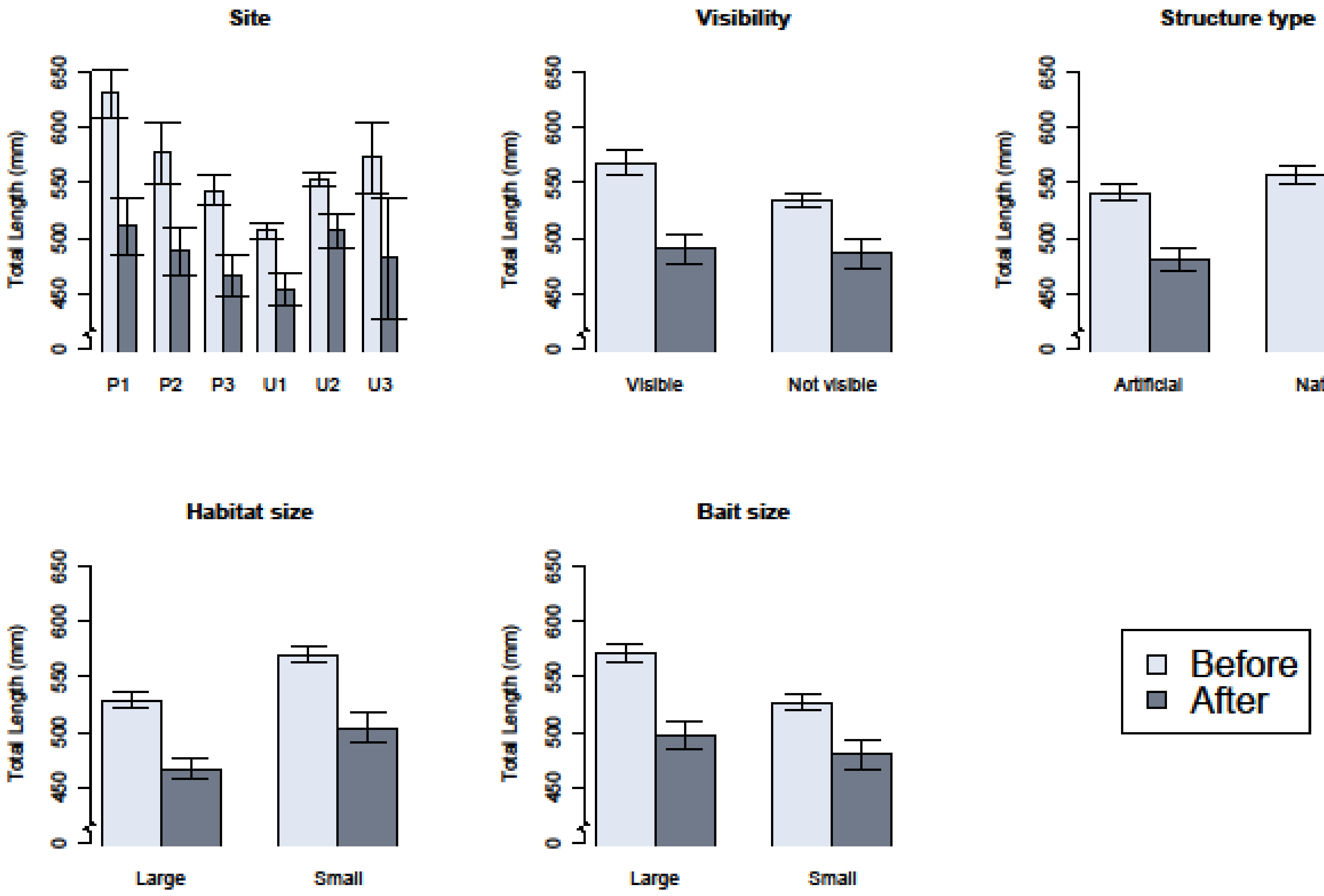


Figure 4.13. Mean (± SE) total length (mm) of Red Snapper caught before and after the recreational Red Snapper season across site variables. Significant differences were tested using a two-way ANOVA with site variable and season as fixed factors along with the interaction (see Table 4.3 for significance).

Table 4.3. Two-way ANOVA table of variables tested for catch-per-unit-effort (CPUE) and total length (mm) from four sampling trips. Season variable divided into two sampling trips before the recreational Red Snapper fishery open season.

	Catch-per-unit-effort (CPUE)					**Total Length (mm)**				
Variable	*Sum Sq*	*df*	*F*	*p*		*Sum Sq*	*df*	*F*	*p*	
Site	198.39	5	17.526	< 0.001	***	231317	5	6.148	< 0.001	***
Season	53.78	1	23.755	< 0.001	***	385708	1	51.253	< 0.001	***
Site x Season	76.89	5	6.793	< 0.001	***	47683	5	1.267	0.278	
Residuals	298.83	132				2528591	336			
Visibility	32.11	1	8.592	< 0.01	**	27925	1	3.453	0.064	
Season	53.78	1	14.390	< 0.001	***	302876	1	37.456	< 0.001	***
Visibility x Season	18.78	1	5.024	< 0.05	*	15618	1	1.932	0.166	
Residuals	523.22	140				2781652	344			
Structure type	1.39	1	0.340	0.561		25157	1	3.074	0.080	
Season	50	1	12.227	< 0.001	***	254777	1	31.132	< 0.001	***
Structure type x Season	0.22	1	0.054	0.816		577	1	0.070	0.791	
Residuals	572.5	140				2815224	344			
Habitat size	2.25	1	0.561	0.455		120676	1	15.357	< 0.001	***
Season	53.78	1	13.401	< 0.001	***	318625	1	40.547	< 0.001	***
Habitat size x Season	10.03	1	2.499	0.116		423	1	0.054	0.817	
Residuals	561.83	140				2703212	344			
Bait size	7.11	1	1.759	0.187		73103	1	9.238	< 0.01	**
Season	53.78	1	13.302	< 0.001	***	290618	1	36.726	< 0.001	***
Bait size x Season	1	1	0.247	0.620		15461	1	1.954	0.163	
Residuals	566	140				2722154	344			

DISCUSSION

Using acoustic telemetry and catch-per-unit-effort data, I found that sow Red Snapper have similar site fidelity and residency patterns as smaller Red Snapper in the western Gulf of Mexico. I also documented that large-scale movement and small-scale habitat use patterns of sow snapper were also not substantially different than small snapper. Acoustic returns of sow snapper tagged and tracked using mobile acoustic telemetry had 79% recovery at initial tag sites after three months and 36% after one year. This is similar to observed patterns of small adult Red Snapper, which have high site fidelity on the order of 1 – 2 years before emigrating from the site over longer time periods (SEDAR 2012). Stationary acoustic telemetry showed sow snapper tagged on one platform had similar long-term habitat use patterns as small Red Snapper, residing at depths near the seafloor and within close proximity to structure. There was a strong recreational fishing season effect in catch-per-unit-effort data. Based on these results, sow Red Snapper in the western GOM have high site fidelity, use similar habitats, and have similar movement patterns as small adult snapper. The site fidelity characteristics of sow Red Snapper and use of small and typically unknown habitat features support our hypotheses that a portion of the spawning stock of sow Red Snapper may have been overlooked and that the high recruitment observed in the stock may be originating from these non-targeted sources.

Previous speculation regarding sow snapper habitat use patterns were that they persisted higher in the water column and off-structure compared to their smaller snapper counterparts. Red Snapper are known to have high site fidelity (Patterson & Cowan 2003, Szedlmayer & Schroepfer 2005, Diamond et al. 2007, Strelcheck et al. 2007, Westmeyer et al. 2007, Topping & Szedlmayer 2011a) but specifics regarding sow habitat use patterns have been minimal. Small Red Snapper seek refuge within structured environments to avoid predation while sow snapper, which have effectively outgrown this predation window, are capable of moving freely and using all depths of the water column. However, sows also preferred depths closer to the bottom and proximities nearer to structure similar to smaller Red Snapper. The majority of detections from depth sensors attached to sow Red Snapper were received from depth less than 10 m off the seafloor. Tagged fish spent more days on site than away from it and did not move far off the structure. These sow Red Snapper appear to have high site fidelity and residency times.

Red Snapper registered significantly more detections during daylight hours than night hours, which supports the existence of diel movement patterns, whereby fish seek refuge within or nearby the structure during the day and venture off site during night hours presumably to forage. This pattern is well documented for Red Snapper (Ouzts & Szedlmayer 2003, McCawley et al. 2006, Peabody & Wilson 2006, Topping & Szedlmayer 2011a), and results in this study corroborate these findings. More recently, however, researchers found that the detection efficiency of acoustic receivers is highly dependent on environmental conditions (How & de Lestang 2012, Mathies et al. 2013) and can also be highly variable depending on time of day (Payne et al. 2010). To account for this variability in detection efficiency across different environmental landscapes, researchers should deploy reference tags at research sites to account for detection variability unrelated to the actual fish movement (Kessel et al. 2013). I did not use control/sentinel tags to monitor the variability in detection efficiency, so it is not possible to conclude that the differences in the number of night and day detections I witnessed represents true diel movement of tagged sow snappers or potentially an artifact of detection variability.

During the period of stationary array deployment on sites P2 and U1, a drastic temperature increase was recorded in the temperature sensors attached to fish 5, 6, and 12 for approximately one week beginning August 26. This pattern was documented in all three fish that were tagged at two different sites, which suggests that the temperature change was an artifact of uniform changes in water temperature during this time and not a product of individual fish movements. The depth sensors attached to the fish did not show any exceptional vertical movements towards the surface where temperatures are typically much warmer during summer months due to the formation of the summer thermocline. Instead, fish remained at similar depths throughout this time period as they had previous to this temperature increase.

Initial methodology for tracking Red Snapper with the VR28 mobile hydrophone included performing search patterns around the area where fish were tagged if they were not detected immediately on site. This technique proved to be of limited success. First, the search pattern methodology is very time-intensive. Each search pattern requires a full day and would have resulted in sacrificing visiting other tagging sites to relocate other tagged fish. My solution was therefore to spend up to two hours maximum searching at one site for tagged fish before moving on to the next site. In this way, I could maximize our charter time and visit all study sites during one relocation trip. Additional complications that are characteristic of mobile hydrophones became prevalent during later relocation trips. The development of a thermocline and nepheloid layer during the summer months restricted the detection ability using the VR28 mobile hydrophone. The VR28 could be towed at a maximum depth of 15 m, which was still above the thermocline and nepheloid layer. The inability to penetrate through these layers seemed to interfere with successful detection of the acoustic transmitters on the fish. Westmeyer et al. (2007) witnessed a near complete truncation of detections coinciding with the existence of a thermocline below receiver depth. It is possible that we experienced a similar effect during our warmer water trials that reduced the number of detections substantially. To get below the thermocline, we had to supplement the VR28 mobile system with stationary VR2W acoustic receivers. Finally, the strong site-attachment of these fish was largely unanticipated. Thus, the fixed-array passive method proved to be more successful in capturing fish detections than the VR28, which led us to focus on this method over the mobile VR28 for the majority of relocation trips.

Fishing effort clearly influences size and abundance of localized Red Snapper populations. Catch-per-unit-effort trials were most influenced by whether sampling was conducted pre- or post-season. In all two-way comparisons for both catch and total length, the season variable was significant: CPUE and mean total length were both significantly higher before the recreational fishing season opened than after it closed. This result illustrates that above all else, acute concentrated fishing effort can drastically reduce abundance on a site-specific level. Additionally, mean total length is reduced as recreational anglers discard smaller fish in order to catch and retain the largest fish available. This effect results in an overall reduction in mean total length over time.

Sites not visible from the surface, including an artificial reef “cut-off” platform and two natural reef habitats, had significantly increased catch of fish than visible standing platform sites, but there was no difference in total length when compared to visible sites. A clear seasonal effect was seen in catch at non-visible sites, which were severely depleted as a result of the open recreational fishing season. The same effect was not present in visible sites, however. The division of fishery sectors may be the potential cause driving this effect. Commercial fishermen may be preferentially targeting visible standing platform sites over non-visible sites throughout the recreational off-season (approximately 90-95% of the year) where it is more efficient to fish or the commercial target size is more abundant. Commercial fishermen receive a higher price per pound for 16-inch, “dinner plate” size fish than they do for fish either smaller or larger than this optimal size. Thus, it is more economically beneficial for them to target this size class. Though I witnessed similar size fish between our artificial and natural sites, natural habitats typically hold larger fish than artificial ones and the age structure is more skewed towards age 2-3 fish around oil and gas platforms (Wilson & Nieland 2001, Gitschlag et al. 2003, Gallaway et al. 2009). This may be why commercial fishermen tend to focus on visible platform sites. Constant year round fishing pressure from the commercial fishery on these sites keeps catches relatively low compared with not visible sites. Conversely, in not visible sites, fishing pressure is reduced during the recreational off-season, resulting in increases in abundance. With the beginning of the recreational fishing season, recreational anglers targeting larger snappers tend to focus fishing effort on these not visible sites. While these sites may not be visible from the surface they still may be well-known by experienced charter captains. The overwhelming increase in recreational fishing effort on these not visible sites during the open season results in a rapid depletion in abundance. This explains why a large reduction in abundance occurs after the open recreational season on not visible, underwater sites compared to visible platform sites.

Neither catch nor total length significantly differed between artificial and natural structure types. Several researchers have reported smaller adult Red Snapper tend to aggregate around artificial habitats and larger fish around natural habitats, but I did not see any partitioning of size between the different habitat types in my study. Recreational fishing pressure during the open season uniformly depleted abundance and reduced mean total length similarly between these habitats. This result also has key management implications. If artificial habitats are experiencing similar abundances and exploitation rates as natural habitats, then there undoubtedly is value in retaining these artificial platforms that currently exist or constructing and deploying new structure to supplement existing habitat for recruitment of Red Snapper. Thus, artificial structures represent a viable fishery management tool to maintaining or increasing spawning stock biomass and may represent one source of the increased recruitment delivered to the Red Snapper fishery.

While I did not see any differences between artificial and natural habitat types regarding catch or total length, the habitat size revealed differences in fish size: smaller habitats showed increased mean total lengths than larger habitats; larger fish were seen at smaller structures. One explanation for this pattern may be larger sows are outcompeting smaller fish on small sites for resources. This effect is not seen on larger sites where there is more available space to allow resource partitioning even in the presence of competition from large sow snapper. Depth sensor data show that this partitioning of the structure is independent of vertical relief and occurs on a two-dimensional scale, with fish not using available vertical structure independent of size, and both size classes tending to reside nearer to the seafloor. Thus, smaller fish will tend to occur in higher abundance on large sites, where there is enough space available for them to persist even in the presence of larger sow Red Snapper.

Data from catch-per-unit-effort trials revealed that larger baits and hooks resulted in catching larger fish. This effect is quite intuitive and is well-recognized among researchers (Cooke et al. 2005, Gregalis et al. 2012, Patterson et al. 2012) and anglers in the recreational Red Snapper fishery. When targeting sow fish, it is well known by anglers (and the basis of how we developed our gear), to use a specialized “sow rig” that contains larger, often whole, baits to maximize the possibility of landing the largest fish possible. While this strategy typically limits the number of smaller fish landed on large hooks, large fish themselves were not deterred by small hooks with small baits in our study. Several sow snapper were caught each trip on small hooks baited with cut fish or squid. However, this gear modification might help in targeting sow snapper and eliminating the substantial number of discarded smaller fish (Gregalis et al. 2012, Patterson et al. 2012). The fate of these discarded fish, especially when afflicted with severe symptoms of barotrauma from fishing in deep waters, remains highly ambiguous and the effects of delayed mortality may further restrict the future growth of the spawning stock.

Two important management implications came out of this study. First, I found that Red Snapper have remarkably high site fidelity, with some fish remaining on the initial tagging habitat for the duration of the project. Some fish moved short distances and this movement increased in small increments with time. Nonetheless, if large snapper that have been relatively removed from key predation windows and are relatively site specific, then these fish could be contributing to the spawning stock. Moreover, there are numerous areas of low relief throughout the Gulf that are uncharted, and these areas harbor populations of these fish. Because these fish are site specific, an “indexed” survey that is employed has the potential to miss these fish in the abundance survey process. Ironically, fishery-independent surveys are conducted on sites specifically away from Red Snapper habitat; however, it is assumed Red Snapper have an equal probability of encountering this gear. This may not be the case. Because these fish are not randomly distributed, their encounter rate would be artificially low.

Second, I found that certain areas could be easily depleted of Red Snapper by fishing activity, particularly well-known areas, even in shortened fishing seasons. Certainly, this would reduce the abundance of the larger sow fish and may lead to erroneous conclusions if indeed they do exist at higher abundances and are site-attached to other areas. For example, assessments at these structures would likely show the abundance of large fish would be underestimated for two reasons: (1) localized depletion and (2) missing fishes in surveys because many are on less-sampled areas that likely stay in these habitats due to their site-specific nature. I also found no differences in size or depletion rates over natural vs artificial habitat types. These data have clear implications that artificial reefs can supplement or at least produce similar catch rates of Red Snapper as natural structures. Thus, these structures represent a viable tool for maintaining or increasing spawning stock biomass for the Red Snapper fishery.

Based on acoustic tracking results, sow Red Snapper appear to be using the same habitats, showing similar depth profiles in the water column, and having comparable site fidelity and residency patterns as smaller Red Snapper. They are not residing nearby but off-structure, where they have escaped fishing efforts targeted by the directed fishery as I hypothesized. Acute and intense fishing pressure is extremely capable of depleting the stock on a site-specific level as well as reducing the total length of fish caught over the course of the open recreational fishery season as determined by catch-per-unit-effort analyses. The combination of stock and size reductions would project to reduce overall spawning stock biomass and thus future recruitment. However, as reported by fishery independent surveys, this reduction is not occurring and recruitment levels are some of the highest in the history of the stock. The high recruitment observed must be originating from other non-targeted populations. Based on NOAA bottom long-line surveys and high capture rates of large snapper, more structure exists in the western GOM than is realized or can be adequately sampled. The inability to target these populations of sow Red Snapper results in an artificially low abundance, which creates a discrepancy in the stock-recruit relationship for this fishery. The rapid recovery of Red Snapper stocks recently suggests that managers may have underestimated the spawning stock biomass or productivity of this stock, or potentially both. These results highlight one reason why managers cannot reconcile the rapid recovery and high abundance of fish reported by anglers and scientists, particularly for the western Gulf of Mexico, when production models are predicting much less recovery. The site fidelity characteristics of sow Red Snapper and use of small and typically unknown habitat features support our hypotheses that a portion of the spawning stock of sow Red Snapper may have been overlooked. While estimating fish populations is clearly an uncertain process, these findings are important in that it will help improve our understanding of population dynamic and improve the management and recovery of the Red Snapper fishery.

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CHAPTER V:

CONCLUSIONS, MANAGEMENT IMPLICATIONS, AND FUTURE DIRECTIONS FOR THE RED SNAPPER FISHERY IN THE NORTHERN GULF OF MEXICO

A primary focus of this dissertation was to address some of the key questions regarding discard mortality, recruitment, and connectivity of Red Snapper in the Gulf of Mexico (GOM). Acoustic telemetry using transmitters with accelerometer and depth sensors provided a unique and novel approach for examining hypotheses concerning fate after release, resumption of "normal" activity, and movement and residency of Red Snapper. Findings from these studies will help fishery managers make more informed decisions on best-release practices for discarded Red Snapper and explain why such high levels of recruitment exist in the western GOM when spawning stocks are at very low levels. Ultimately, this information will help advance our understanding of overall population dynamics and improve the management and recovery of the Red Snapper fishery in the GOM.

I used acoustic telemetry with unique sensor tags to estimate the extent of delayed mortality for Red Snapper and attempted to determine the best-release practices for enhancing survival. I tested whether: (1) certain release treatments were more favorable for increasing post catch-and-release survival and if rapid recompression strategies were a better alternative to venting; (2) season of capture associated with differences in water temperatures and presence of thermoclines influence survival, and; (3) depth of capture influences survival. Novel acoustic telemetry technology was used to record acceleration and depth data upon release, allowing estimation of survival rates and delayed mortality events in a series of temperature, depth, and release treatments. Fish were tagged using acoustic transmitters and released in one of three ways: vented at the surface, non-vented at the surface, or rapidly recompressed using a descender device. There was a clear positive effect of venting and rapid recompression on survival. Fish that were not vented were over two and a half times as likely to perish as fish that were vented prior to release. Fish rapidly recompressed by descending and bottom release were nearly four times as likely to survive as fish that were similarly not vented but released at the surface. Increases in water temperature negatively influenced fish survival, particularly when summer thermoclines create large surface-bottom temperature differentials. I suggest that returning the fish to cooler water temperatures by using descending methods enhances post-release survival and appears to be particularly important when seasonal thermoclines are present.

Venting and rapid recompression have the potential to improve recovery and increase survival of regulatory discards in the Red Snapper fishery. Fish in the vented surface release and rapid recompression treatment groups had the highest survival, while non-vented surface-released fish had the lowest. Venting a surface-released fish or rapidly recompressing it will increase the probability of fish surviving barotrauma injuries. Fish suffering delayed mortality perished within a 72-hour period. This appears to be the critical time threshold, whereby fish that survive this vulnerable short-time period will likely experience long-term survival. Overall, these data support that venting and rapid recompression methods are effective tools for alleviating barotrauma symptoms and increasing overall post-release survival.

Of central importance to effective fisheries management is the ability to accurately estimate population demographic parameters for stock assessments. For Red Snapper in the GOM, a high level of uncertainty has surrounded estimates of discard mortality, which represents an important parameter because of the high volume of discards that occur in this fishery. Results from this study enhance our understanding of delayed mortality and post-release behavior of Red Snapper and provide conclusive information documenting the fate of regulatory discards. Estimates of delayed post-release mortality from this study can be integrated into stock assessment models to reduce uncertainty over discard mortality estimates and improve estimates of Red Snapper population dynamics. Determining the best-release practices to enhance survival will further assist and expedite the recovery of this fishery by minimizing the number of discard mortalities that will ultimately result in larger stock sizes.

The next focus was to extend the application of the novel acoustic sensor transmitters beyond simple estimation of discard mortality and analyze the post-release behavior and activity patterns of discarded Red Snapper that survived the catch-and-release process. Specific objectives for this chapter were to: (1) determine if different release methods (e.g., venting, rapid recompression, non-venting) affected long-term behavior of fish surviving the catch-and-release process and if certain methods proved more beneficial for recovery; (2) examine if diel residency patterns, vertical migrations, or acceleration patterns differed in Red Snapper surrounding oil and gas platforms; (3) use accelerometer data to construct an ethogram to illustrate the allocation of energy expended by Red Snapper and determine if energy allocations differed among release treatments, and; (4) classify surviving Red Snapper into discrete character types based on their unique residency, activity, and behavioral attributes derived from accelerometer and depth sensor data.

This study was the first to examine post-release behavior and activity patterns of Red Snapper using acoustic transmitters equipped with accelerometer and depth sensors. Using this novel approach, I determined that Red Snapper display different acceleration and depth activity over diel time periods, and that acceleration and depth are correlated – fish higher in the water column typically exhibited faster acceleration values than fish residing near the seafloor. Venting, non-venting, and rapid recompression release treatments did not differ in their outcome on long-term fitness, behavior, or survival for discarded Red Snapper. Furthermore, fish released using different methods did not have reduced activity or behavior. That various release treatments do not place an added risk of mortality on discarded Red Snapper is a critical piece of information for managers making determinations on the best-release practices for minimizing discard mortality and promoting sustainable catch-and-release.

The final component of this dissertation focused on addressing the current decoupling of the stock-recruit relationship for the Red Snapper fishery by examining whether localized cryptic spawning stock biomass is responsible for maintaining such high recruitment levels when the adult populations were at all-time lows. I tested the hypothesis that older, larger sow Red Snapper in the western GOM have found spatial refuge from fishing by using different habitats than smaller adult Red Snapper. Specifically, I examined whether: (1) movement and habitat use patterns of sow Red Snapper in the western GOM differed compared to smaller adult Red Snapper, and; (2) differences in catch rates and size classes of Red Snapper existed in various habitats and structure types in the western GOM.

Using acoustic telemetry and catch-per-unit-effort data, I was able to show that sow Red Snapper have similar site fidelity and residency patterns as smaller Red Snapper in the western GOM. I also showed that large-scale movement and small-scale habitat use patterns of sow snapper were also not substantially different than small snapper. Acoustic returns of sow snapper tagged and tracked using mobile acoustic telemetry showed 79% recovery at initial tag sites after three months and 36% after one year. This is similar to observed patterns of small Red Snapper, which have been shown to exhibit high site fidelity on the order of 1 – 2 years before emigrating from the site over longer time periods. Sow Red Snapper tagged on one platform had similar long-term habitat use patterns as small Red Snapper as previously reported, residing at depths near the seafloor and within close proximity to structure. Catch-per-unit-effort had a strong recreational season effect. Sow Red Snapper in the western GOM have high site fidelity, use similar habitats, and have similar movement patterns as small adult snapper.

Results from this study have clear implications for Red Snapper management, and these findings will help mangers explain the confounding issue of why recruitment of young fish remains so high while the historical abundance of spawning stock is so low. These findings helped answer a major assessment difficulty facing Red Snapper fisheries management - developing a significant stock-recruit relationship for this fishery due to non-random habitat use. Additionally, these parameters have been very difficult to estimate due to the historic long-term low level of population abundance leaving managers with no baseline for what recruitment would be observed at higher stock sizes. Compounding the problem is that recent recruitment levels are much higher than would be supported by current model-predicted stock sizes. Thus, there is a de-coupling of the stock-recruit relationship making fitting key management tools (i.e. mathematical models) and benchmark proxies leaving uncertainty in predicting future trends. A key management finding of this study was providing evidence of why fishery independent surveys are reporting such high recruitment level of a stock that is purportedly some of the lowest levels in management history. Thus, while addressing this major management goal, I provided key information about how the occurrence of the spawning stock, “sow Red Snapper,” and their behavior leads to likely overlooking these stocks in estimating spawning stock biomass.

The research completed in this study contributed to a better understanding of discard mortality estimates and recruitment dynamics that can be applied to stock assessments and Red Snapper fishery management. However, there is still a significant amount of variability in these estimates depending upon the season, depth, fishery sector, gear type, regional issues, and more. Thus, there is need for additional research. My novel approach using acoustic telemetry to estimate immediate and delayed mortality should be replicated to determine if similar mortality estimates are observed in other locales, water depths, and seasons. One drawback in using this technology is the expenses associated with purchasing acoustic transmitters and receivers, which restricts the number of fish tagged for study and therefore overall sample size. To supplement the low sample sizes associated with acoustic telemetry, simultaneous passive anchor tagging could be used in future experiments. Anchor tags are cheap, easily deployed, and designed for large-volume mark-recapture experiments. Recent analytical methods have been developed to combine both acoustic and passive tag types into a single model for estimating mortality. Another challenge in using acoustic telemetry methods that I encountered that was part of all three studies involved the variability in detection efficiency associated with environmental factors as reported by numerous recent studies in the acoustic telemetry literature. As discussed in the specific chapters, environmental factors such as such as wind, temperature fluctuation, the presence of thermoclines, and ambient biological noise can significantly influence acoustic detection efficiency, which may be misleading in making inferences about fish movement based solely on the number of presence/absence detections or even acceleration and depth sensor data. To account for the variability in detection efficiency across different environmental landscapes, future studies using acoustic telemetry should include control transmitters (or sentinel tags) and more extensive range testing to account for this detection variability.

For the first time since being classified as overfished, the Red Snapper fishery appears to be on the road to recovery. Very recent stock assessments report overfishing has ended and stocks are rebuilding. A full recovery means that the fishery has reached a level with a spawning potential of 26%, and current models project the stock to be fully recovered by the year 2031 (Figure 5.1). Obviously, there is still a long way to go, and critical data gaps remain regarding the population dynamics of this fishery. Findings from this dissertation research have addressed two of these major data gaps – discard mortality and the source of the spawning stock. By identifying the source of the high spawning stock biomass, protection measures and regulations can be implemented to ensure that the current high recruitment to the fishery is sustained. Determining effective release tools and best-release practices to enhance survival by minimizing the number of discard mortalities will result in larger stock sizes. Ultimately, implementation of findings from this dissertation into the management process will further assist and expedite the rebuilding of Red Snapper stocks and promote the recovery towards sustainability in this historically important Gulf of Mexico fishery.

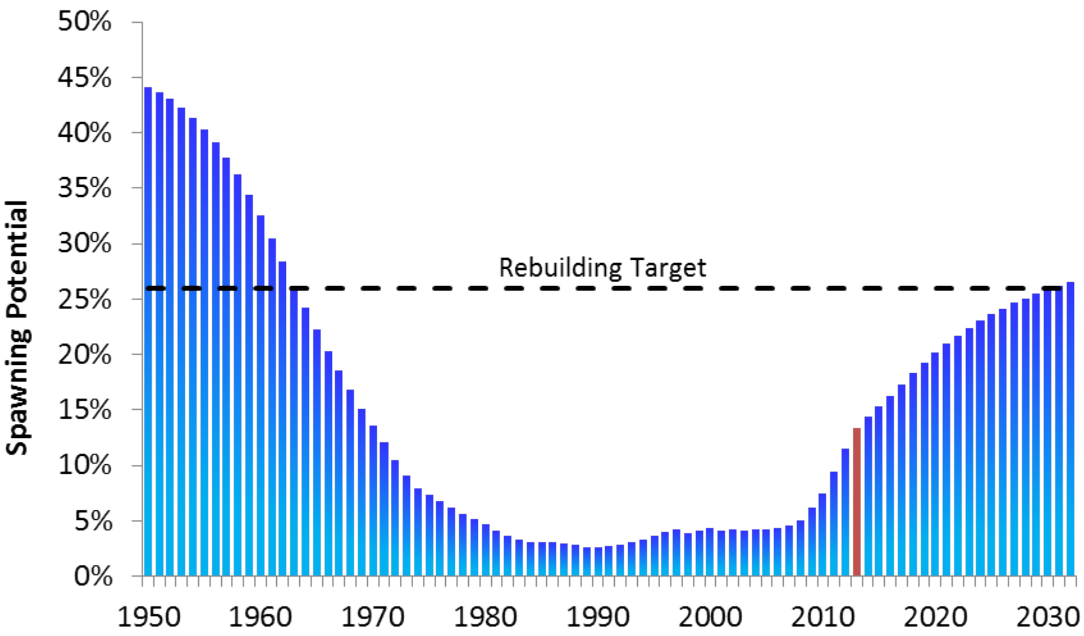

Figure 5.1. Historical spawning potential for Red Snapper in the Gulf of Mexico starting in 1950. Rebuilding target for the fishery with 26% spawning potential to spawning stock biomass ratio is the year 2031. Red bar corresponds to the year 2013. Source: NOAA fisheries, SEDAR 2013.

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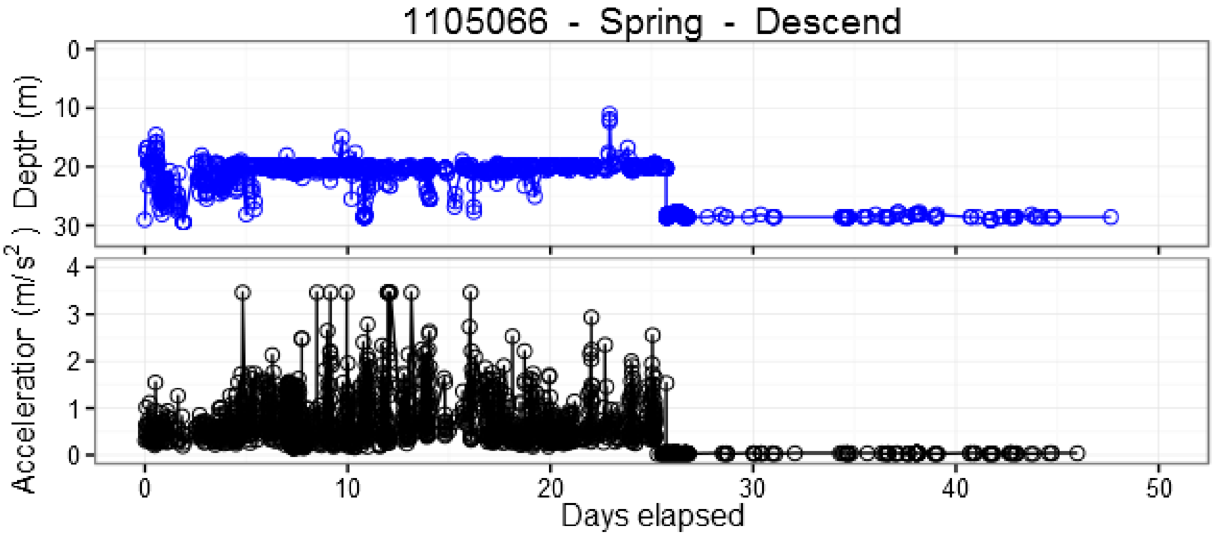
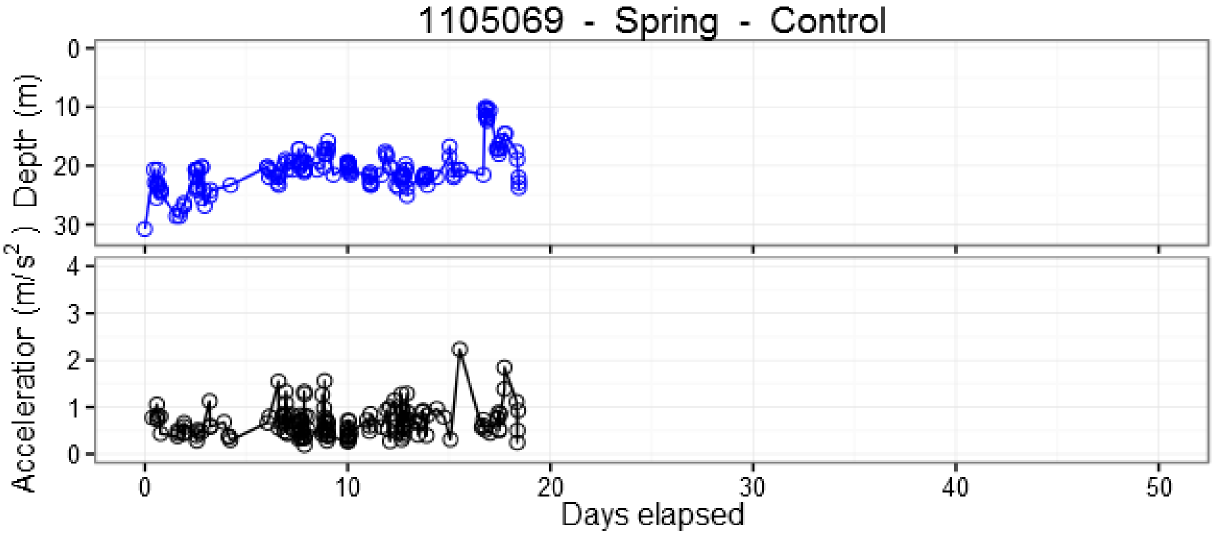
BIOGRAPHICAL SKETCH

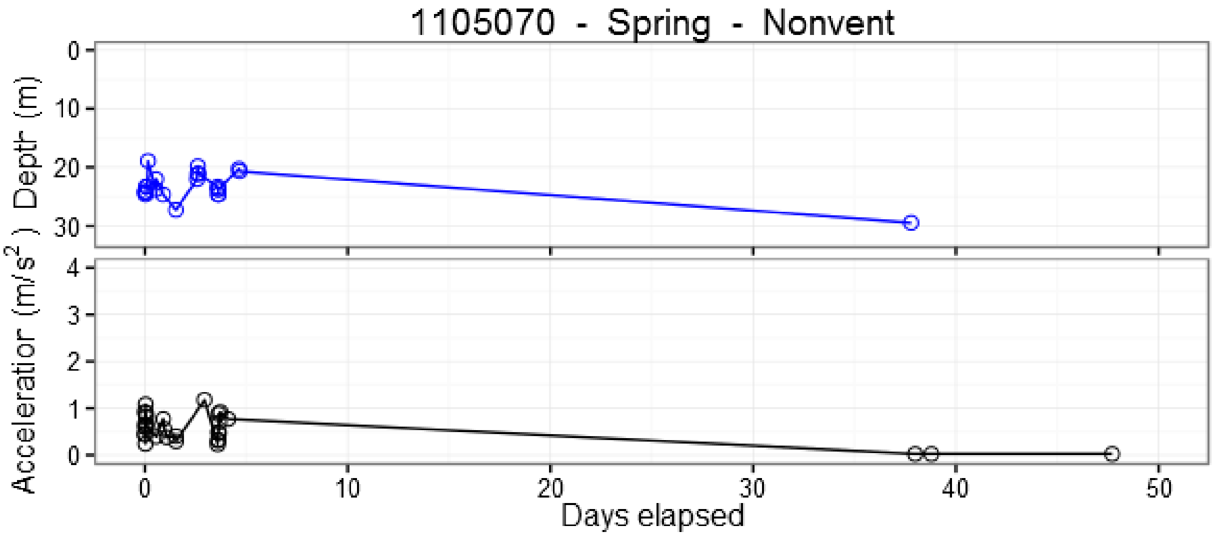
Judson (Judd) Matthew Curtis received his Bachelor's degree from Clark University in Worcester, Massachusetts where he double-majored in Biology and Environmental Science & Policy and graduated *magna cum laude*. During his undergraduate he spent a semester abroad in the Turks & Caicos Islands studying marine ecology and marine resource management at the School for Field Studies, and credits this experience for inspiring him to pursue advanced education in marine fisheries ecology. Upon graduation from Clark University, Judd worked for two years in the biotechnology industry in Worcester before applying for graduate school at Texas A&M University-Corpus Christi under the mentorship of Dr. Greg Stunz in the Fisheries & Ocean Health Laboratory at the Harte Research Institute for Gulf of Mexico Studies. Judd is a member of the American Fisheries Society, Coastal Conservation Association, American Society of Ichthyology and Herpetology, and the Audubon Society, and has presented numerous talks on his dissertation research at national conferences and annual meetings. Upon graduating with his Ph.D., he will continue to study marine fisheries ecology as a post-doctoral researcher at the Harte Research Institute for Gulf of Mexico Studies.

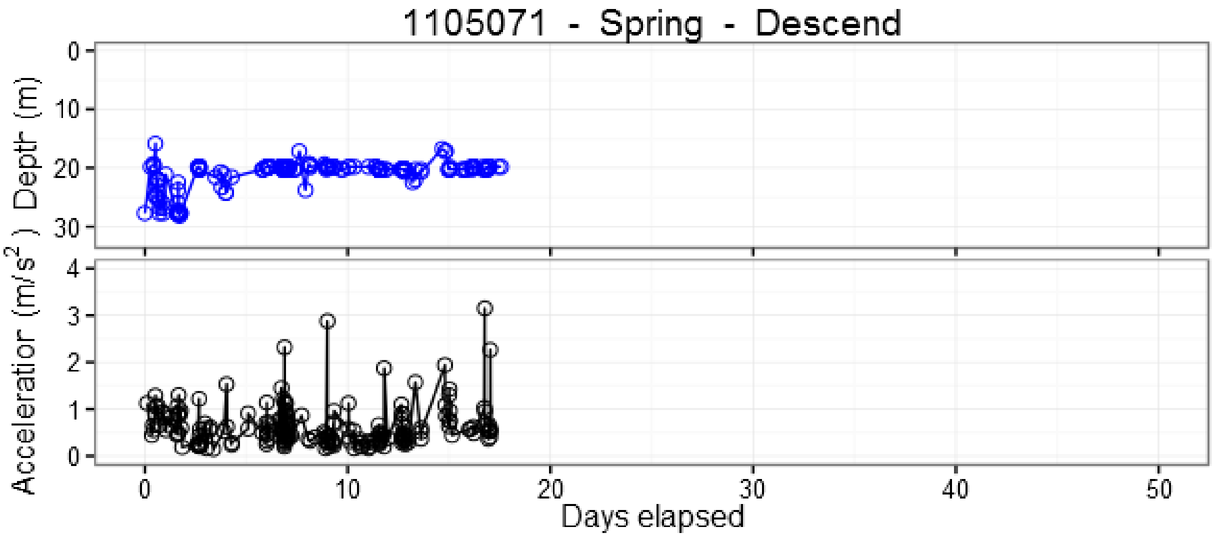
APPENDIX A: SURVIVORS

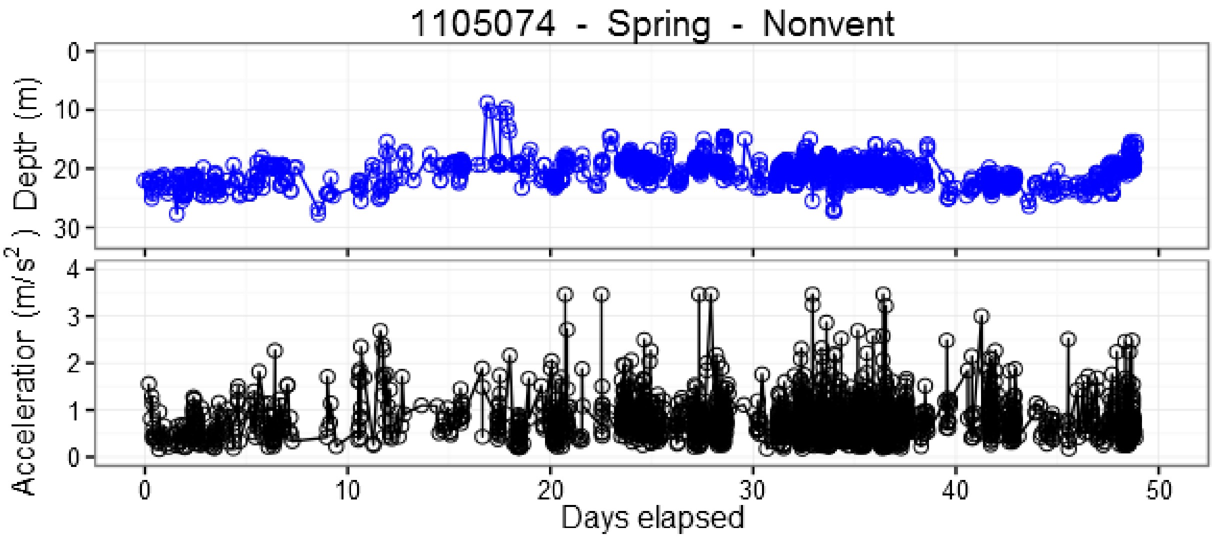
ACCELERATION AND DEPTH PROFILES OF ACOUSTIC DETECTIONS






1105070 - Spring - Nonvent
Depth (m)
0
10
20
30
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed


1105071 - Spring - Descend
Depth (m)
0
10
20
30
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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Depth (m)
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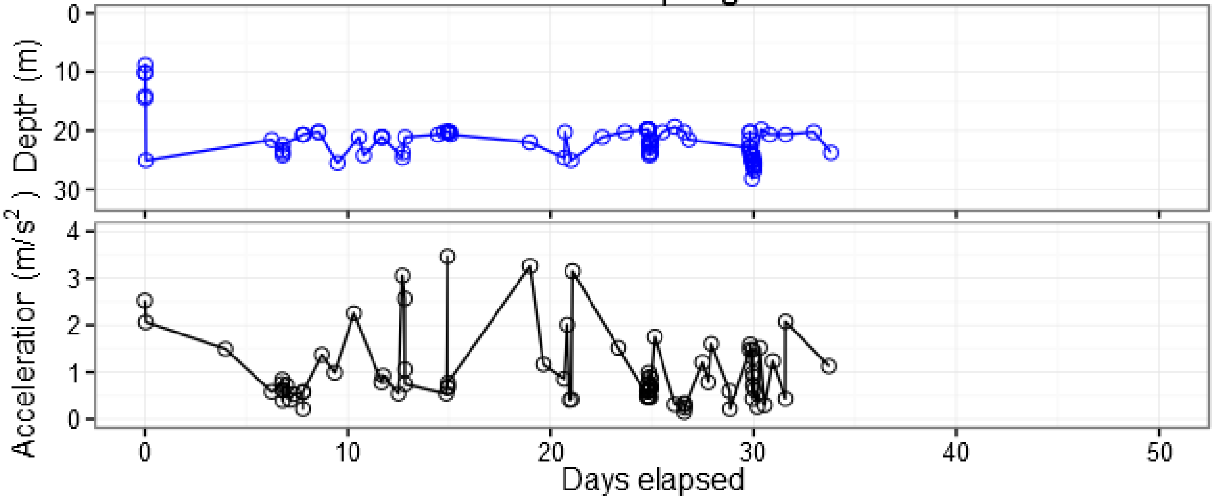
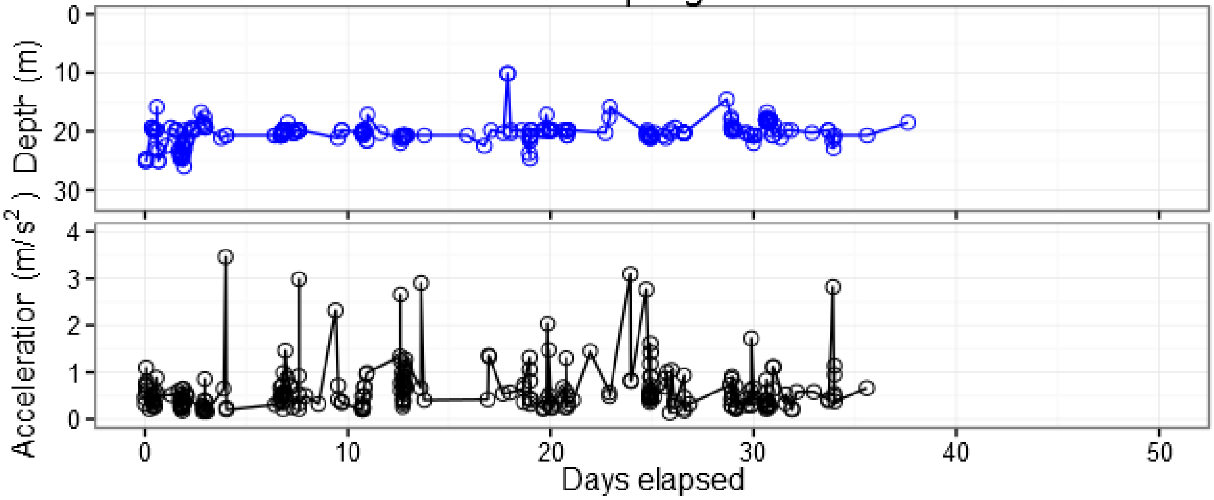
30
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed



1105075 - Spring - Vent



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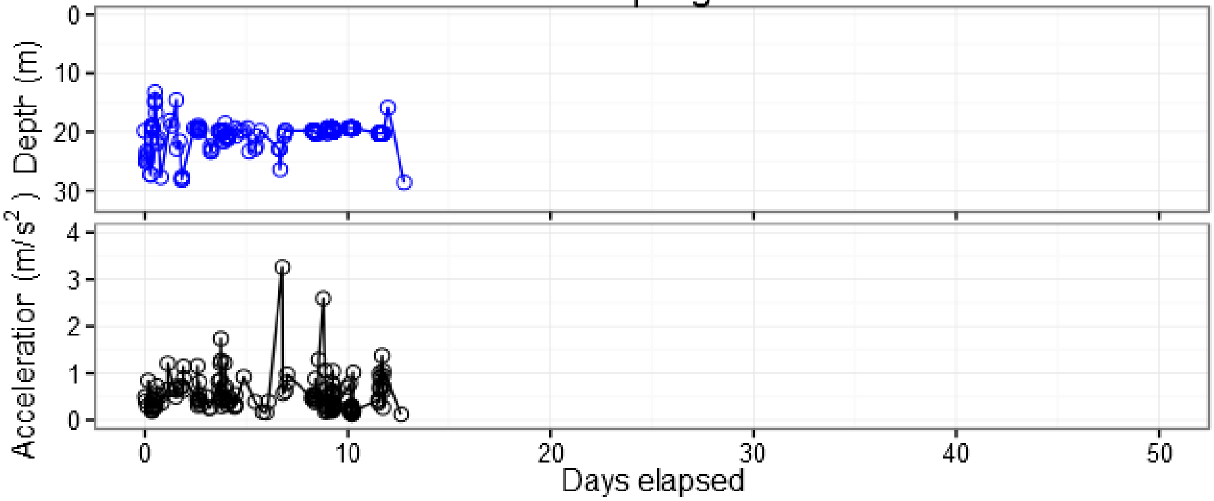

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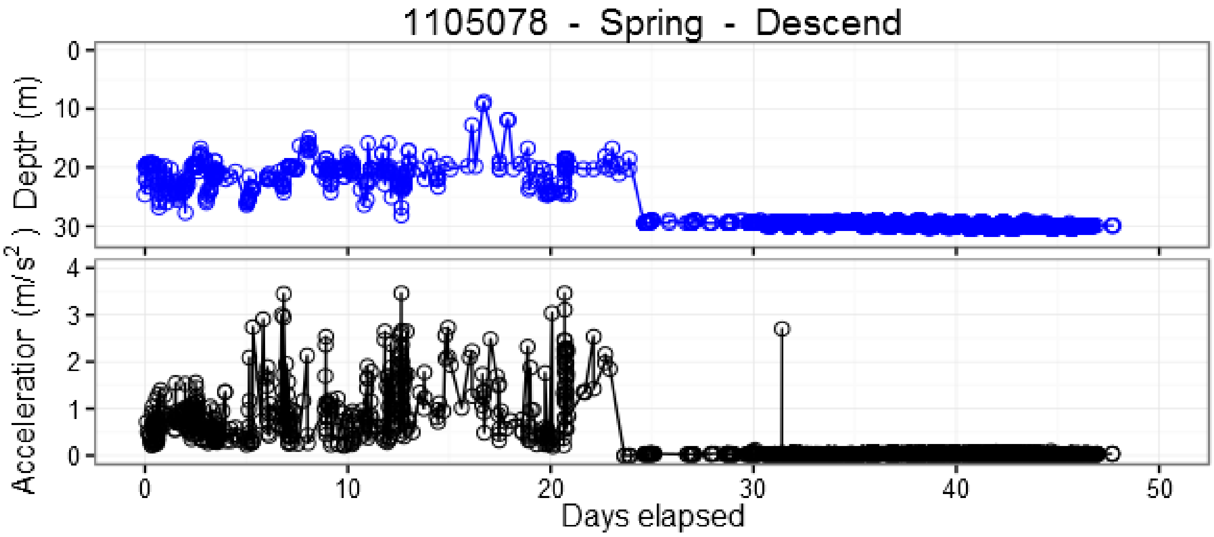

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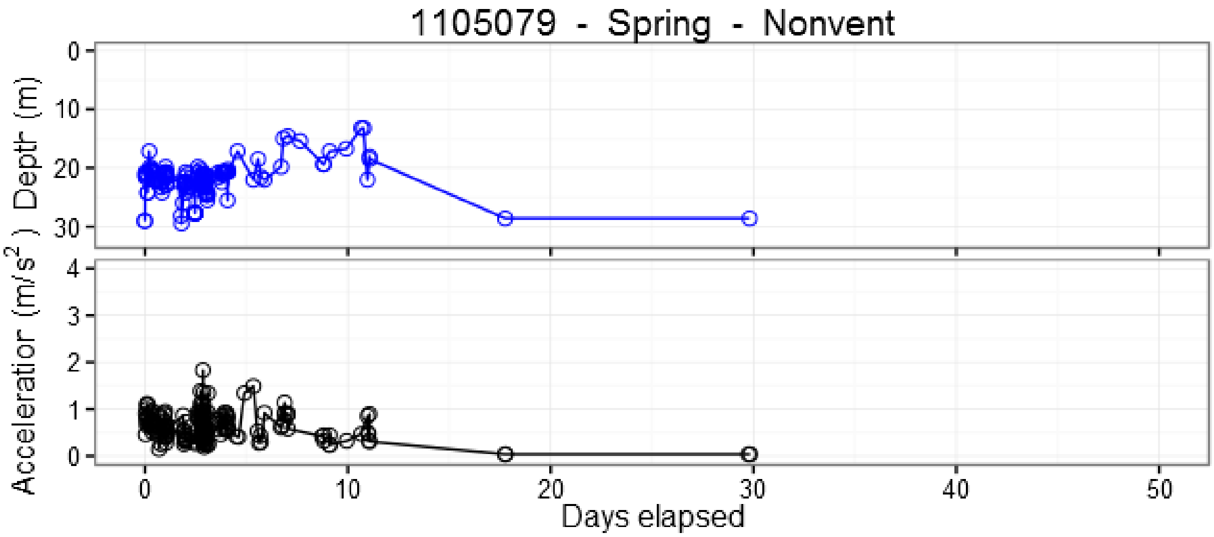

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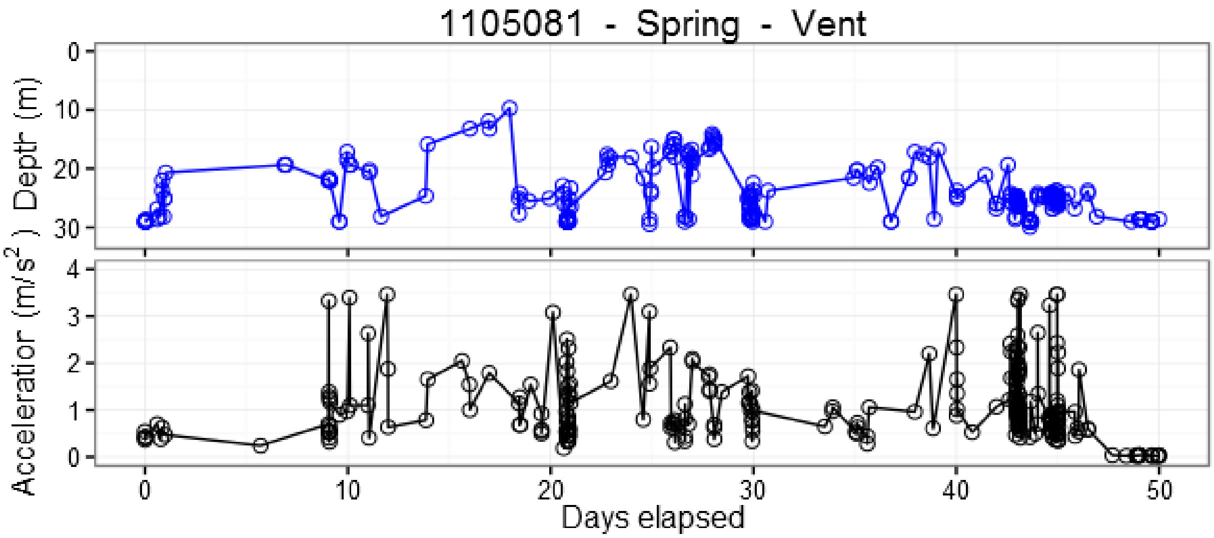
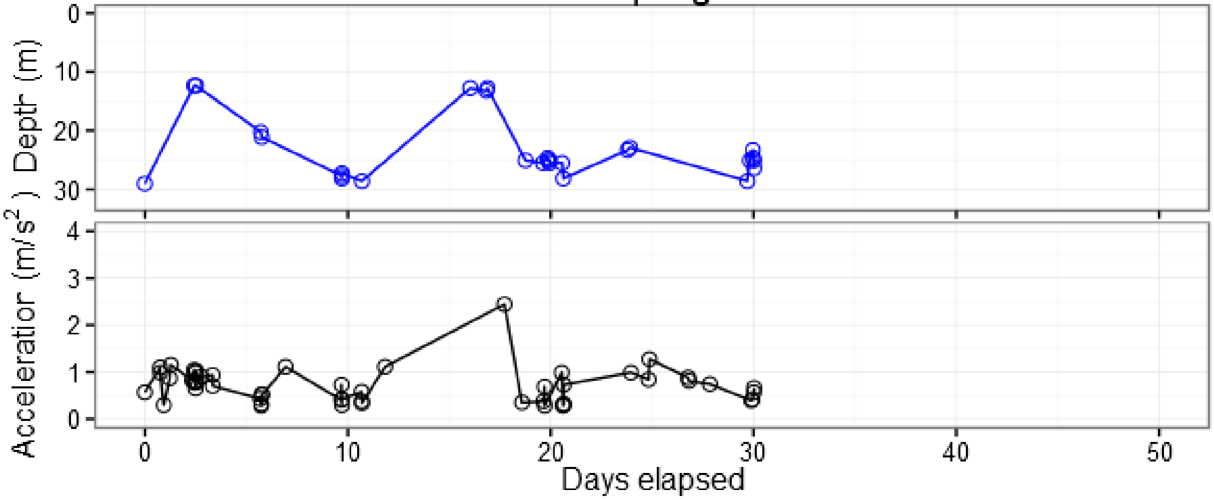


1105081 - Spring - Vent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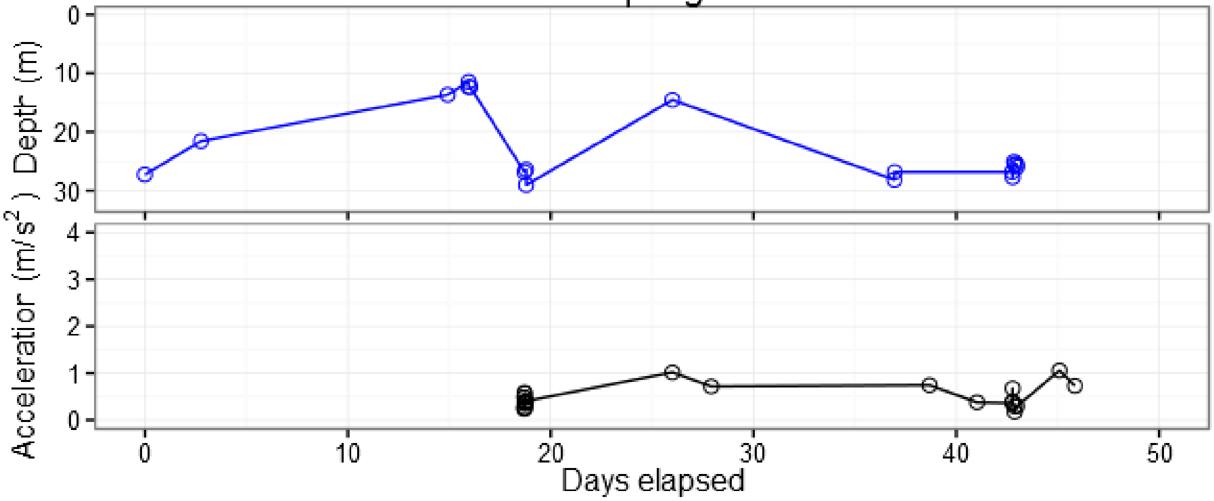
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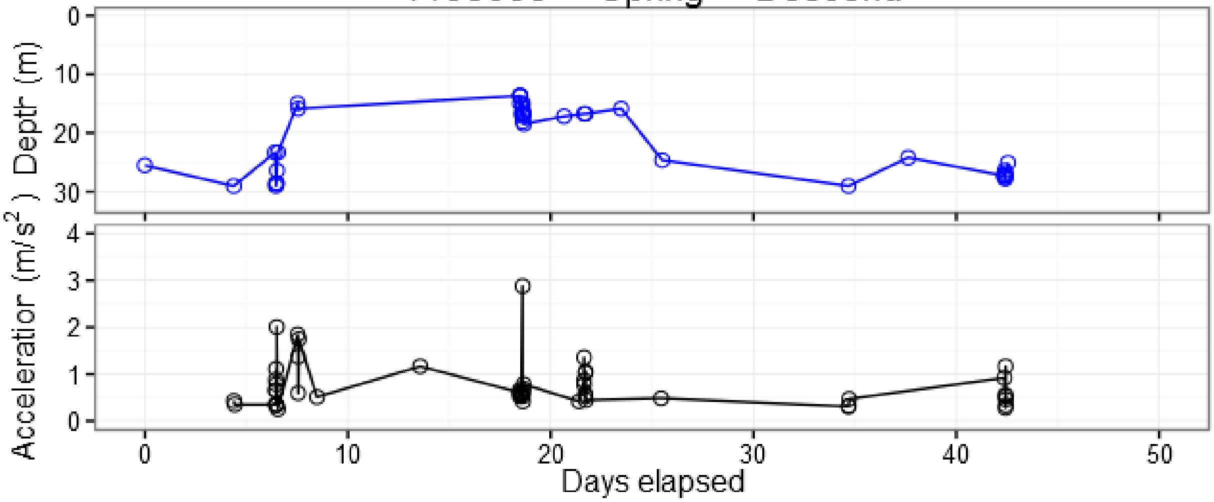
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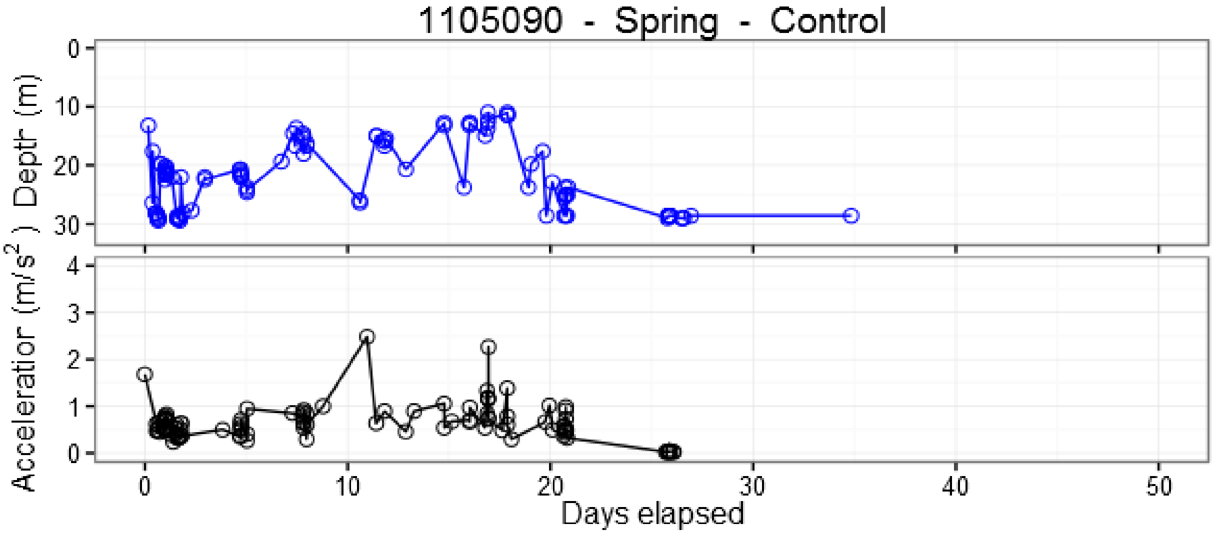
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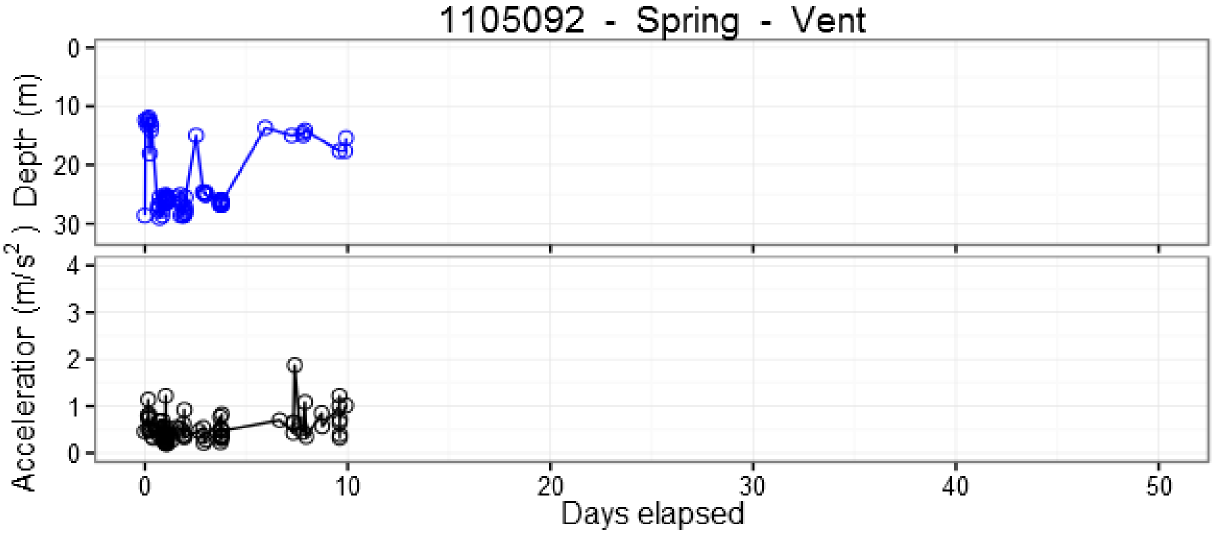
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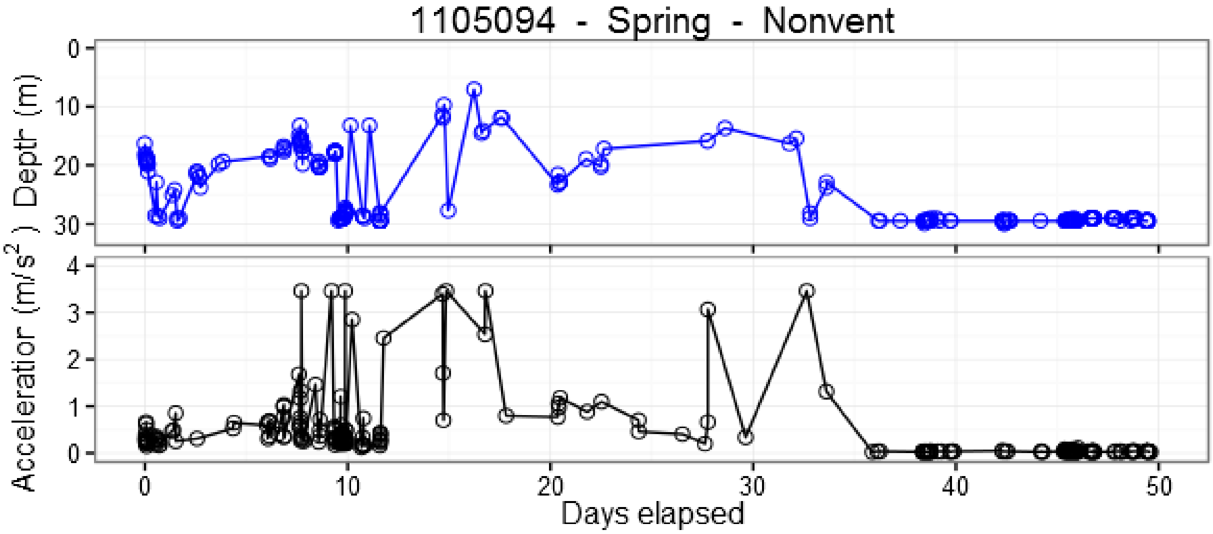
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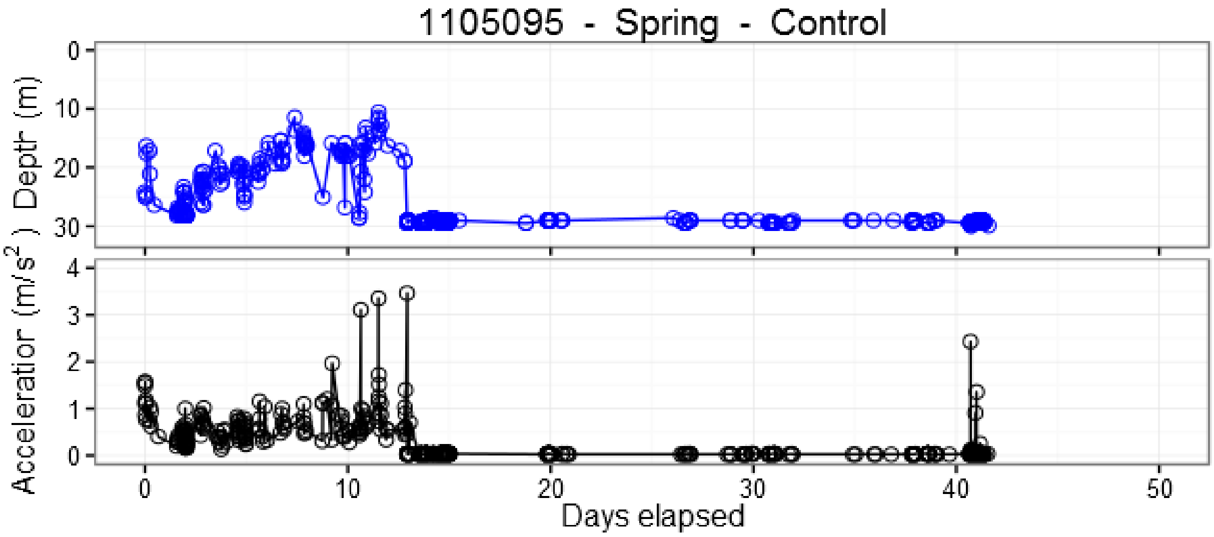
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Depth (m)
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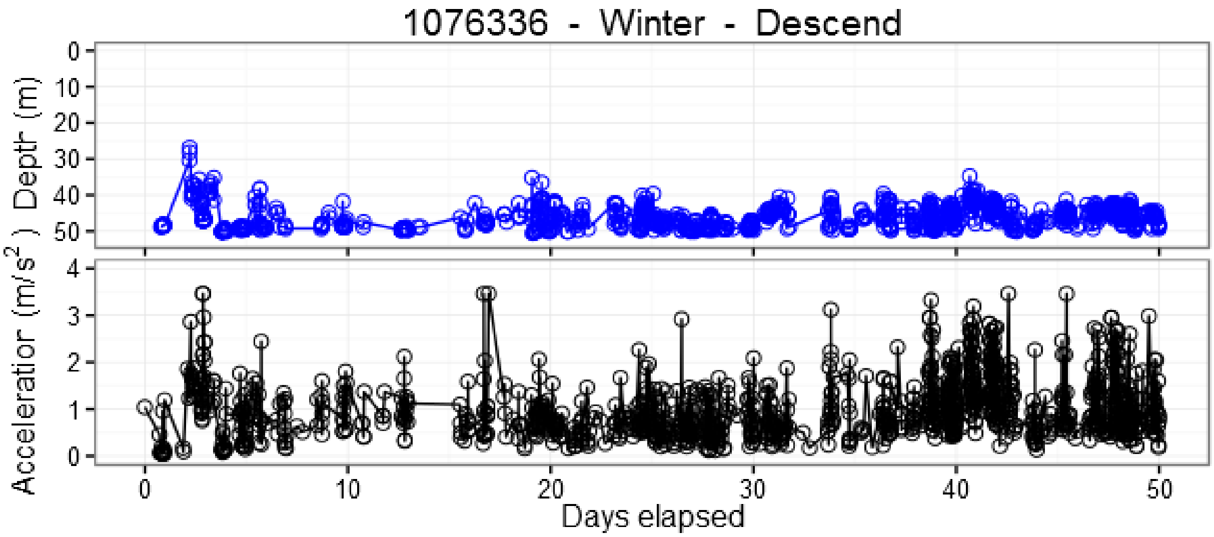
10
20
30
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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Depth (m)
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30
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50
Acceleration (m/s^2)
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2
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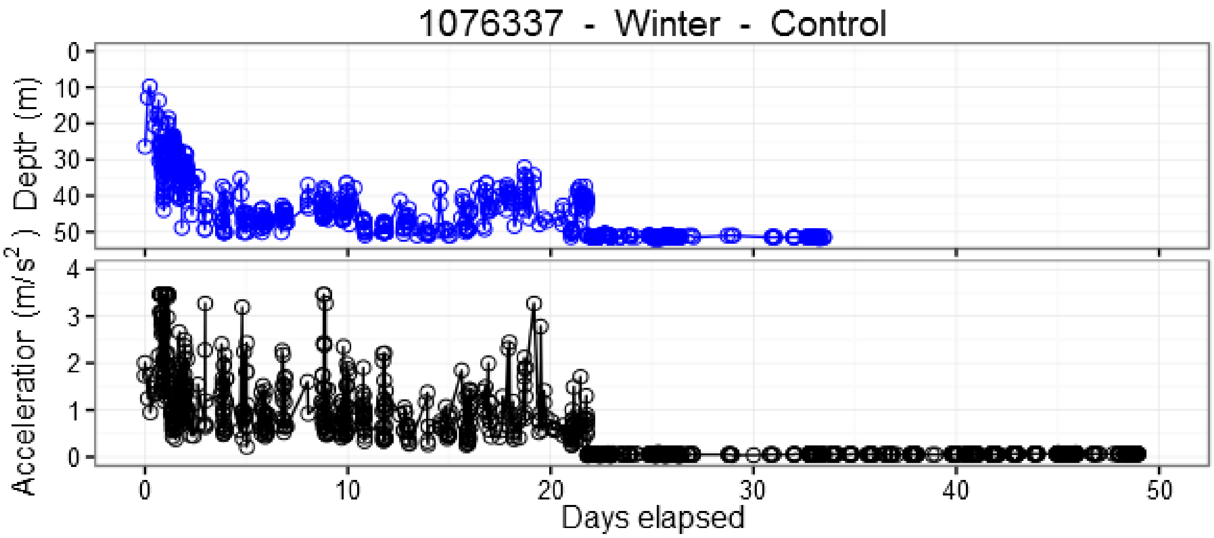
0
0
10
20
30
40
50
Days elapsed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Depth (m)
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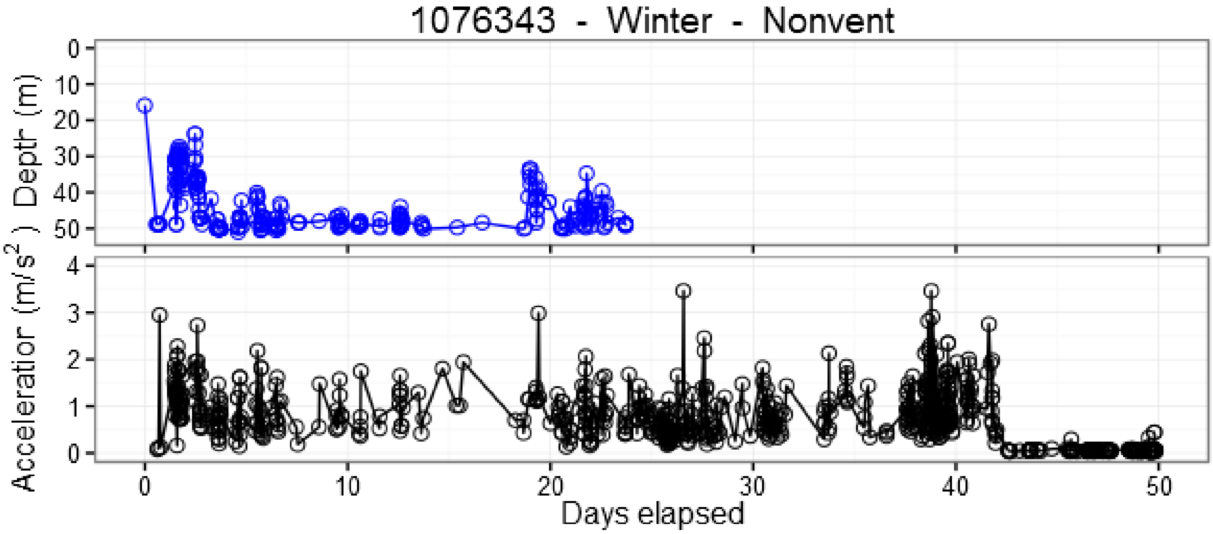
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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Depth (m)
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Acceleration (m/s^2)
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3
2
1
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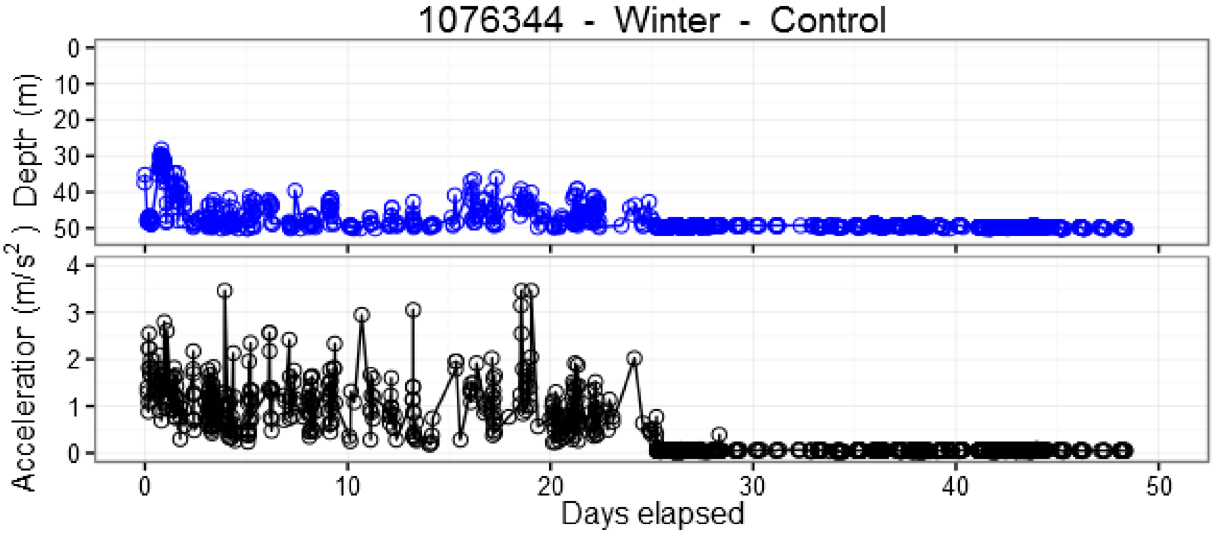
20
30
40
50
Days elapsed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Depth (m)
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50
Acceleration (m/s^2)
4
3
2
1
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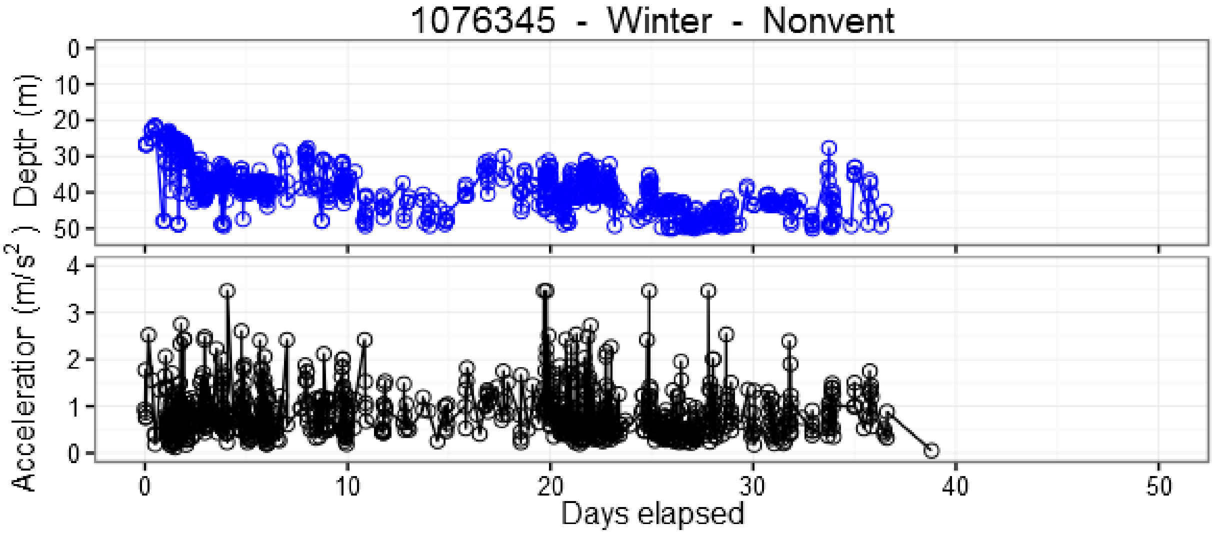
0
10
20
30
40
50
Days elapsed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Depth (m)
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30
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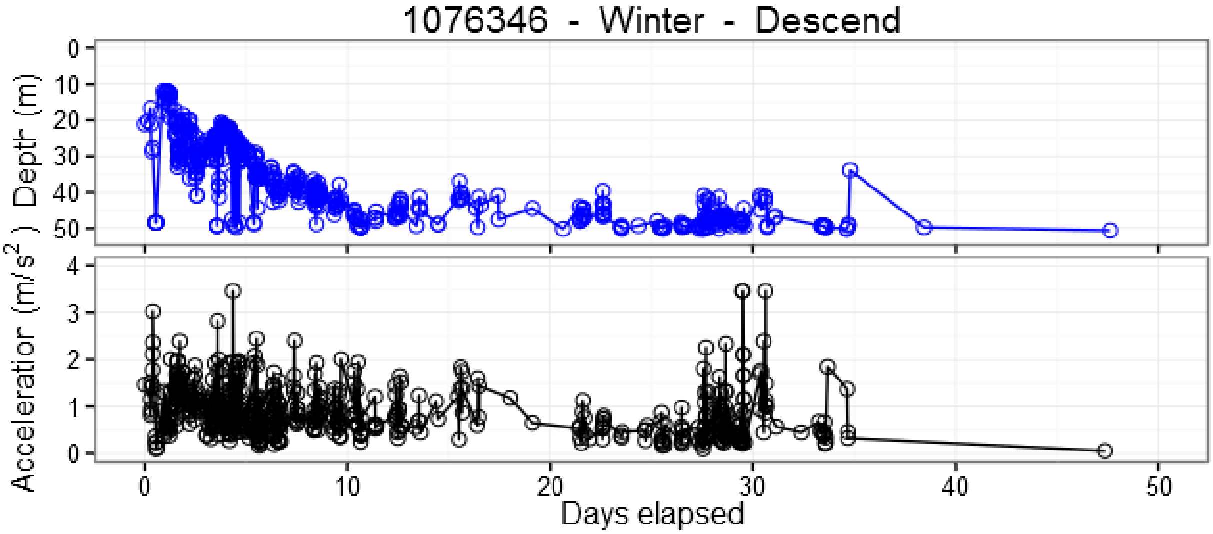
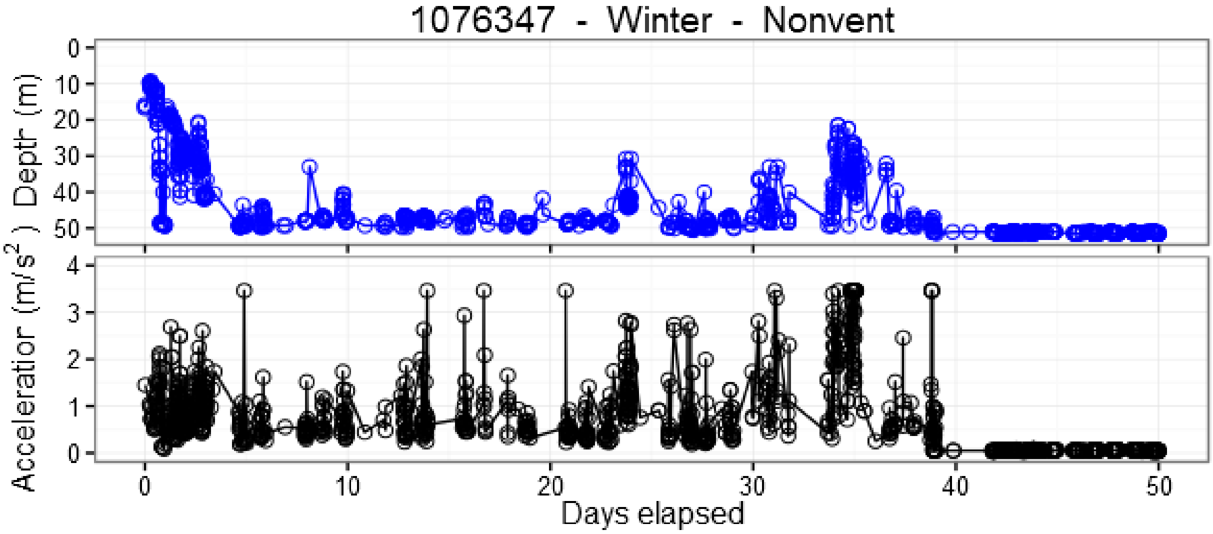
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed


1076346 - Winter - Descend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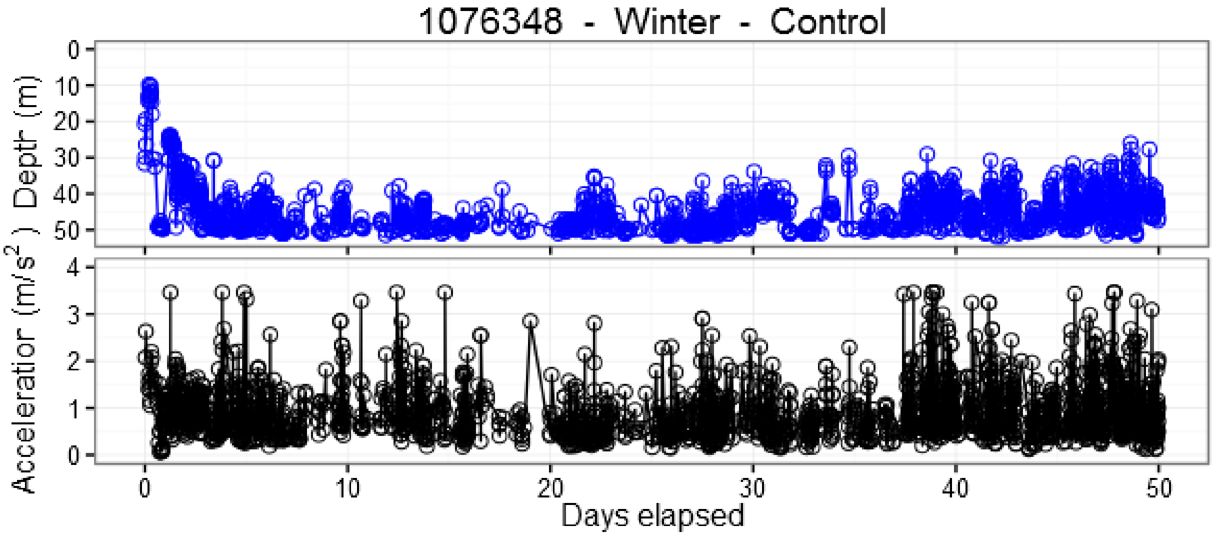
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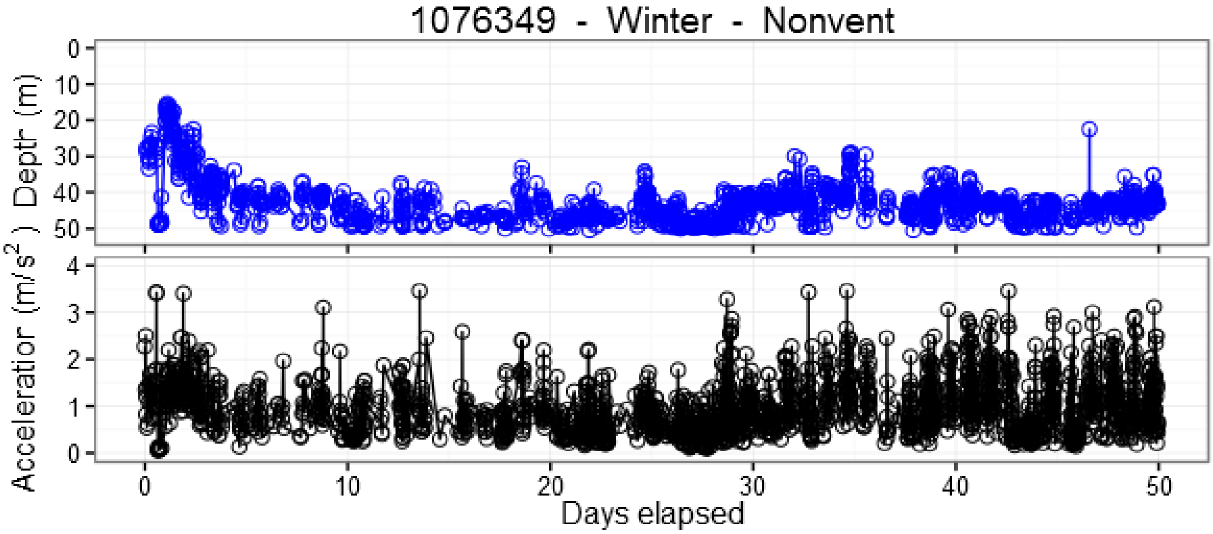
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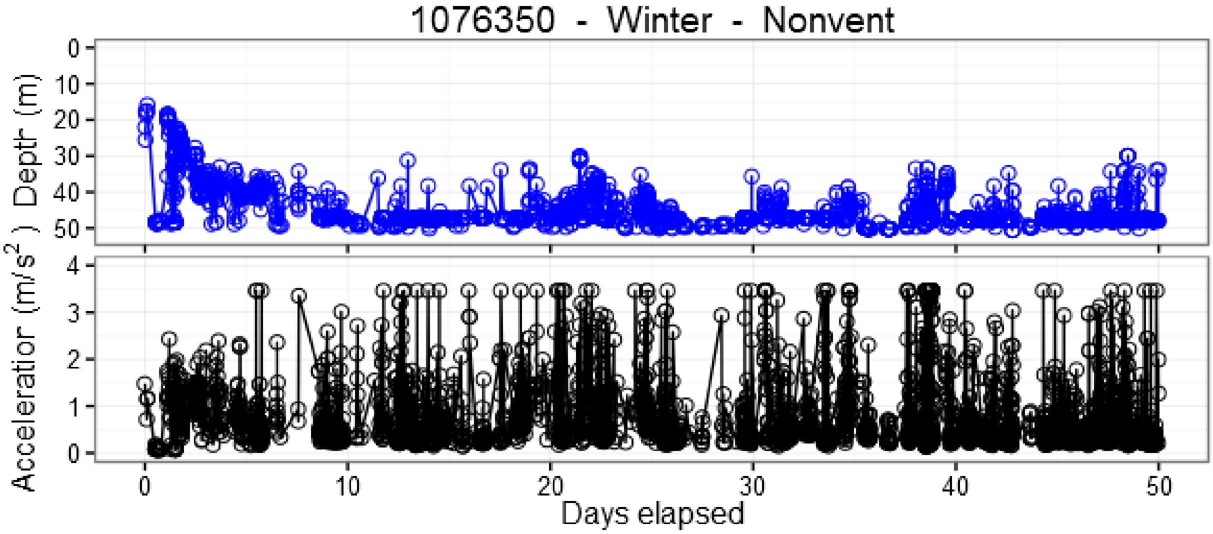
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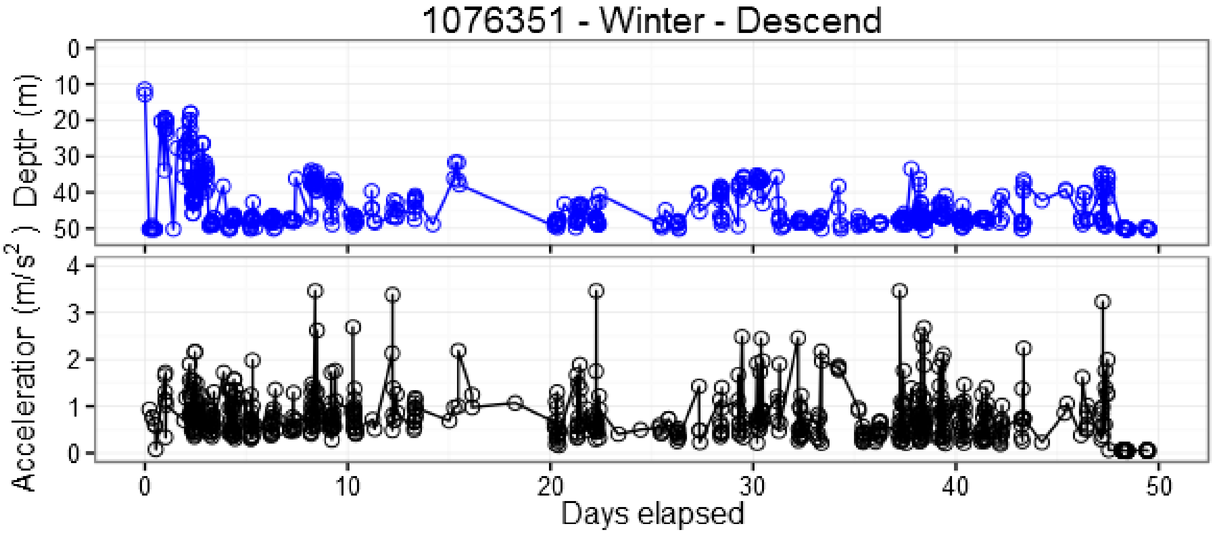
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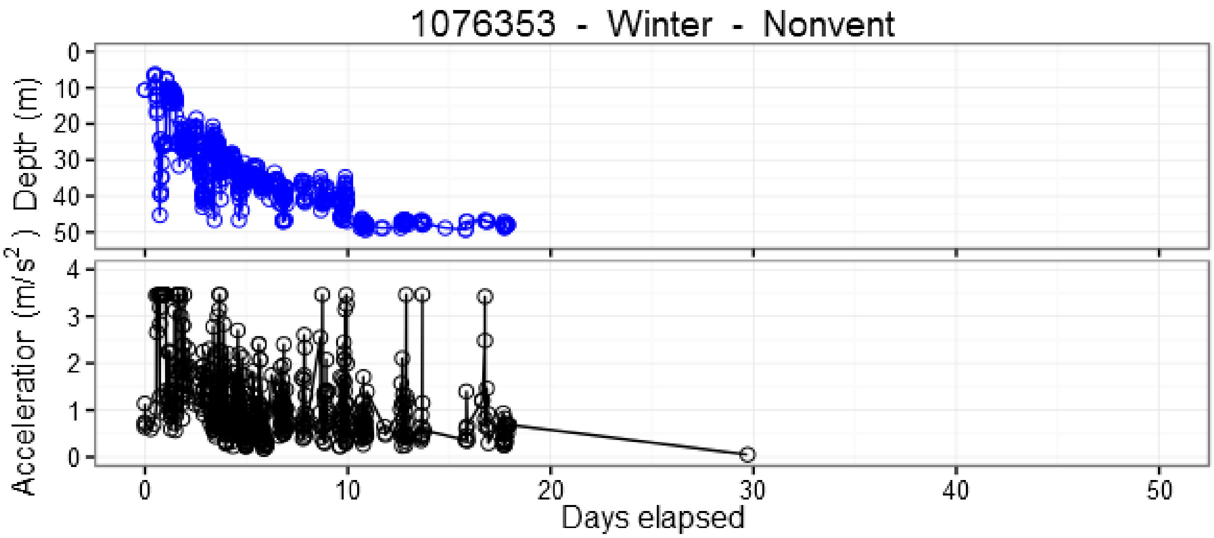
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Acceleration (m/s^2)
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2
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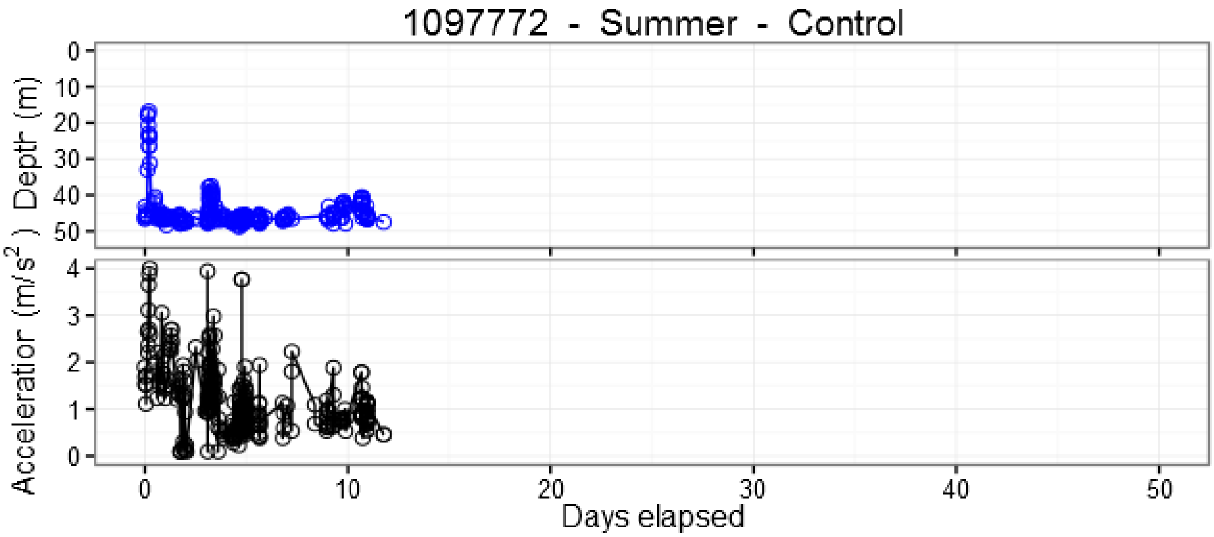
0
0
10
20
30
40
50
Days elapsed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Acceleration (m/s^2)
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2
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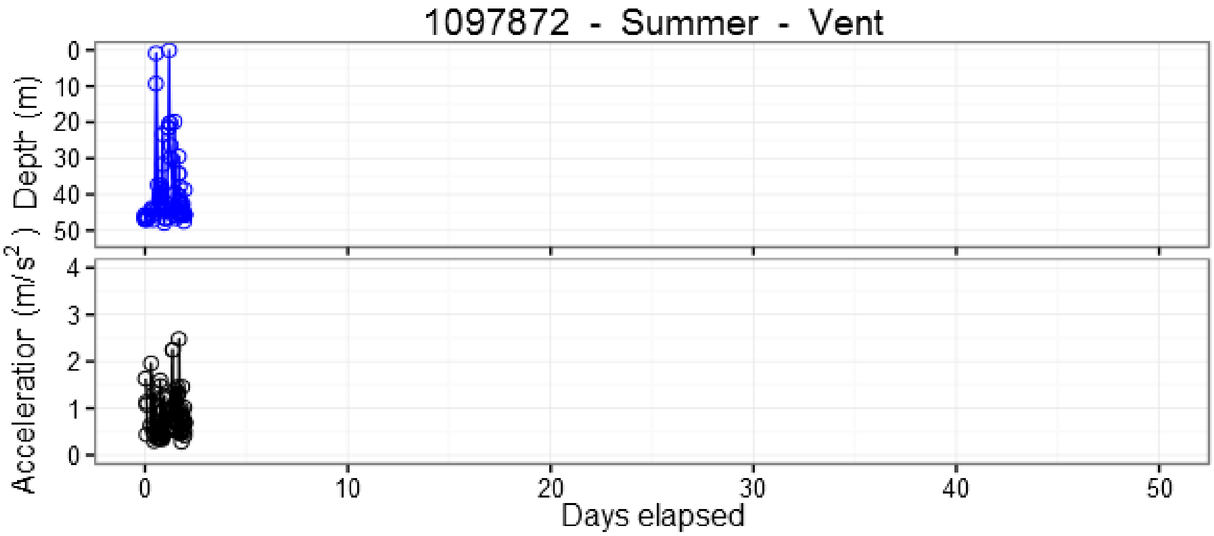
20
30
40
50
Days elapsed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50
Acceleration (m/s^2)
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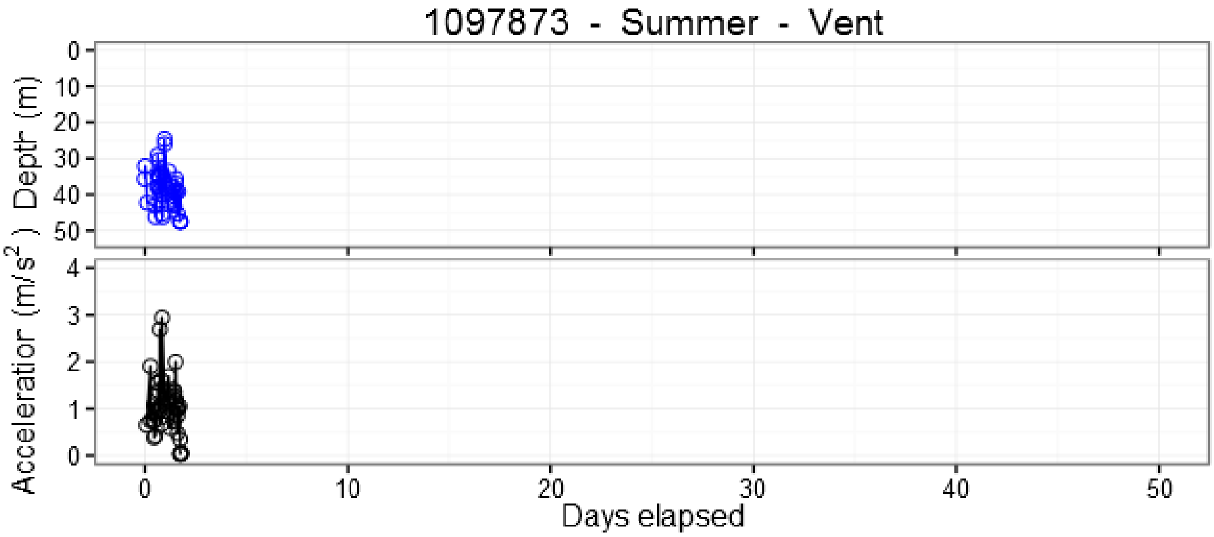
2
1
0
0
10
20
30
40
50
Days elapsed


1097873 - Summer - Vent
Depth (m)
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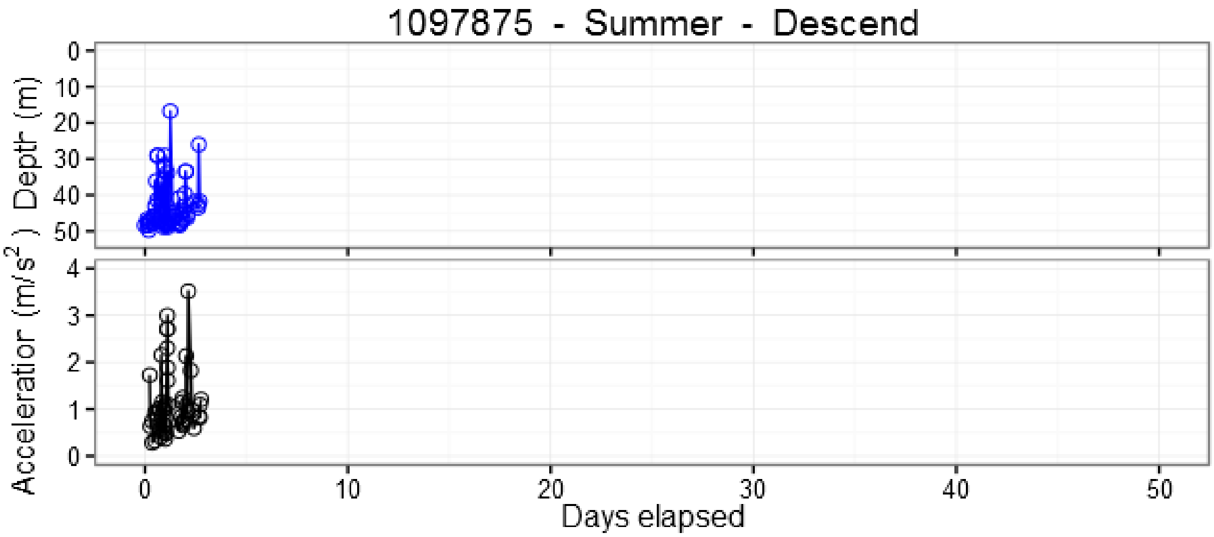
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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Depth (m)
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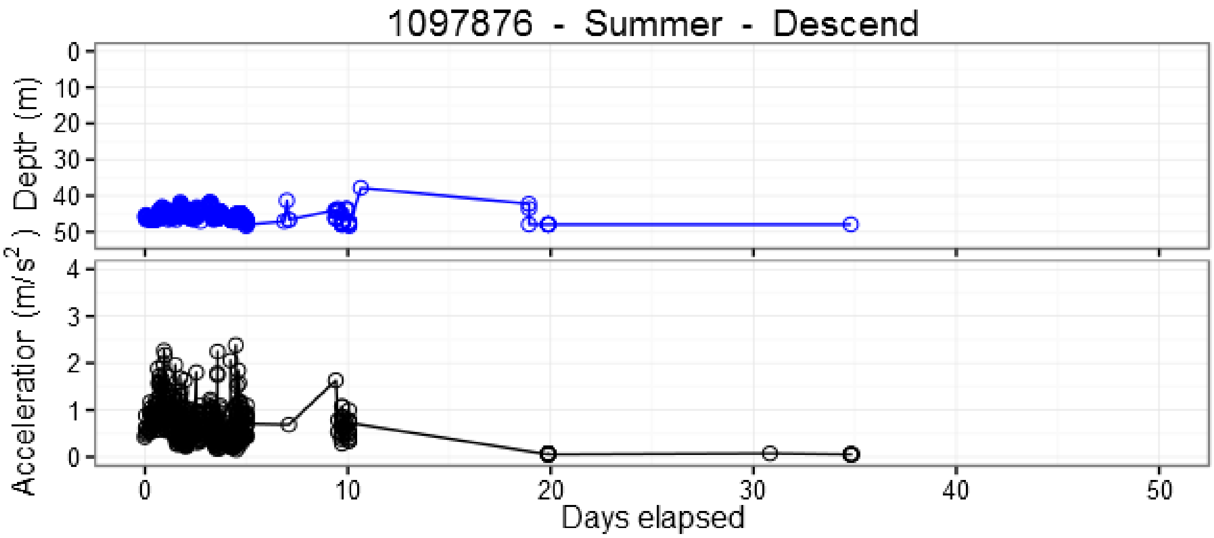
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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Depth (m)
0
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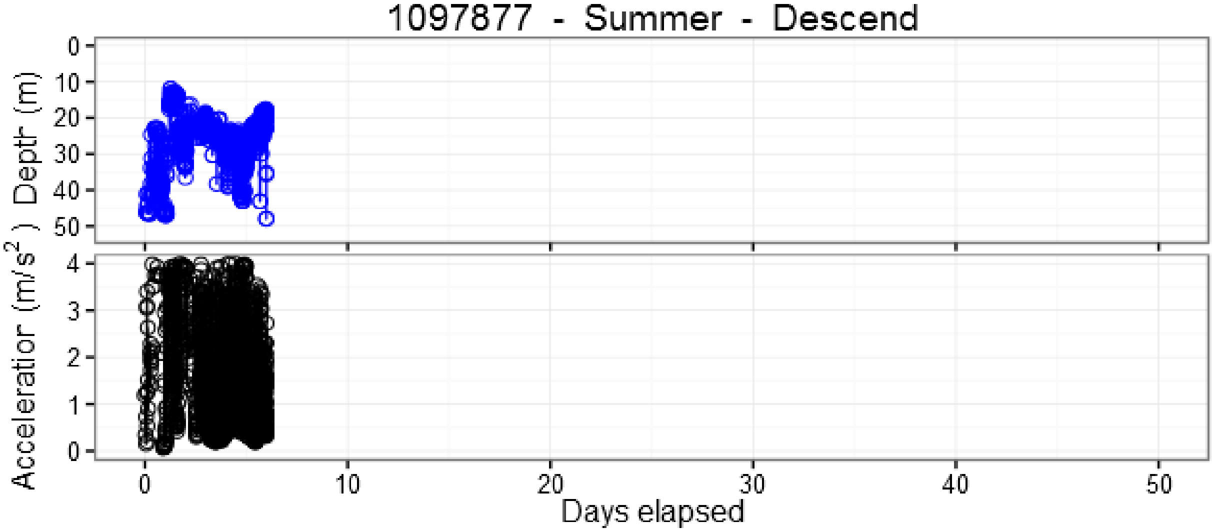
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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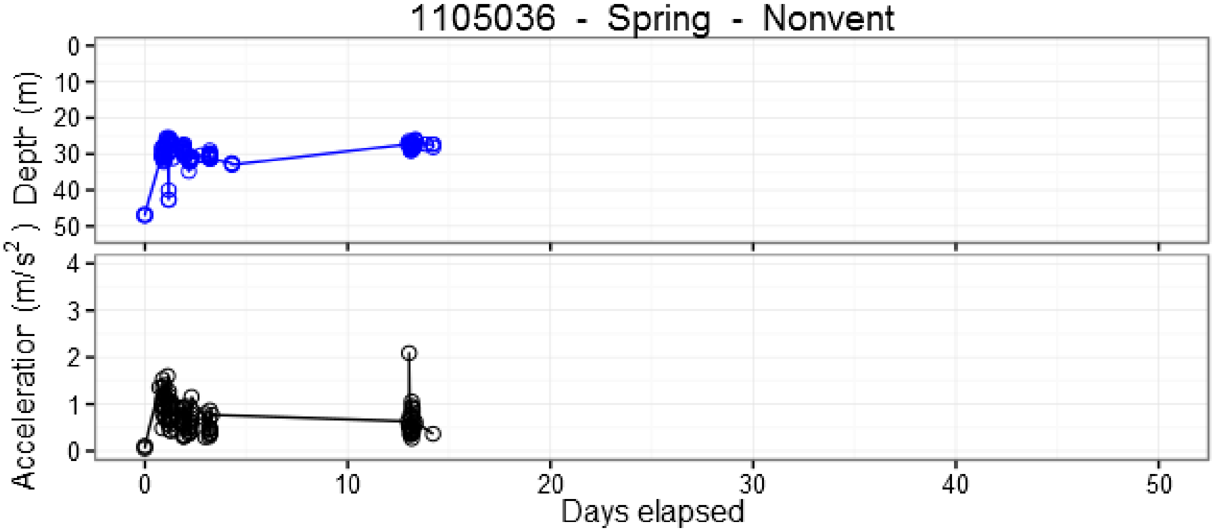
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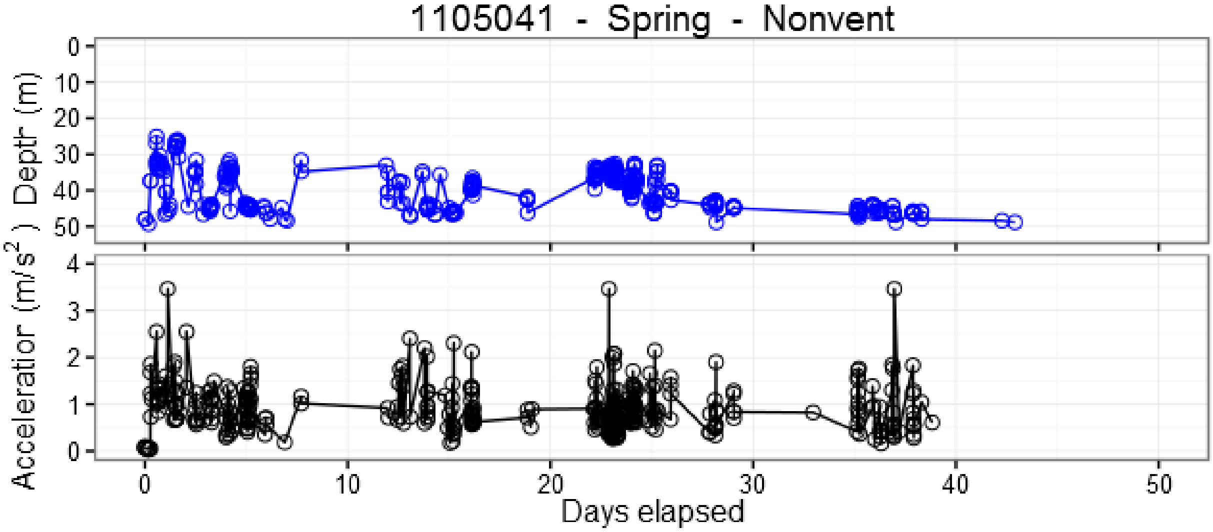
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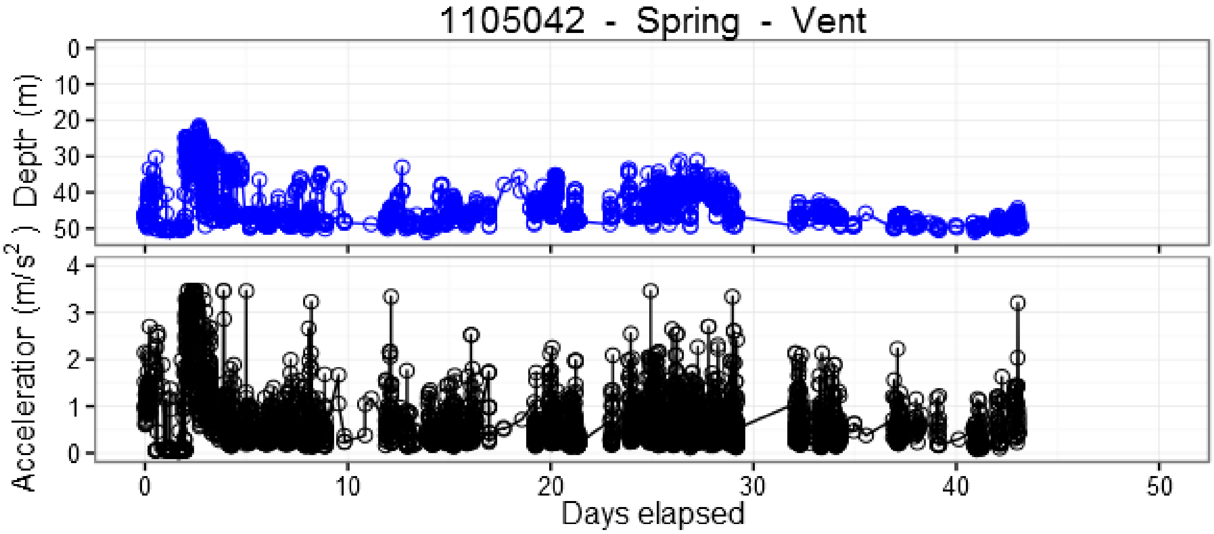
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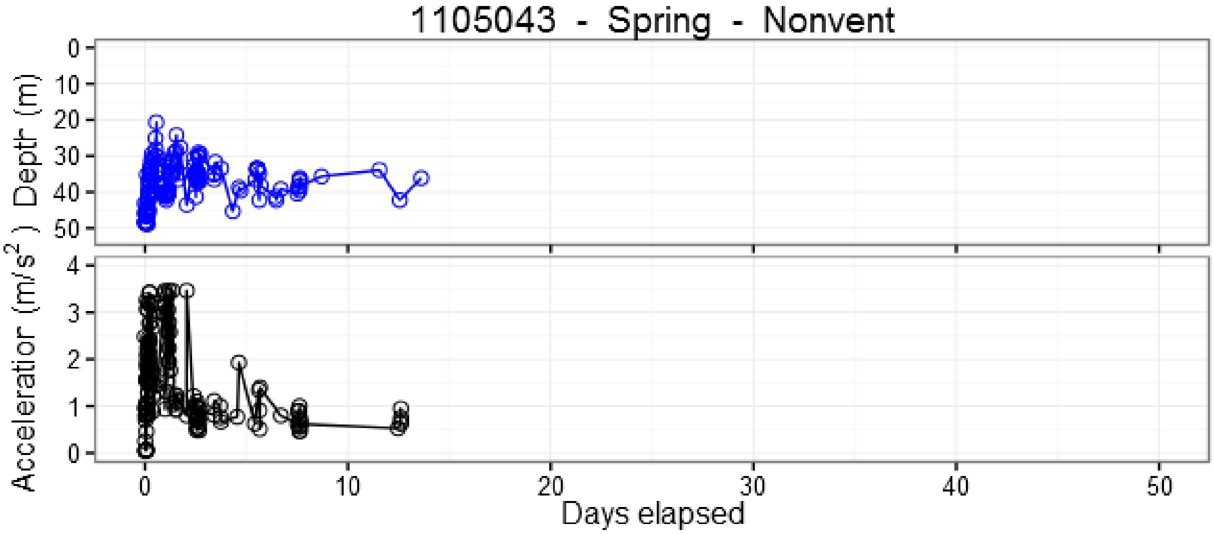
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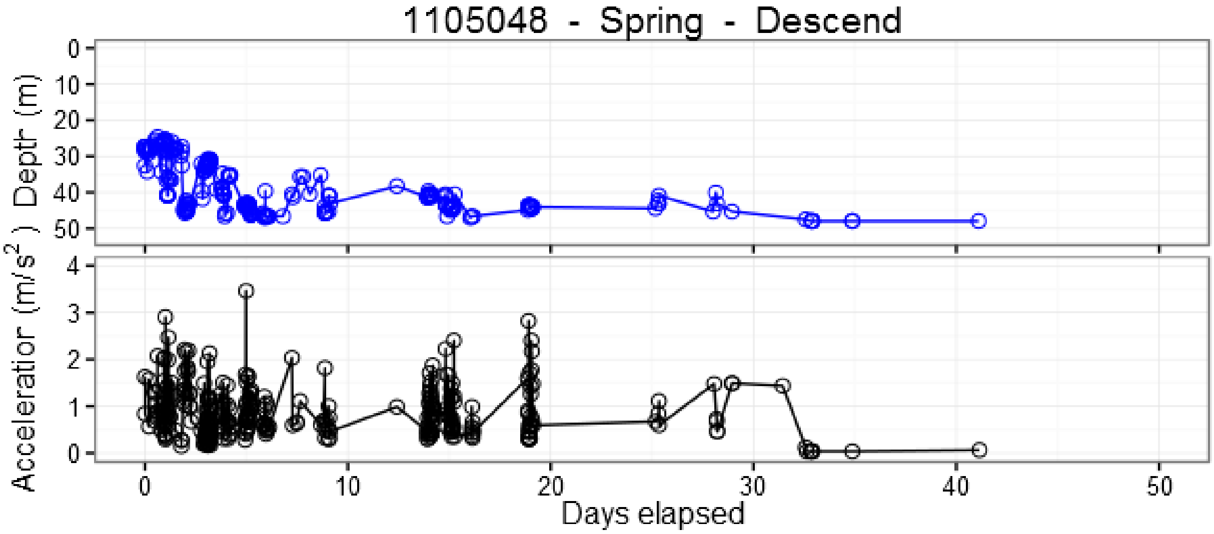
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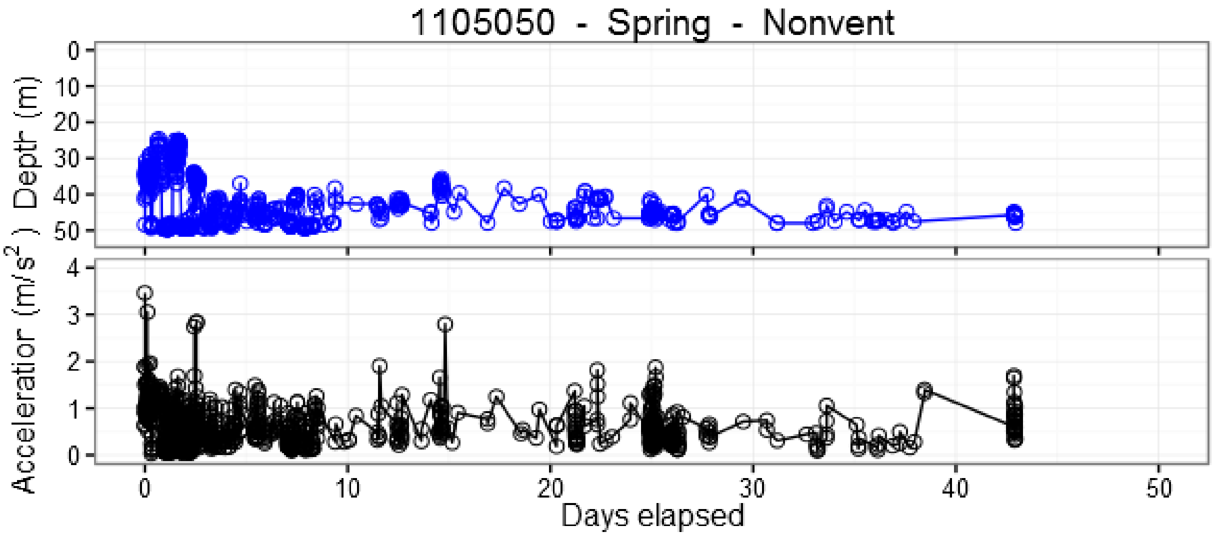
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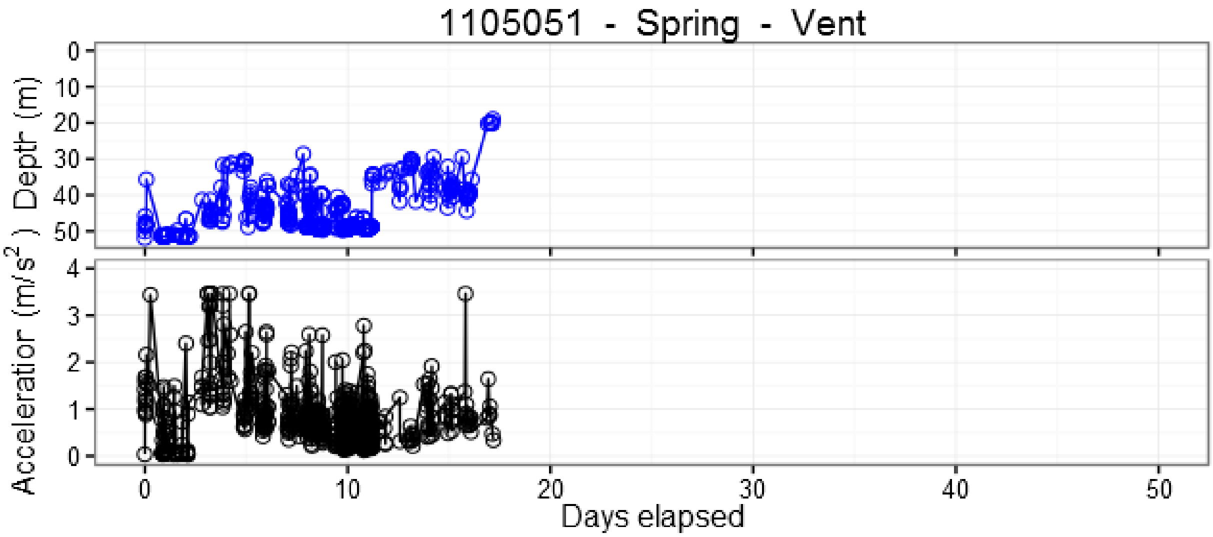
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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50
Acceleration (m/s^2)
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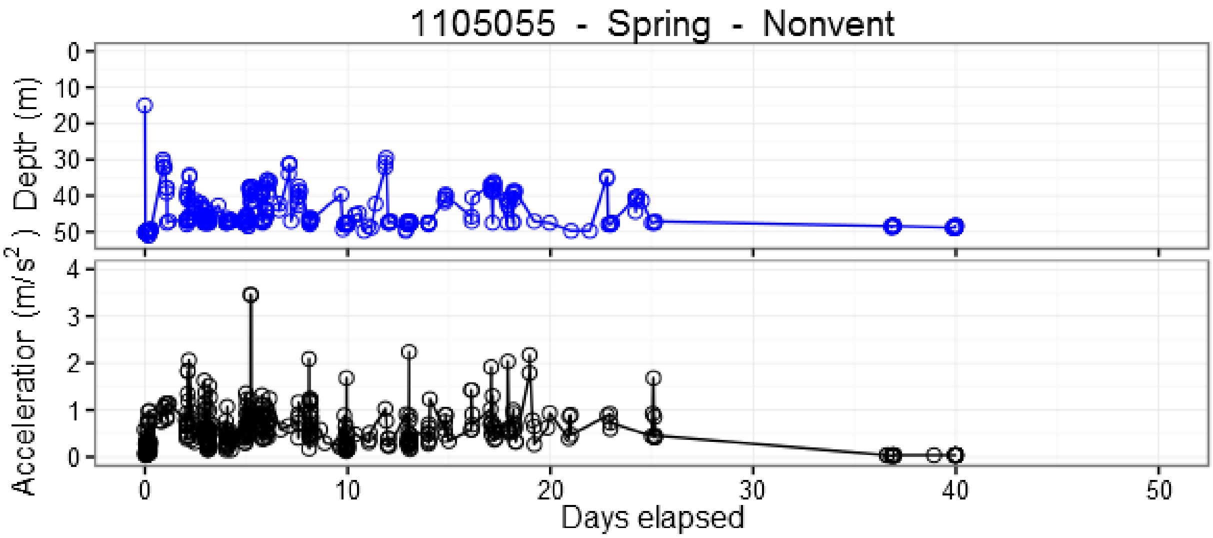
3
2
1
0
0
10
20
30
40
50
Days elapsed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20
30
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50
Acceleration (m/s^2)
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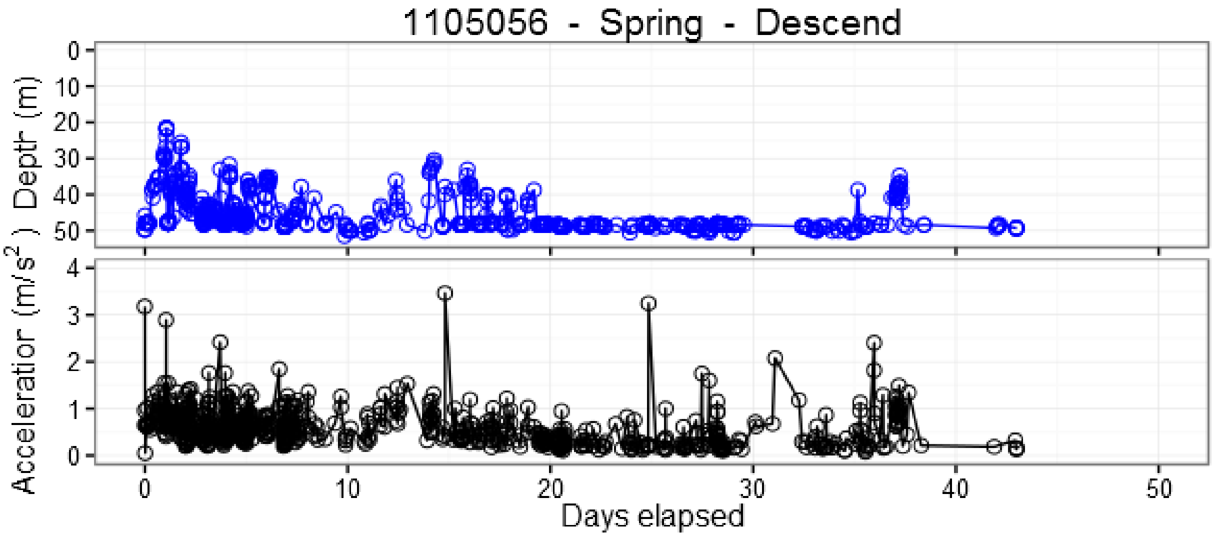
3
2
1
0
0
10
20
30
40
50
Days elapsed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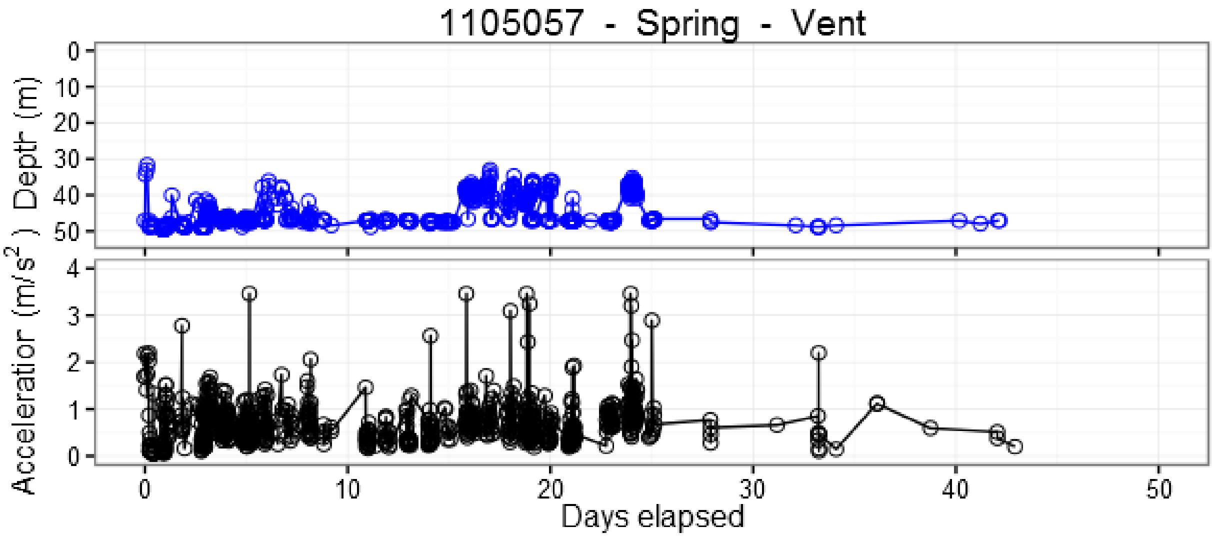
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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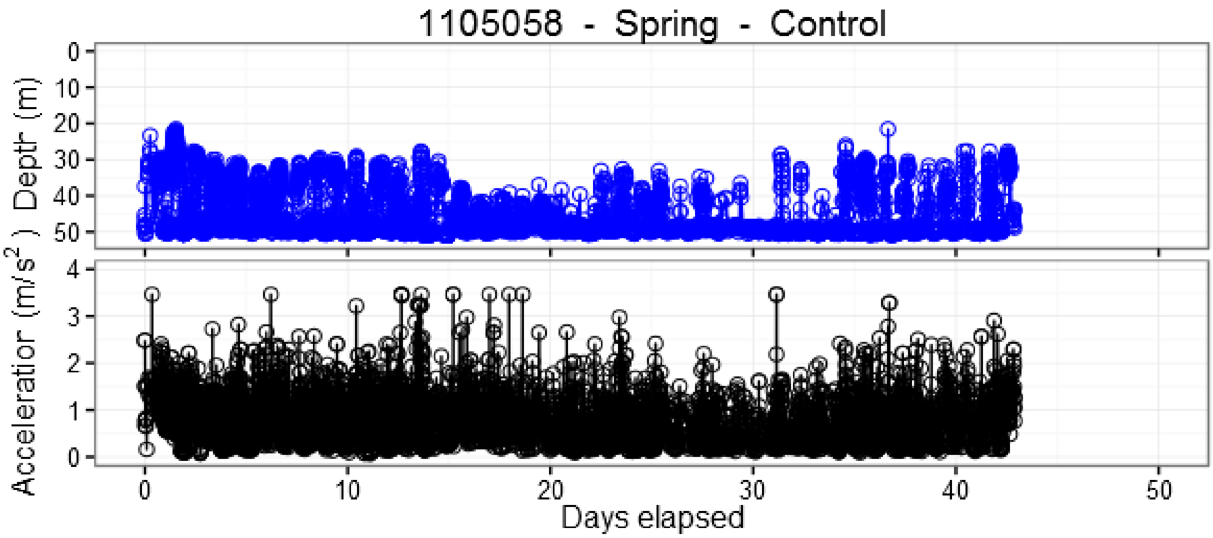
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed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Depth (m)
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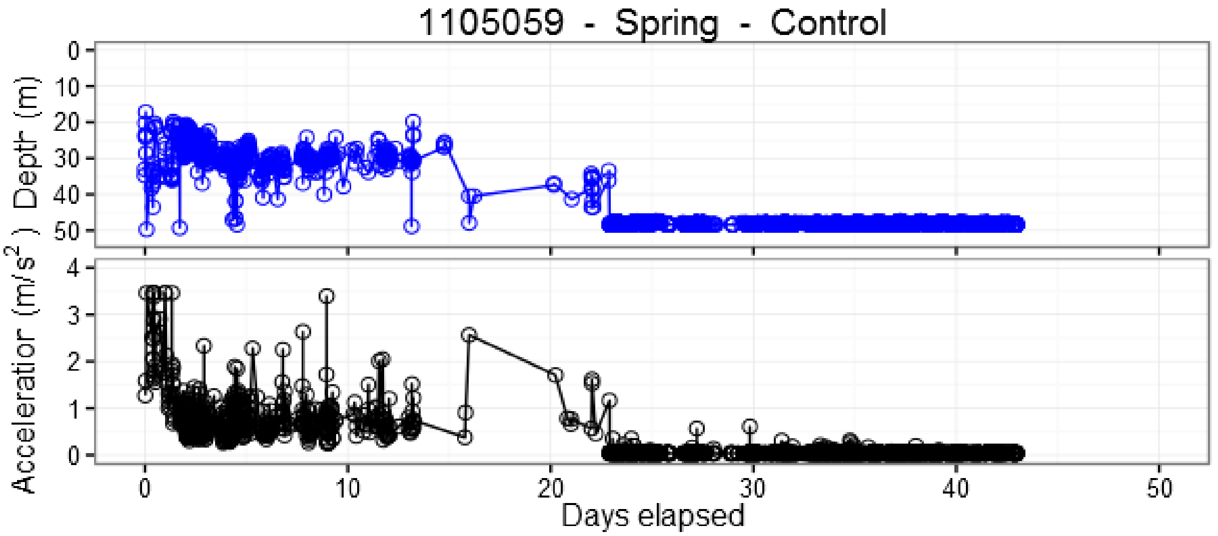
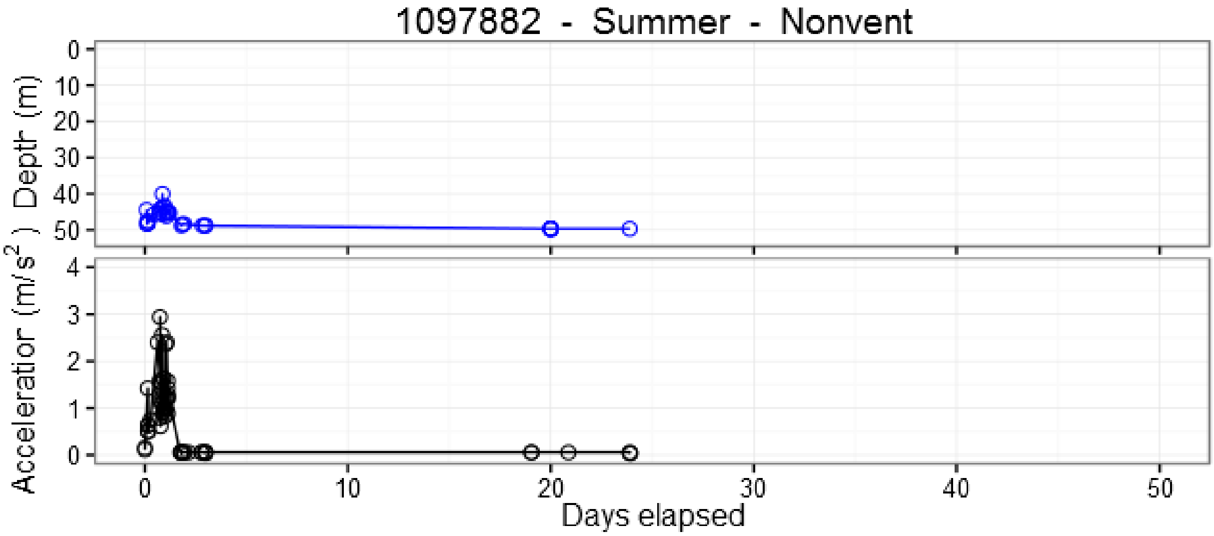
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

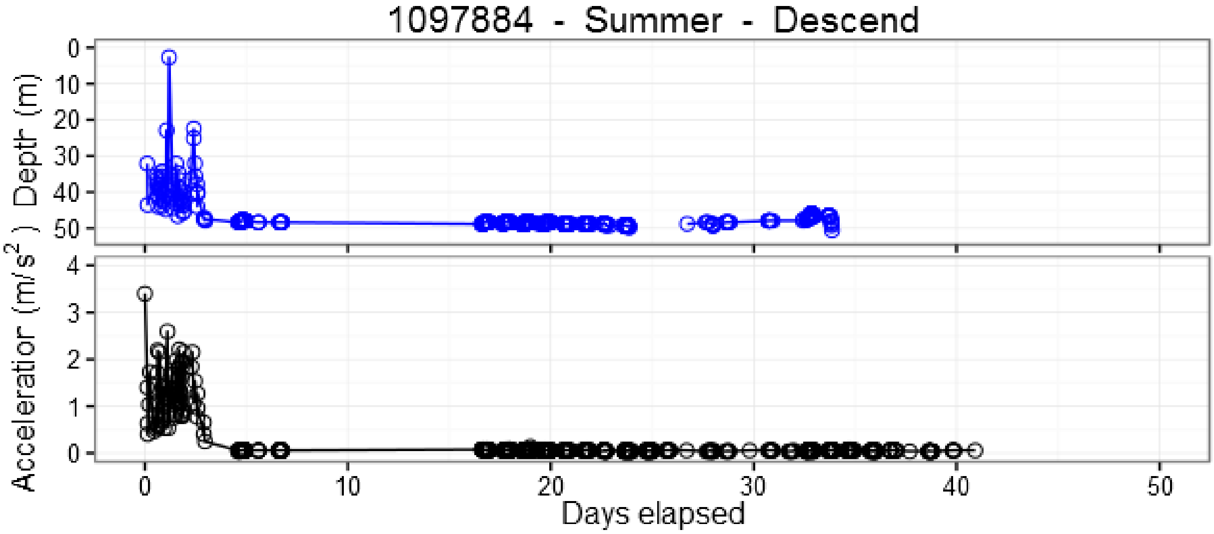

1105059 - Spring - Control
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

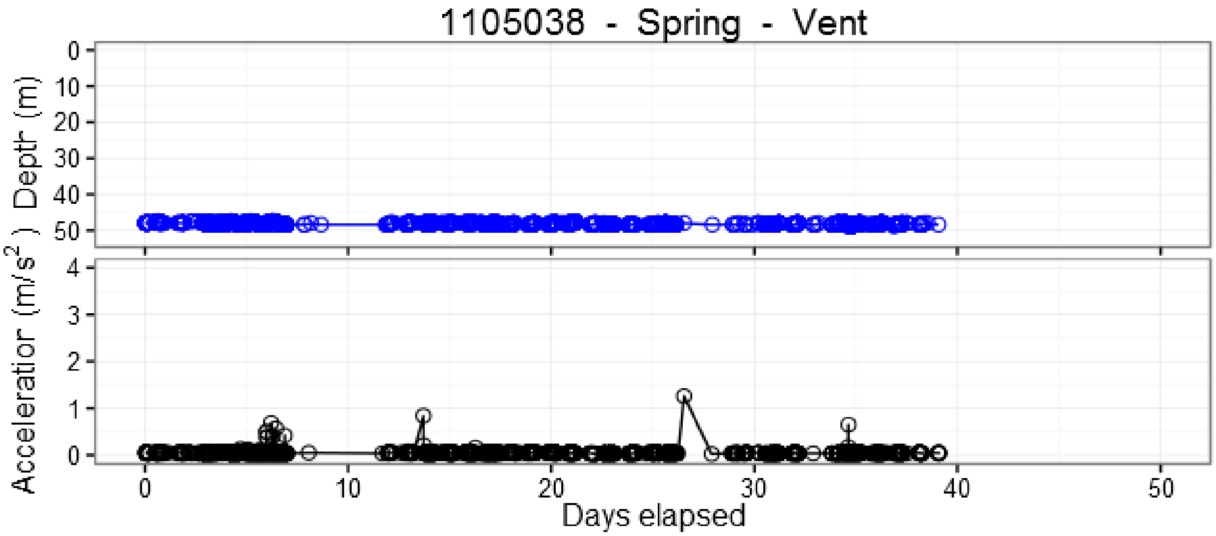

1105061 - Spring - Descend
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

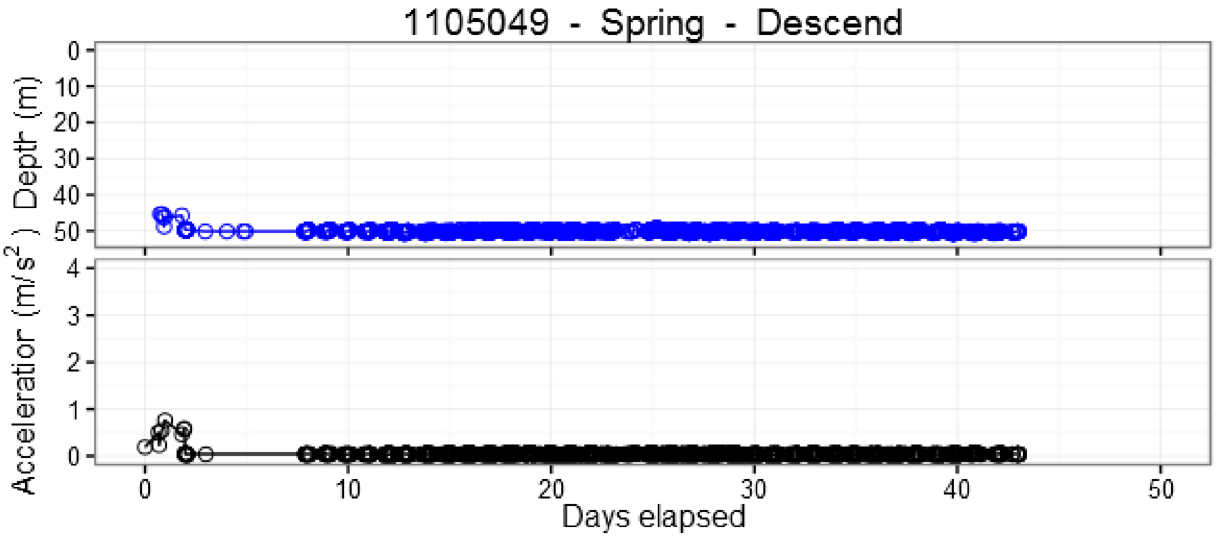
APPENDIX B: DELAYED MORTALITIES

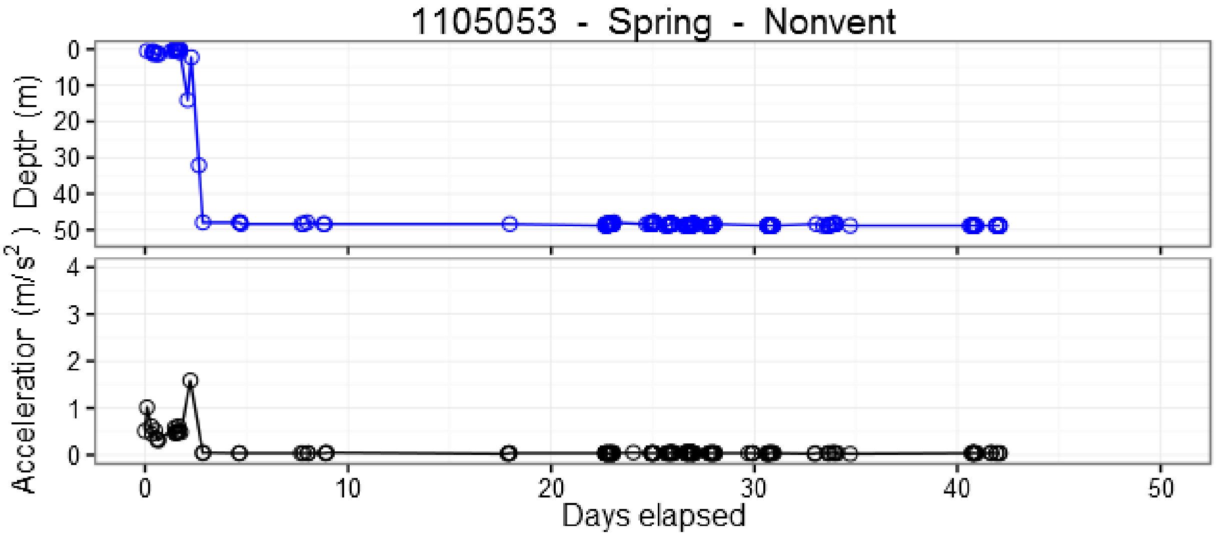
ACCELERATION AND DEPTH PROFILES OF ACOUSTIC DETECTIONS

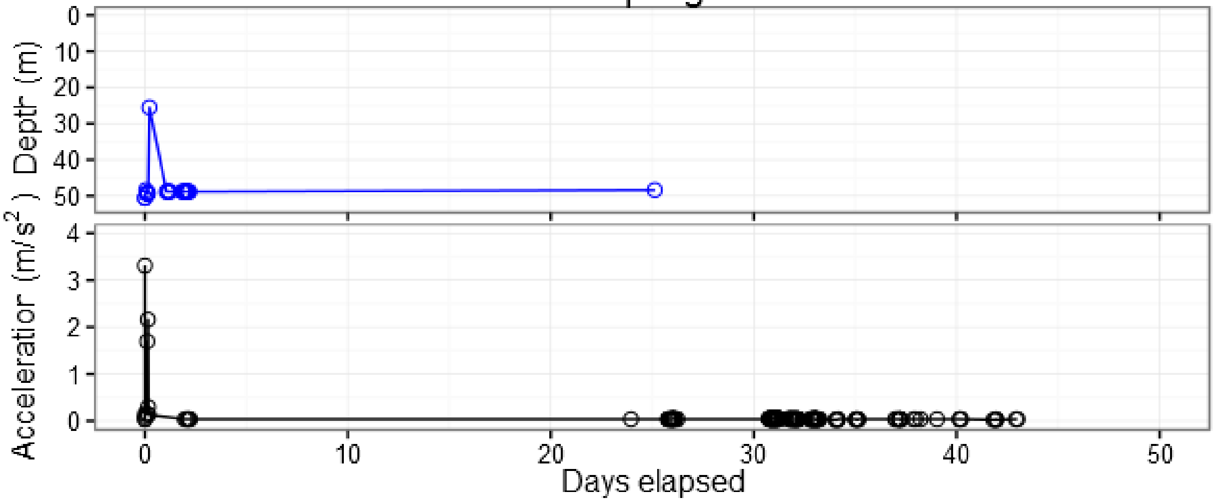




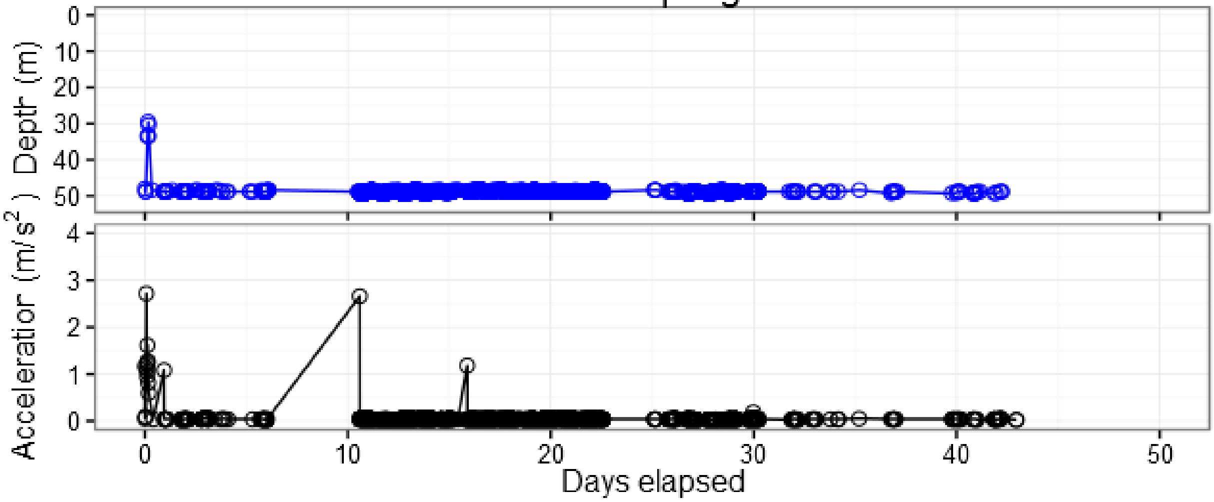

1105038 - Spring - Vent
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed


1105049 - Spring - Descend
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

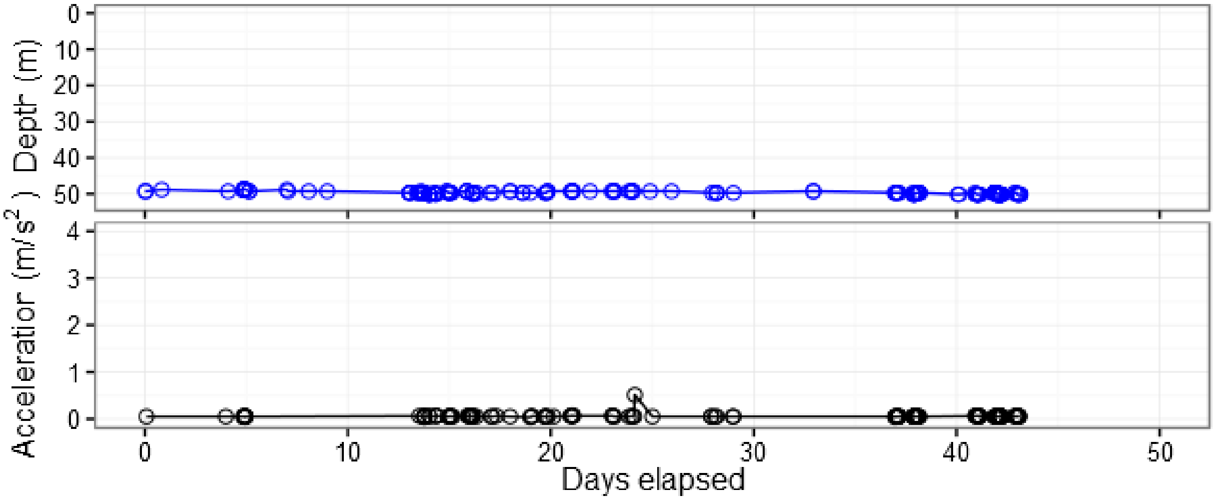

1105053 - Spring - Nonvent
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed



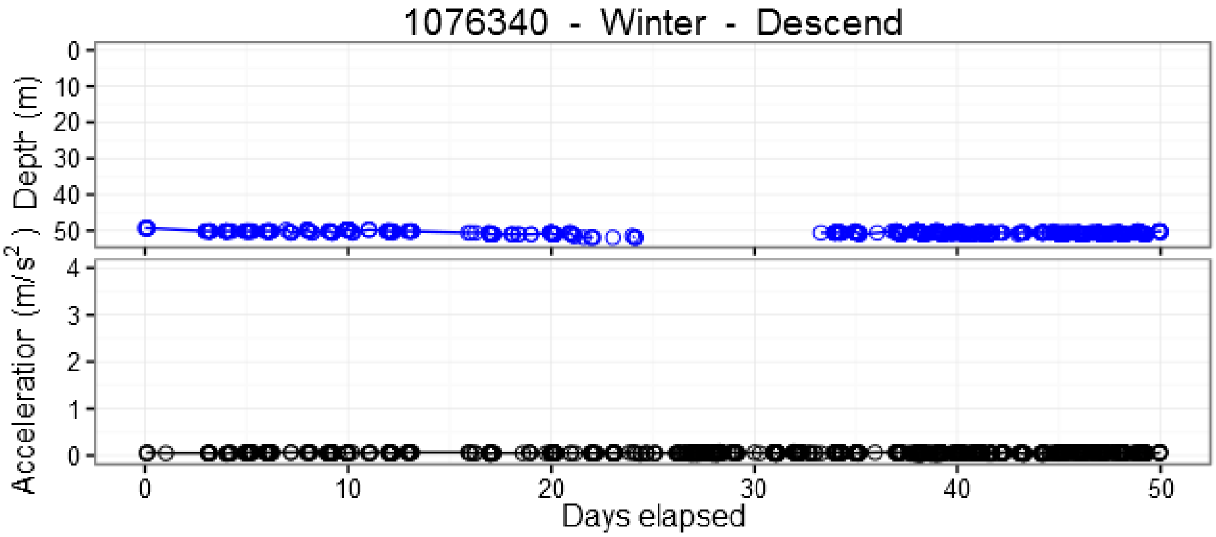
1105060 - Spring - Descend

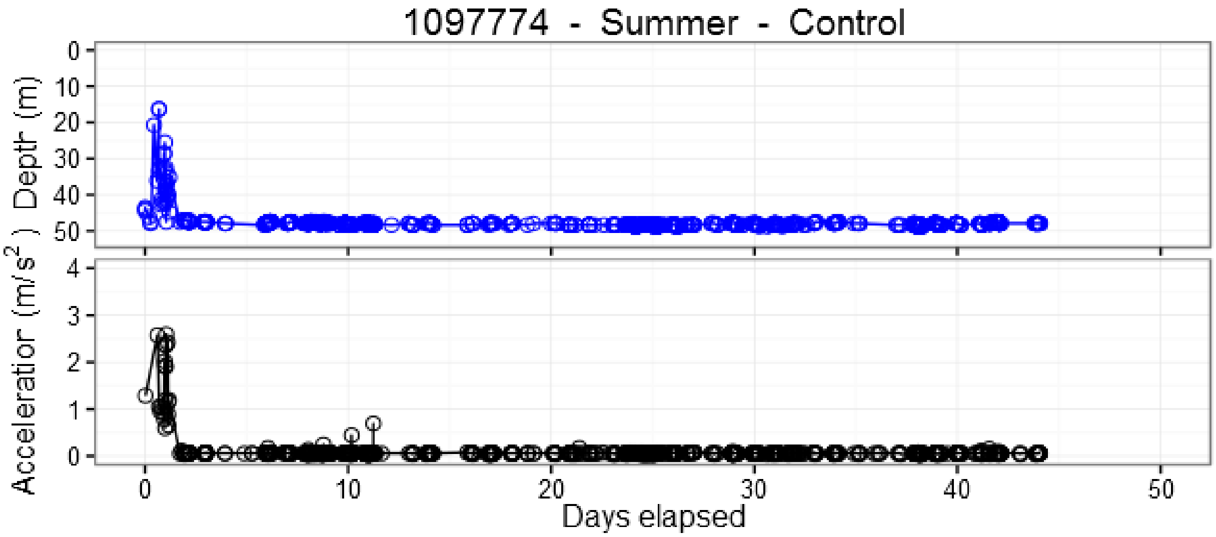


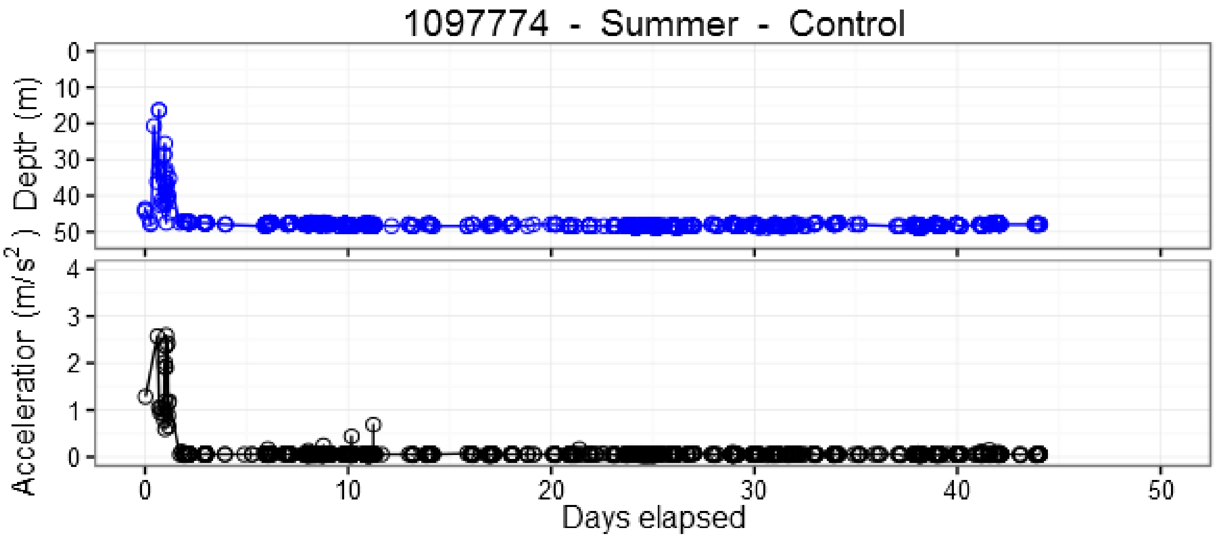
1105065 - Spring - Vent



1076335 - Winter - Descend

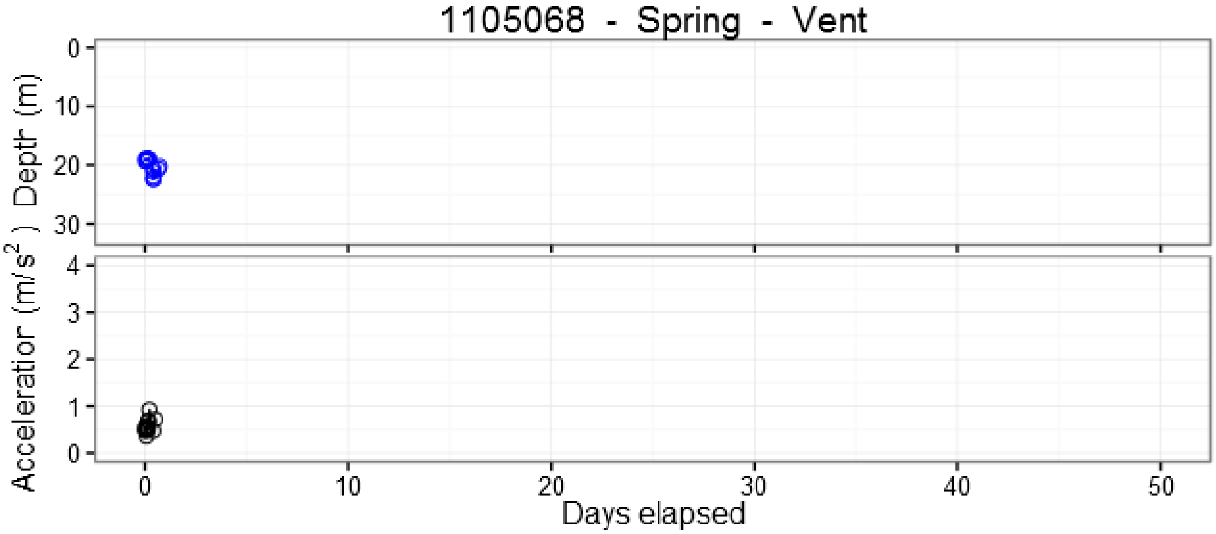

1076340 - Winter - Descend
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed


1097774 - Summer - Control
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

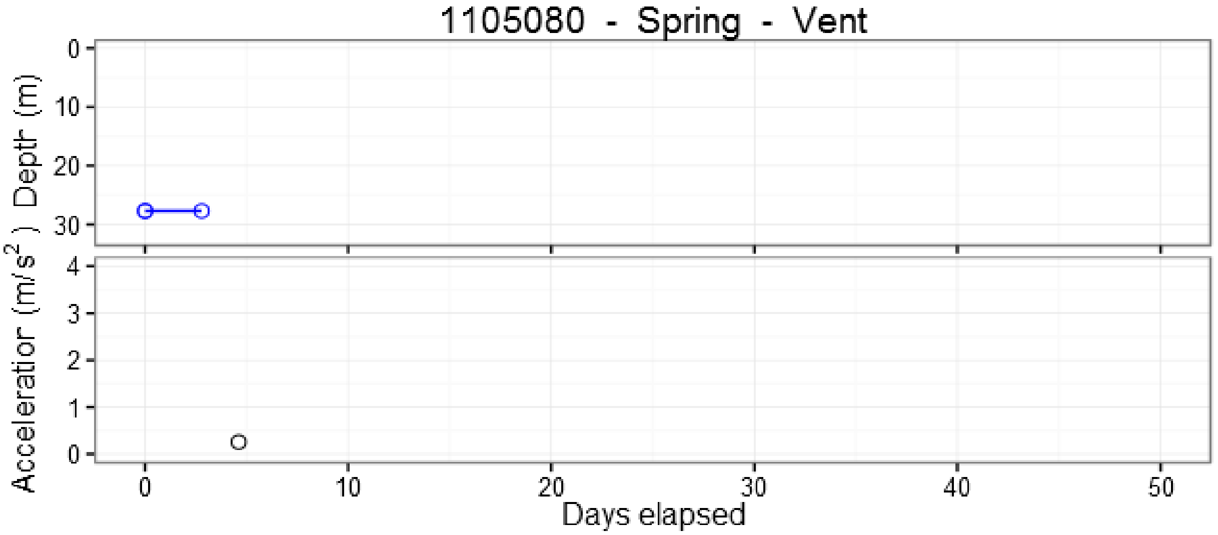

1097774 - Summer - Control
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

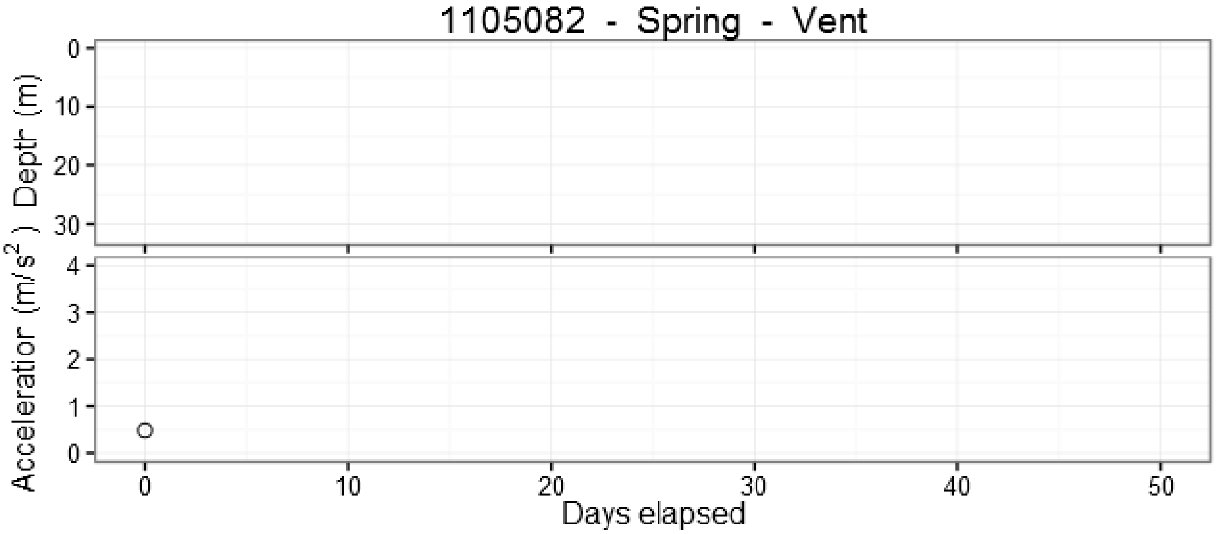
APPENDIX C: UNKNOWNS

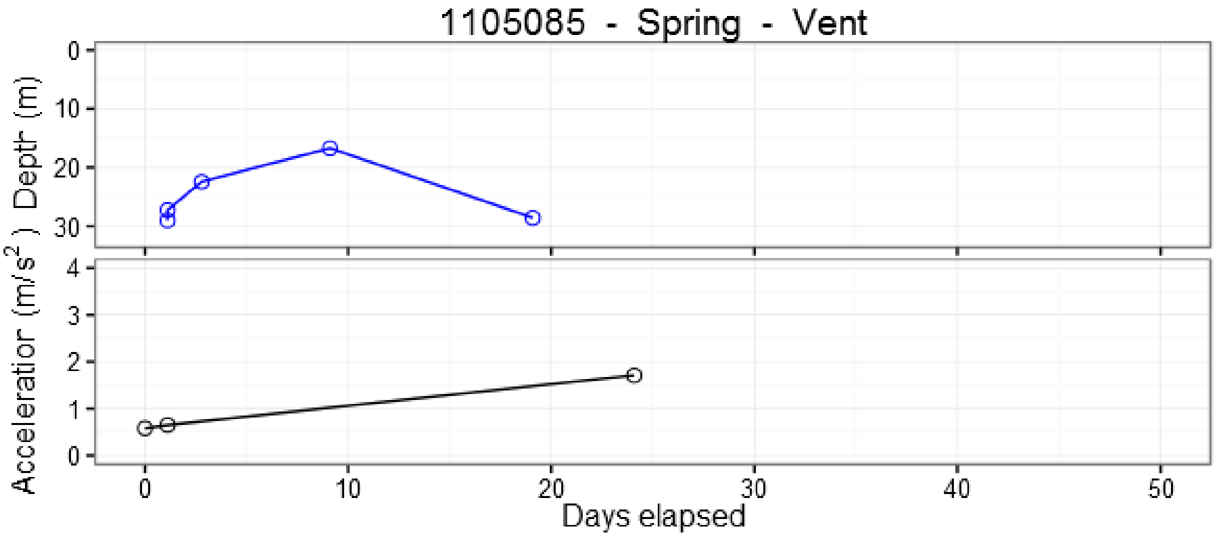
ACCELERATION AND DEPTH PROFILES OF ACOUSTIC DETECTIONS

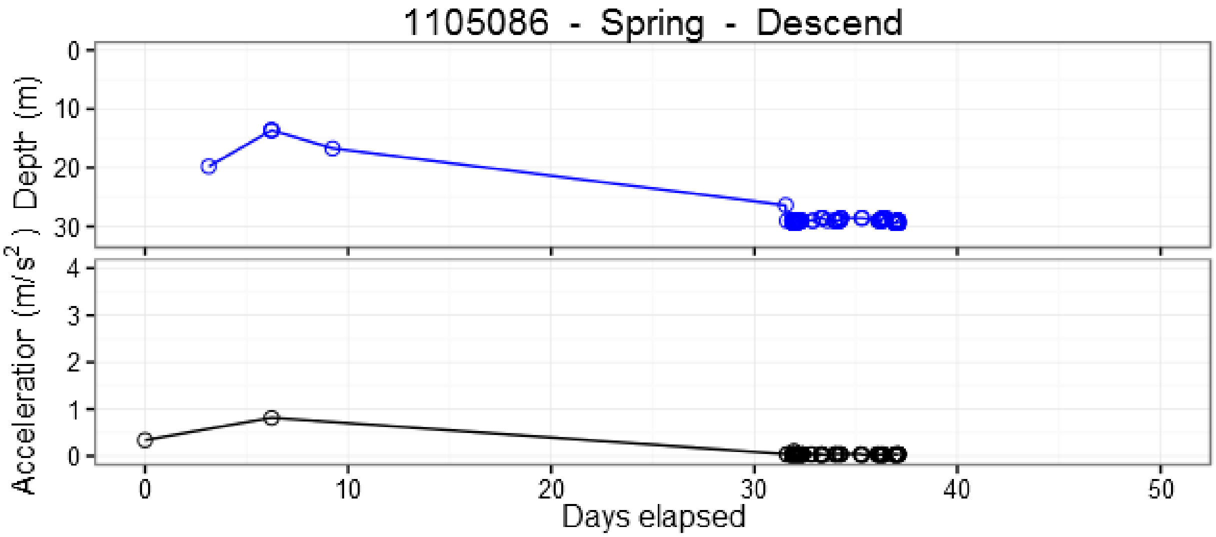


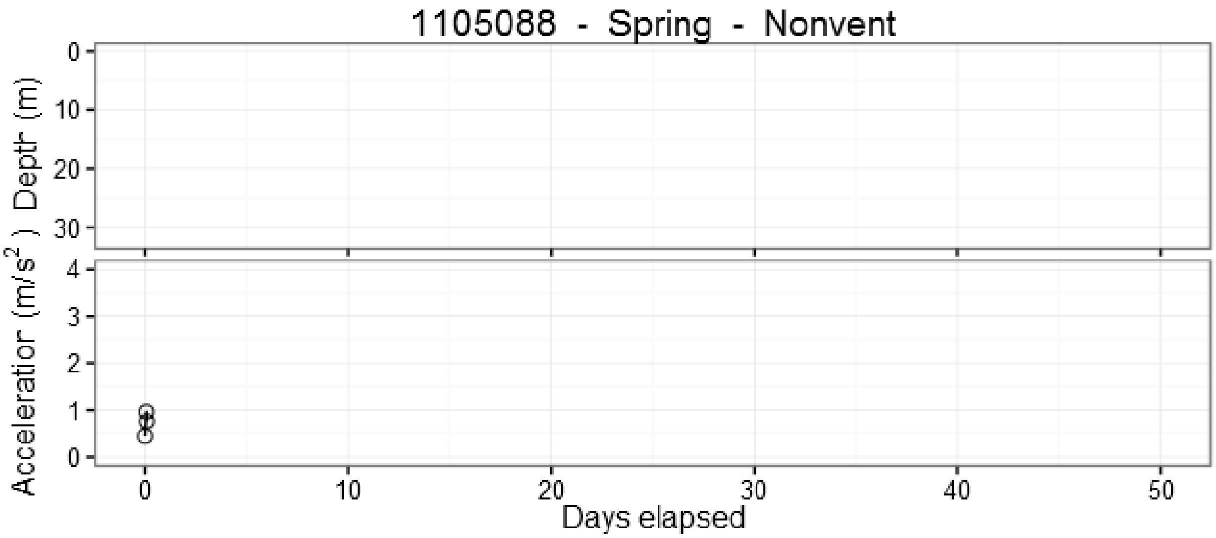

1105073 - Spring - Control

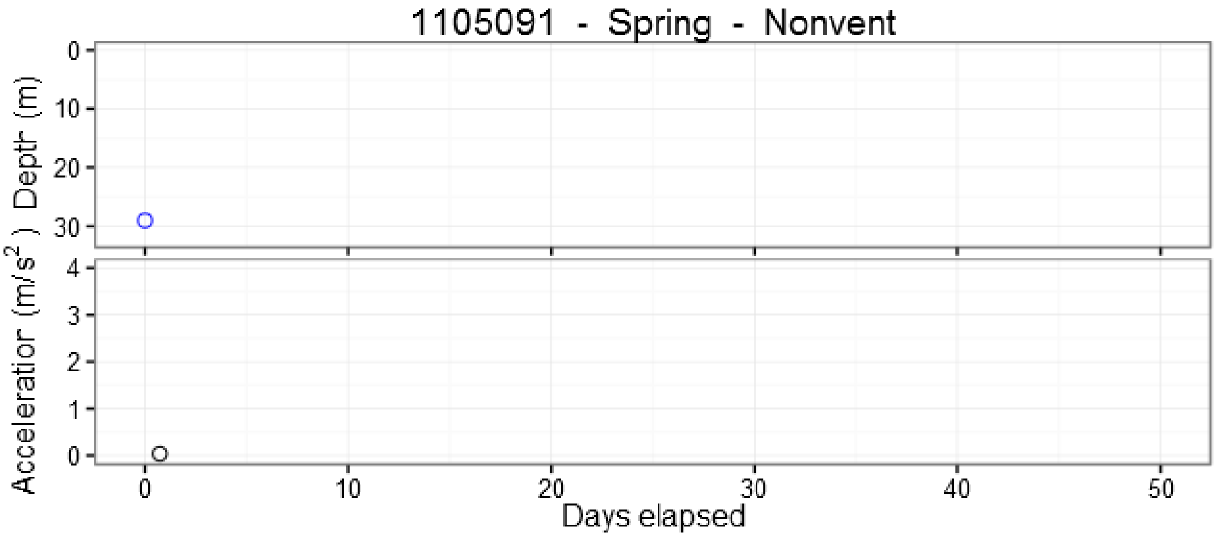

1105080 - Spring - Vent

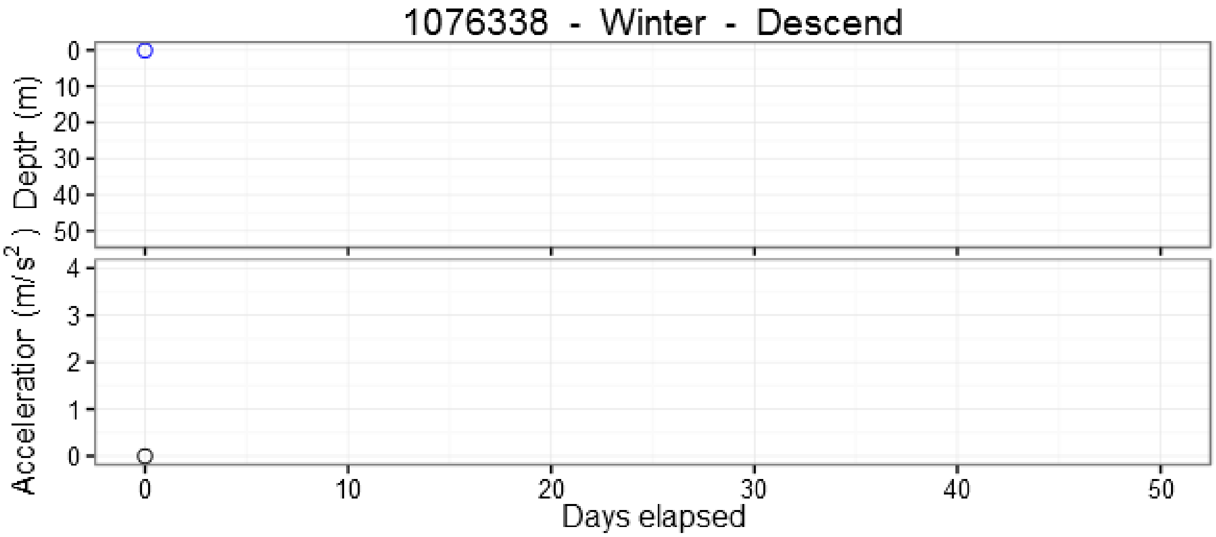

1105082 - Spring - Vent

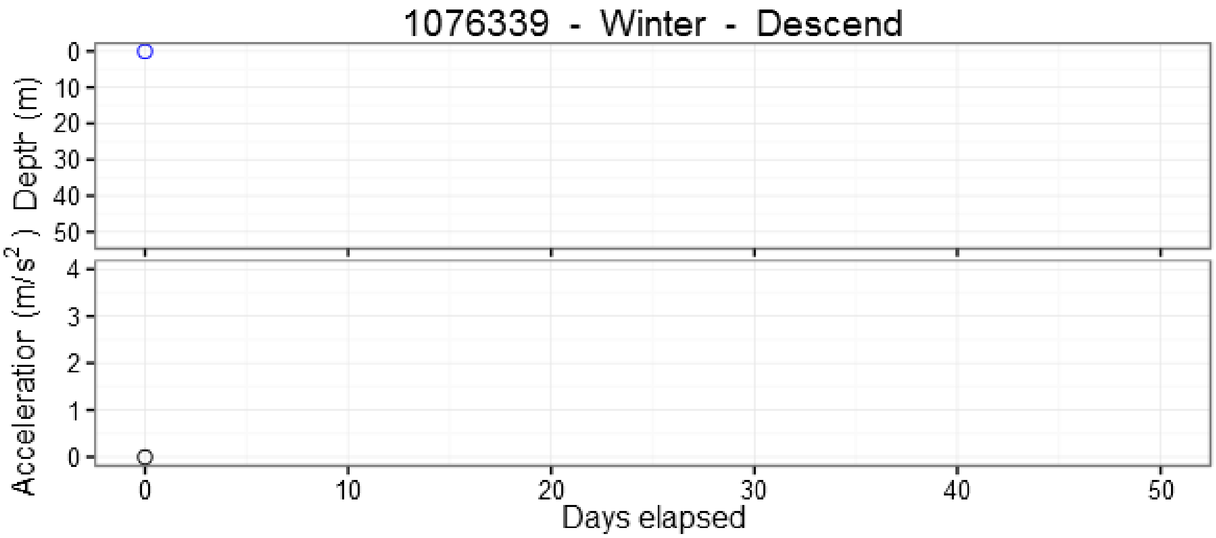

1105085 - Spring - Vent

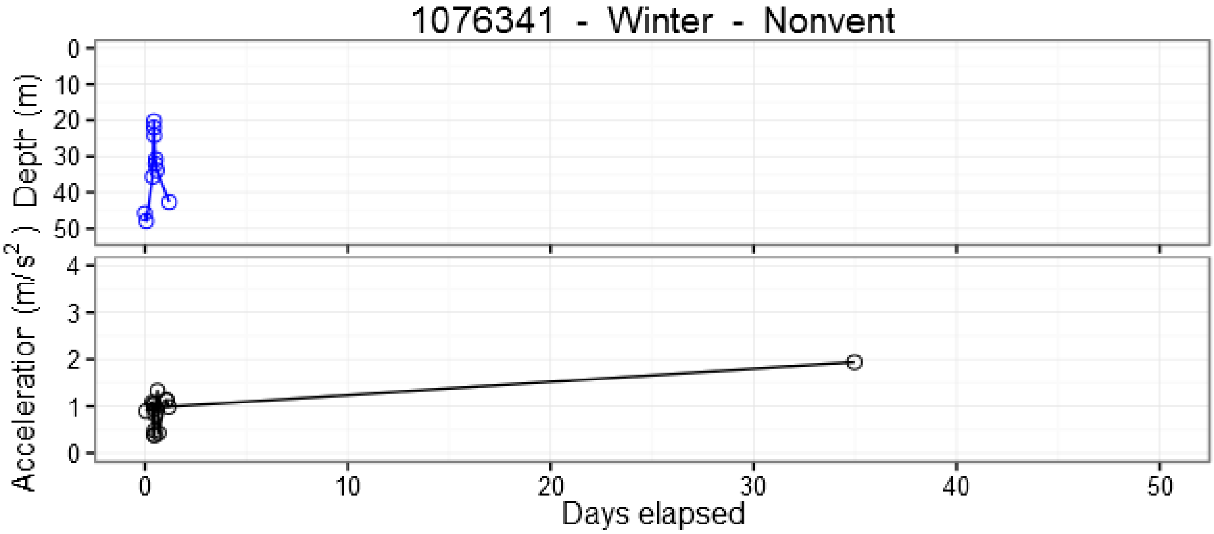

1105086 - Spring - Descend

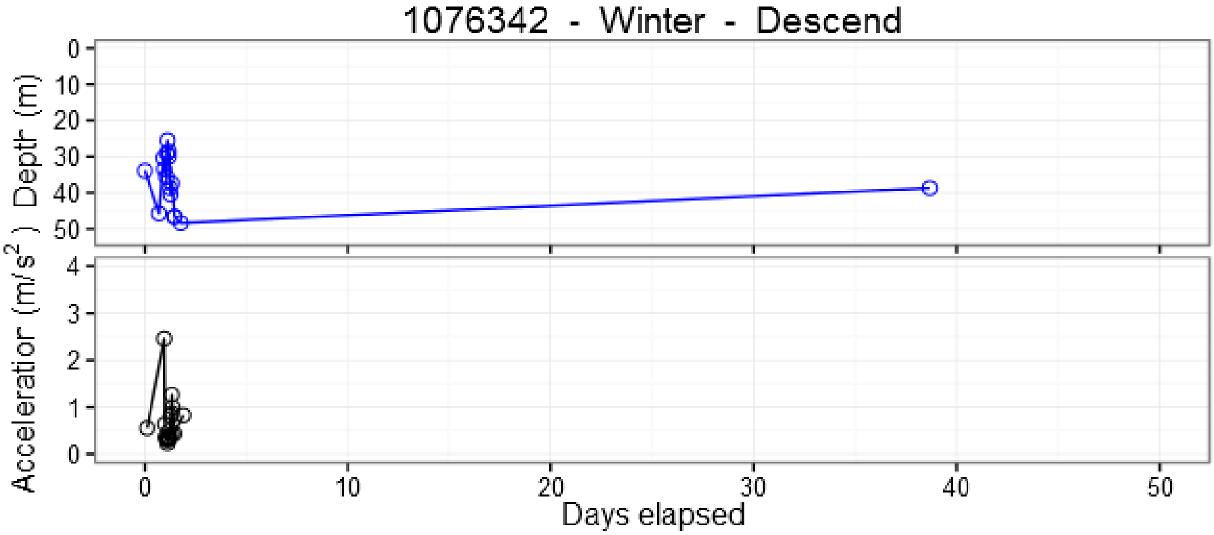

1105088 - Spring - Nonvent

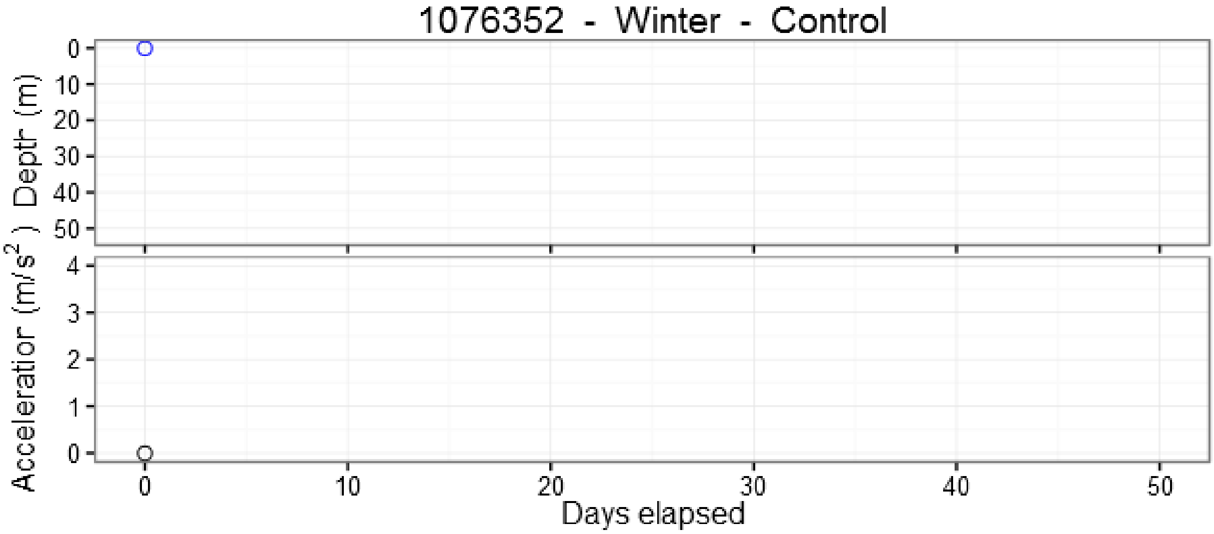

1105091 - Spring - Nonvent

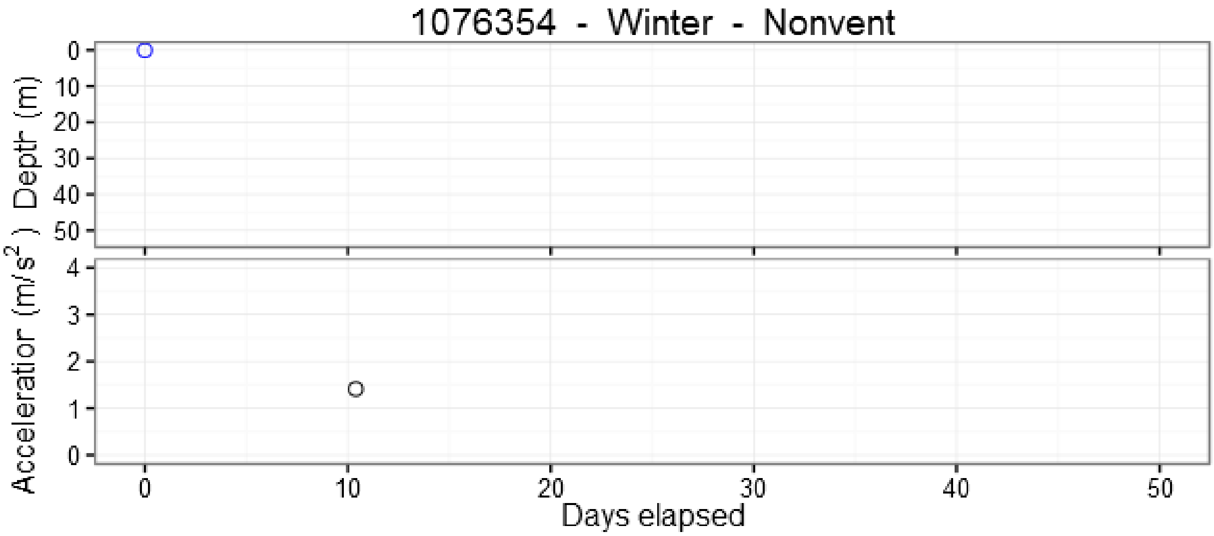

1076338 - Winter - Descend

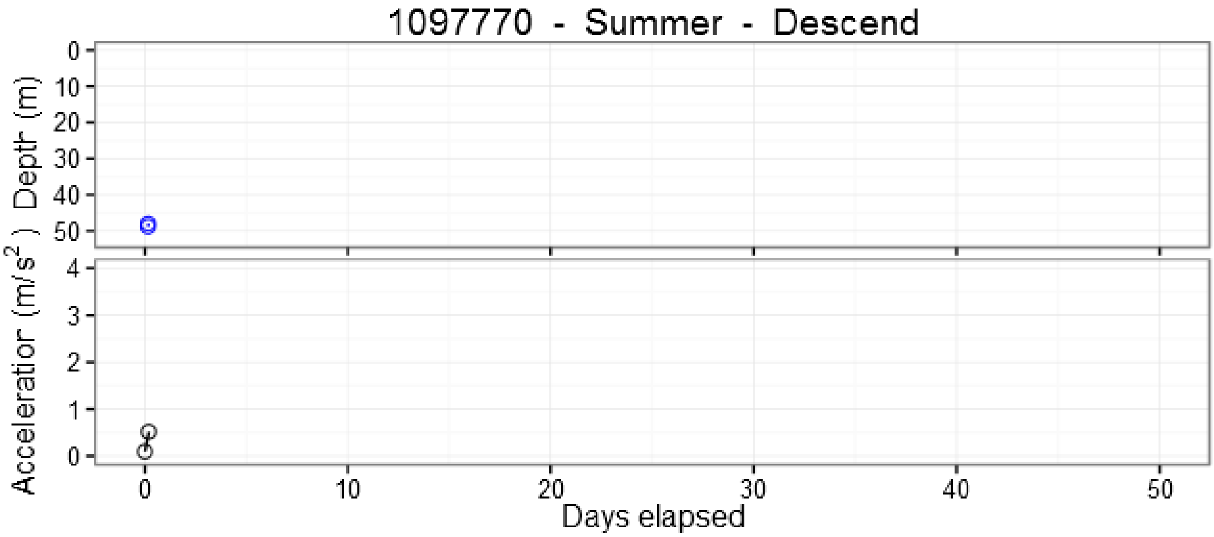

1076339 - Winter - Descend

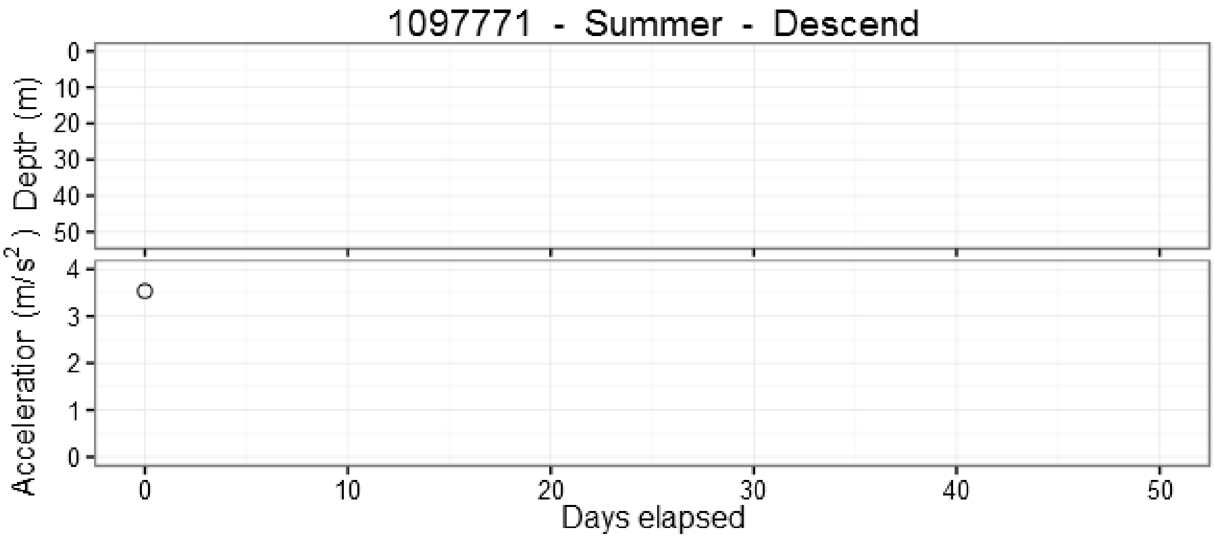

1076341 - Winter - Nonvent

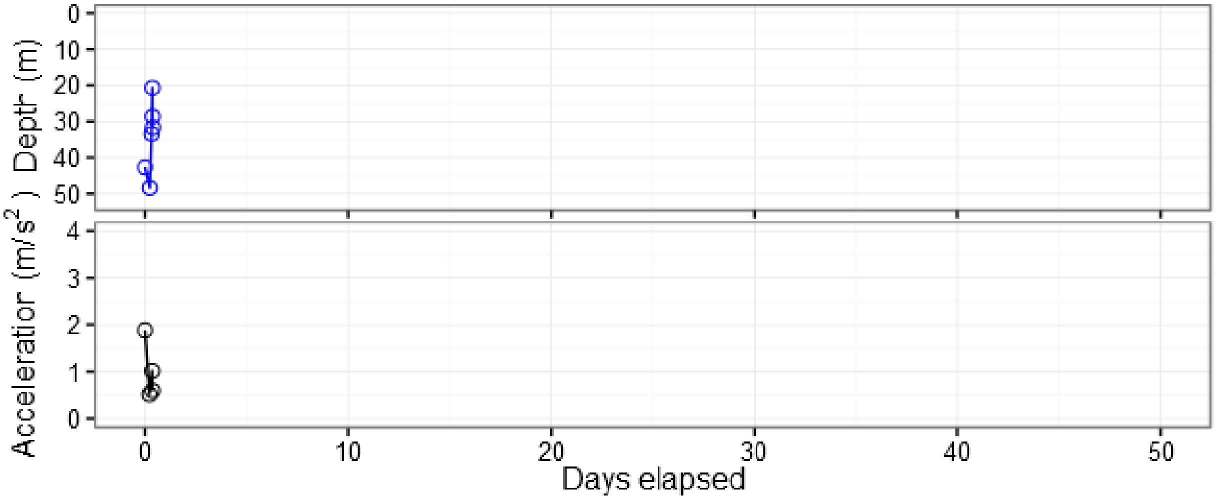

1076342 - Winter - Descend


1076352 - Winter - Control

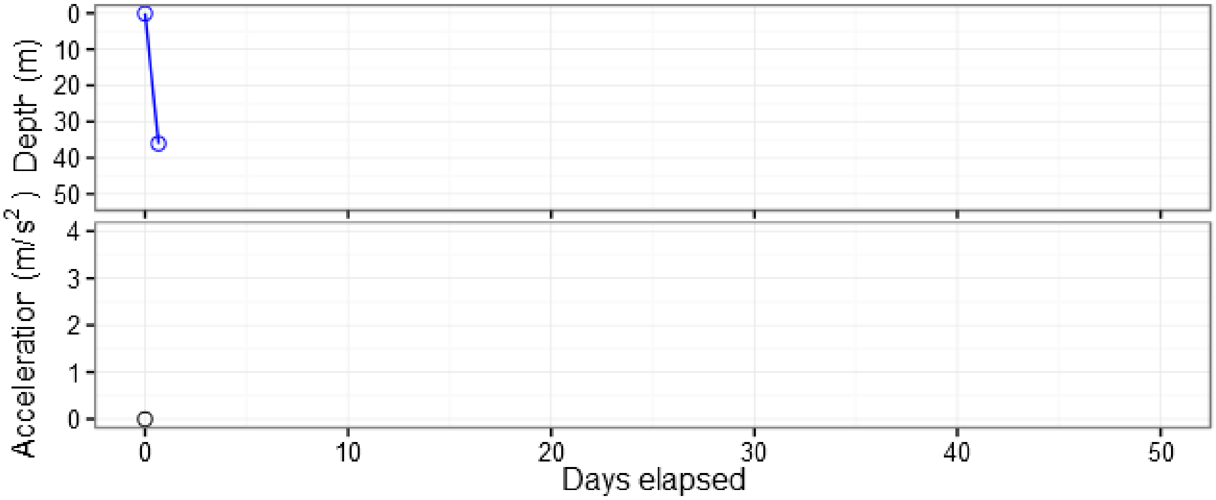

1076354 - Winter - Nonvent
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed


1097770 - Summer - Descend
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

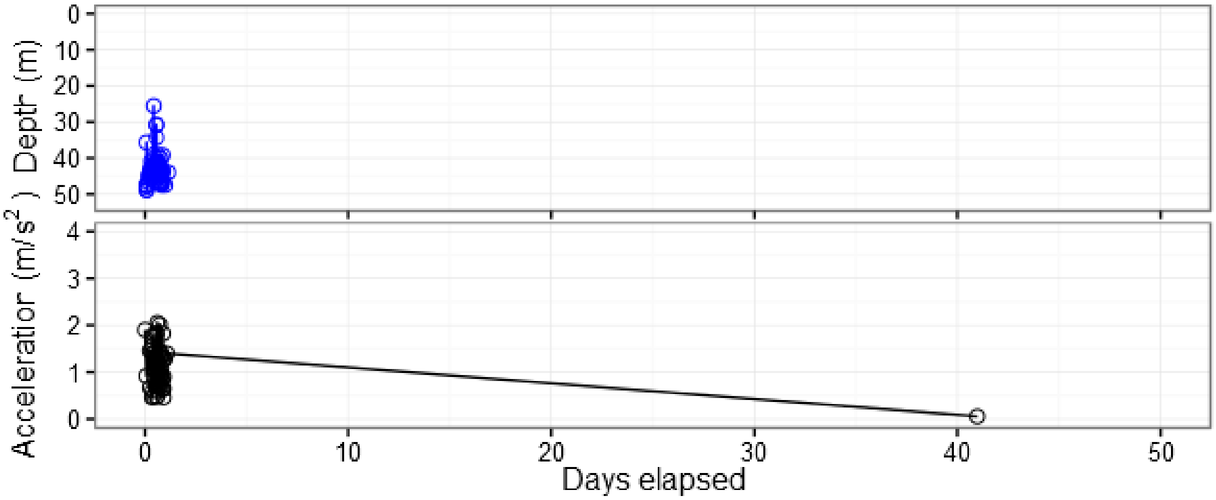

1097771 - Summer - Descend
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed



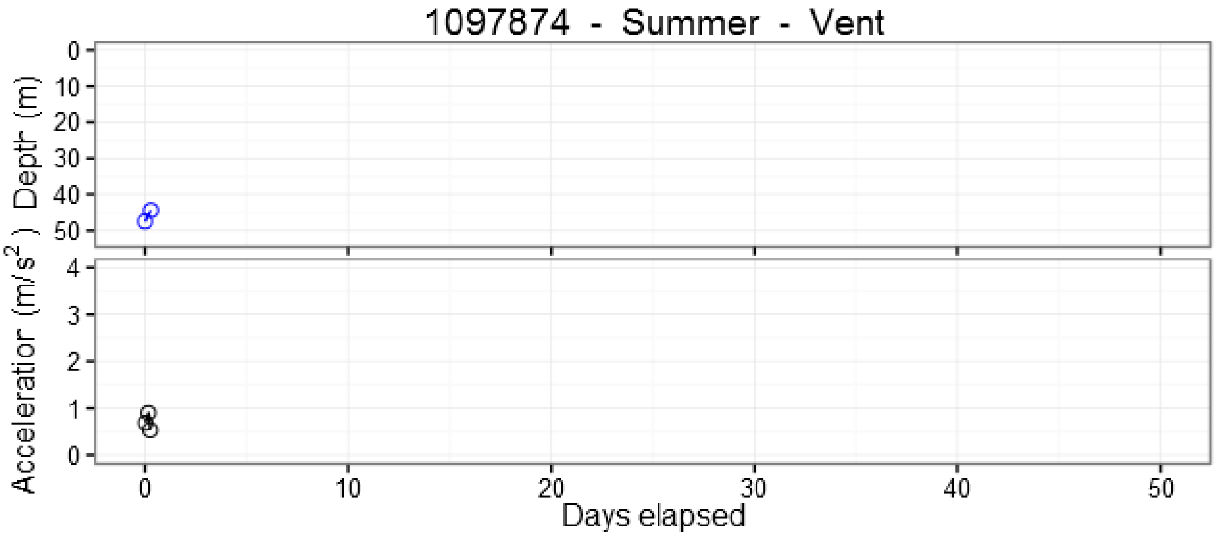
1097773 - Summer - Control

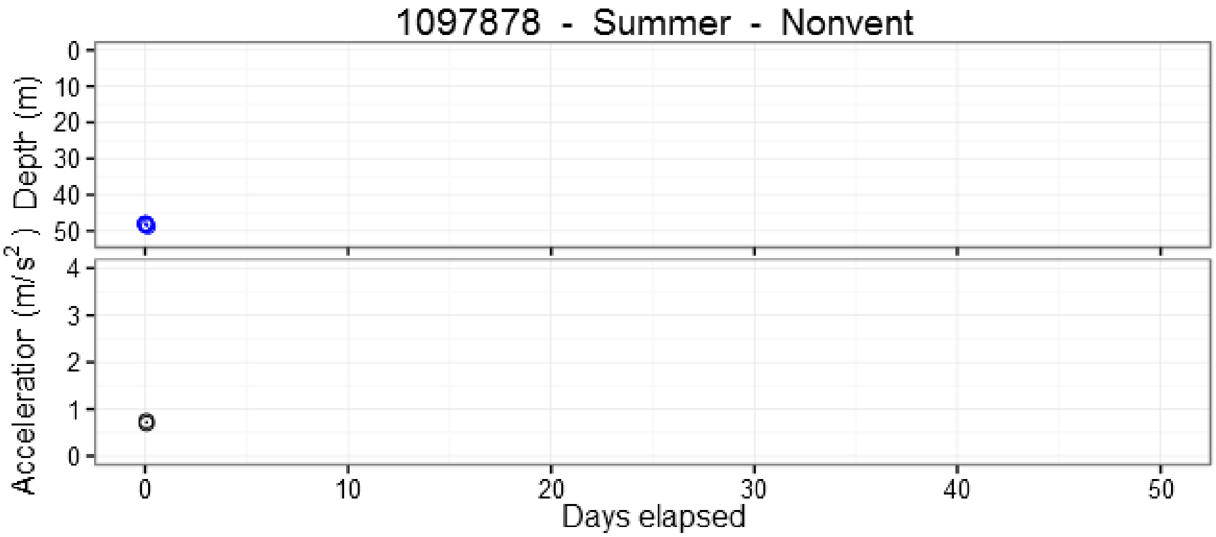


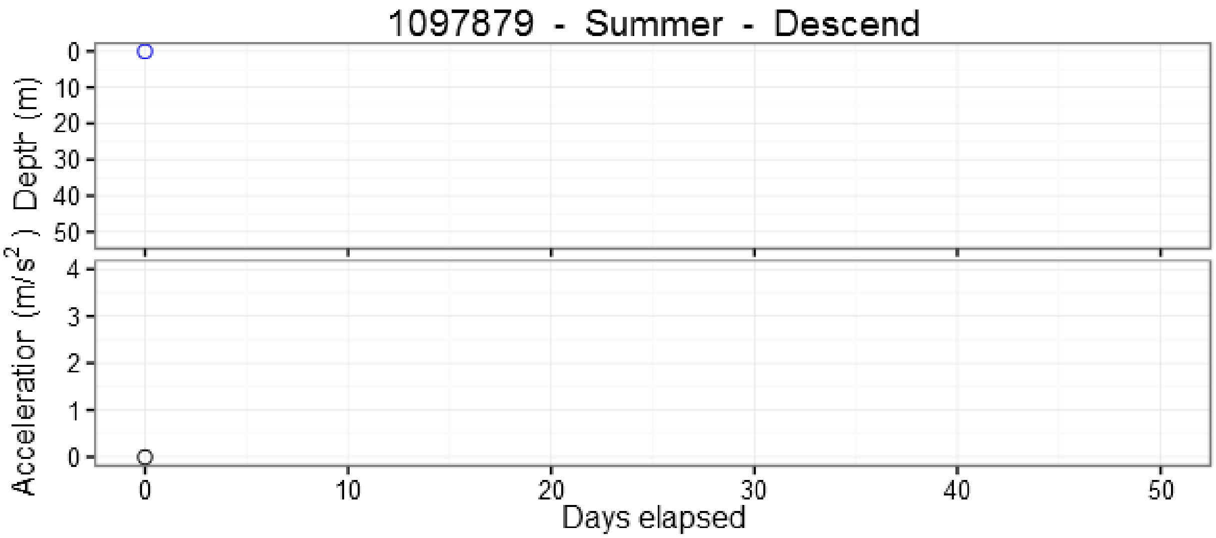
1097870 - Summer - Vent

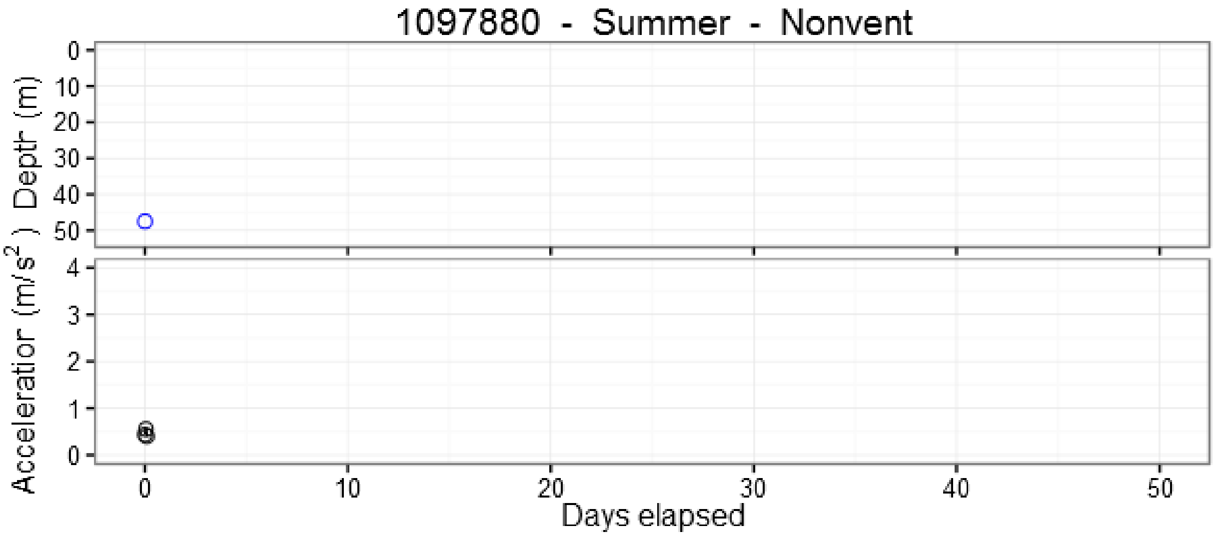


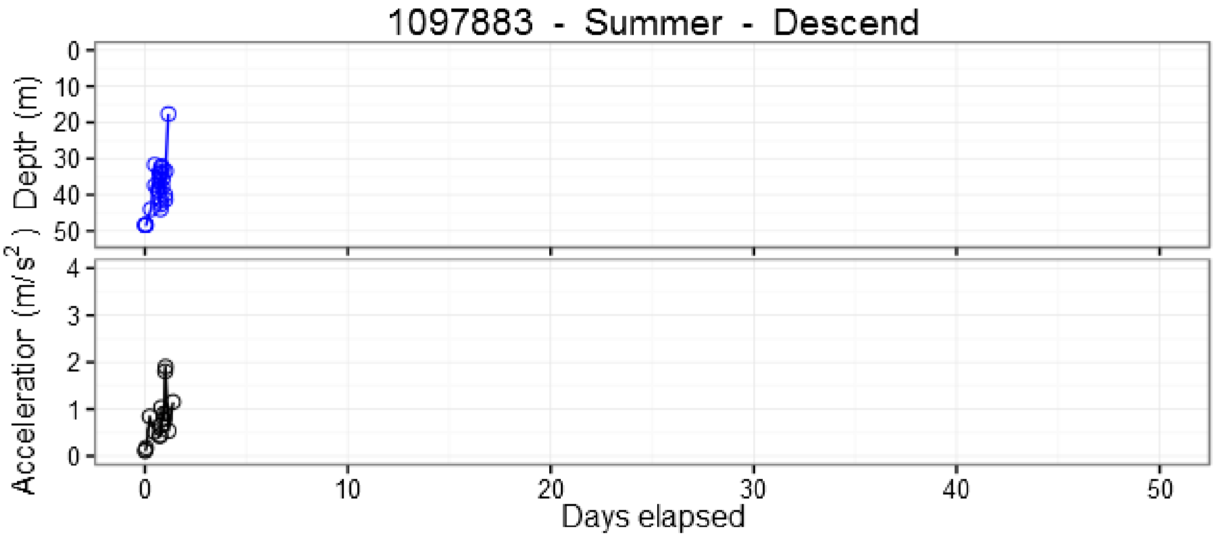
1097871 - Summer - Nonvent

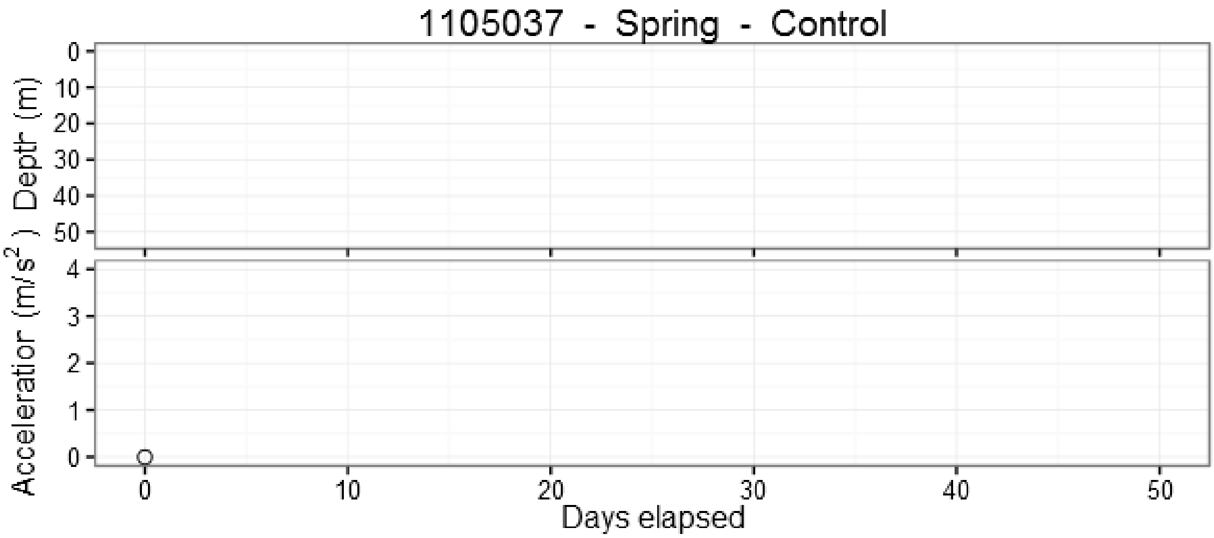

1097874 - Summer - Vent
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

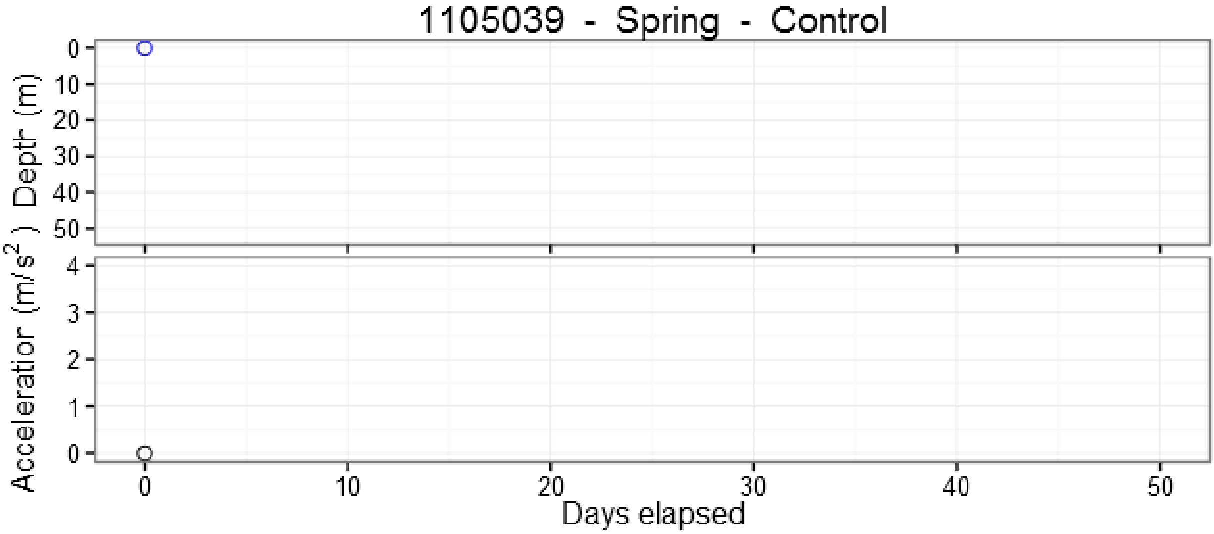

1097878 - Summer - Nonvent
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

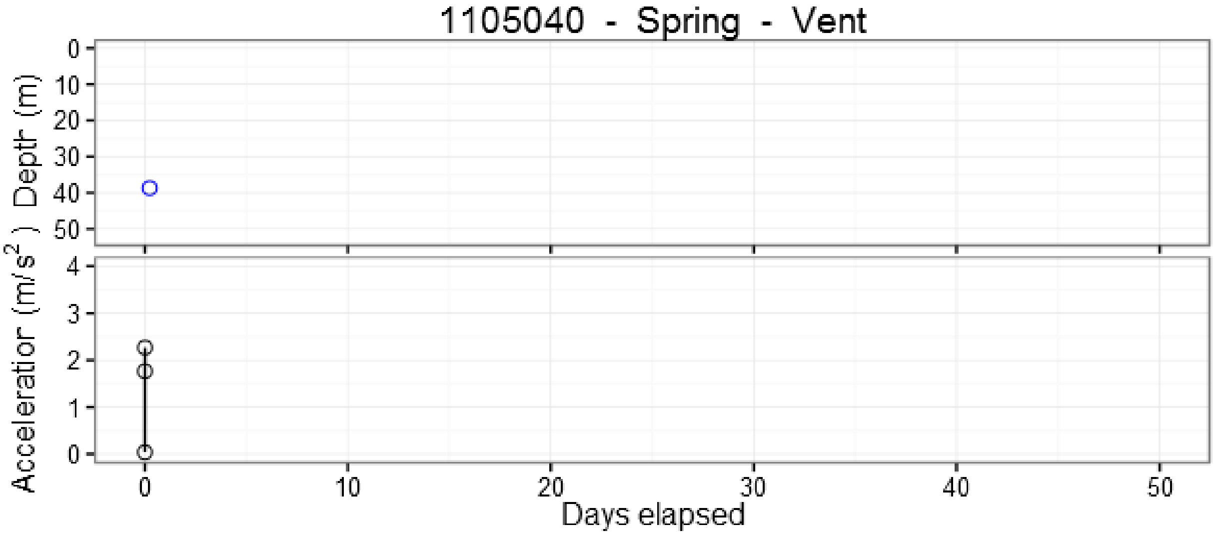

1097879 - Summer - Descend
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed

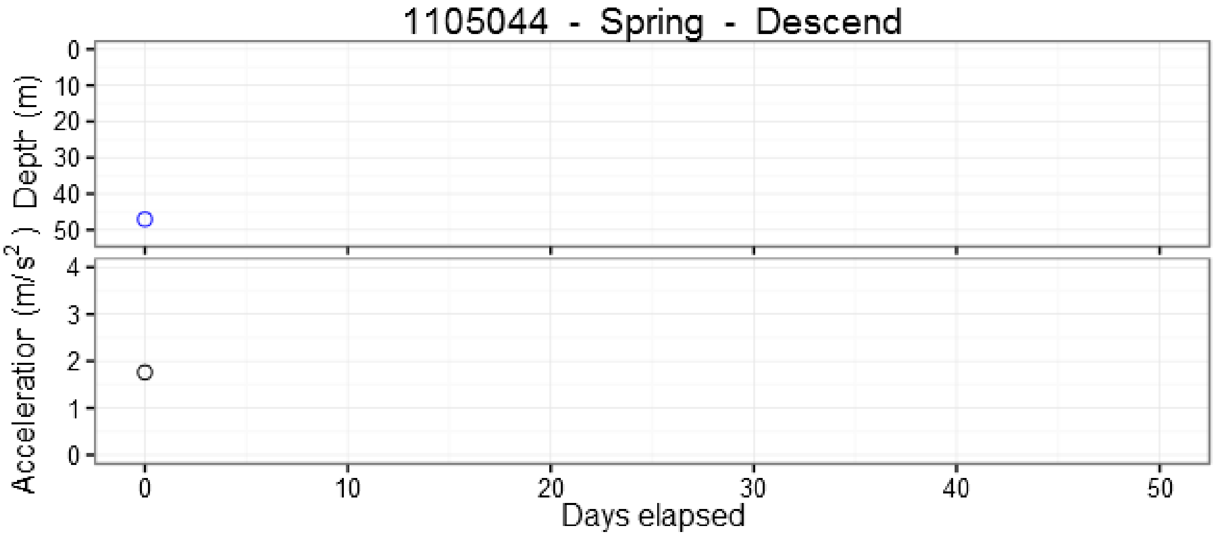

1097880 - Summer - Nonvent

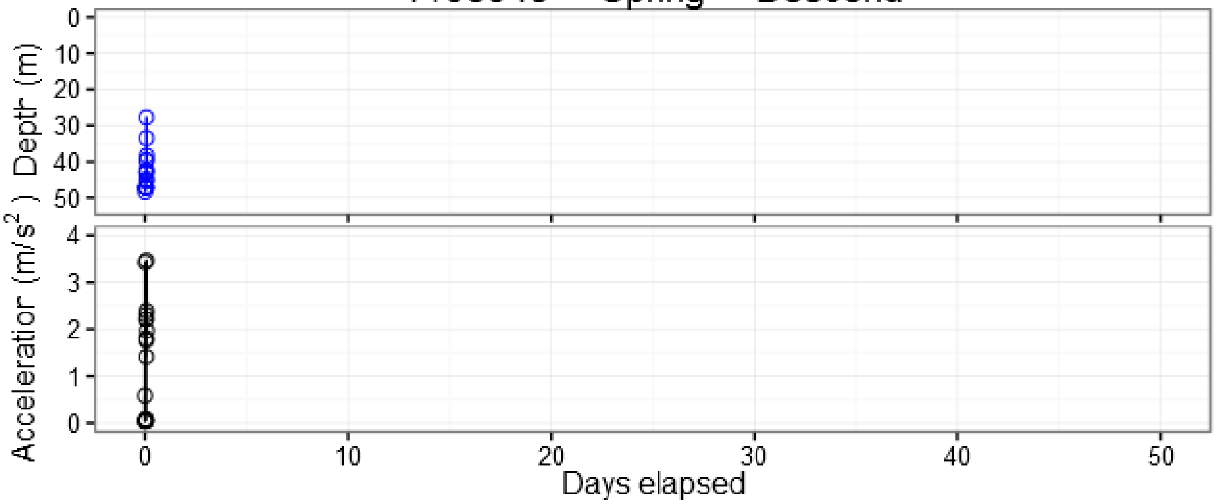

1097883 - Summer - Descend

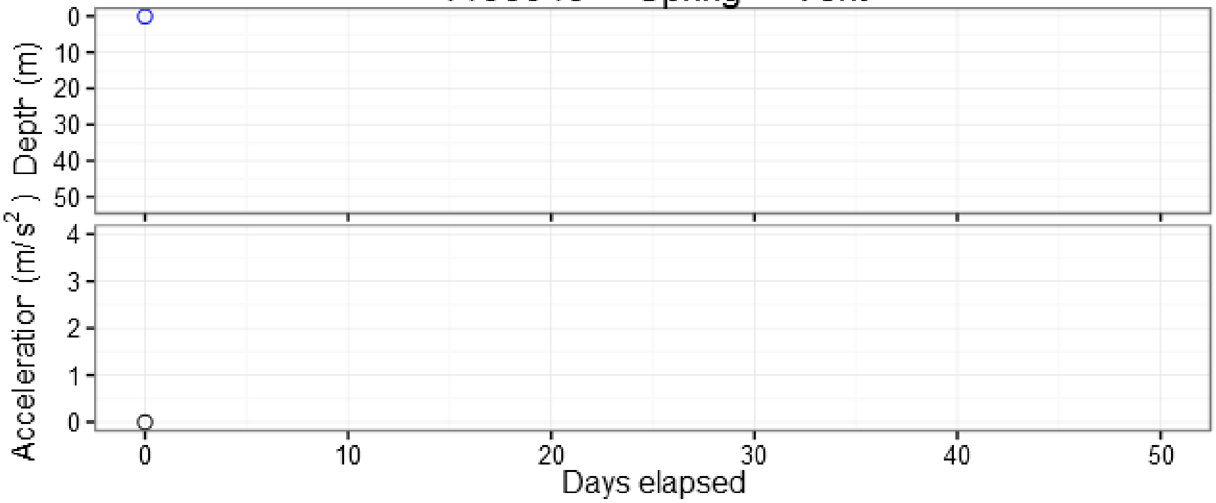

1105037 - Spring - Control

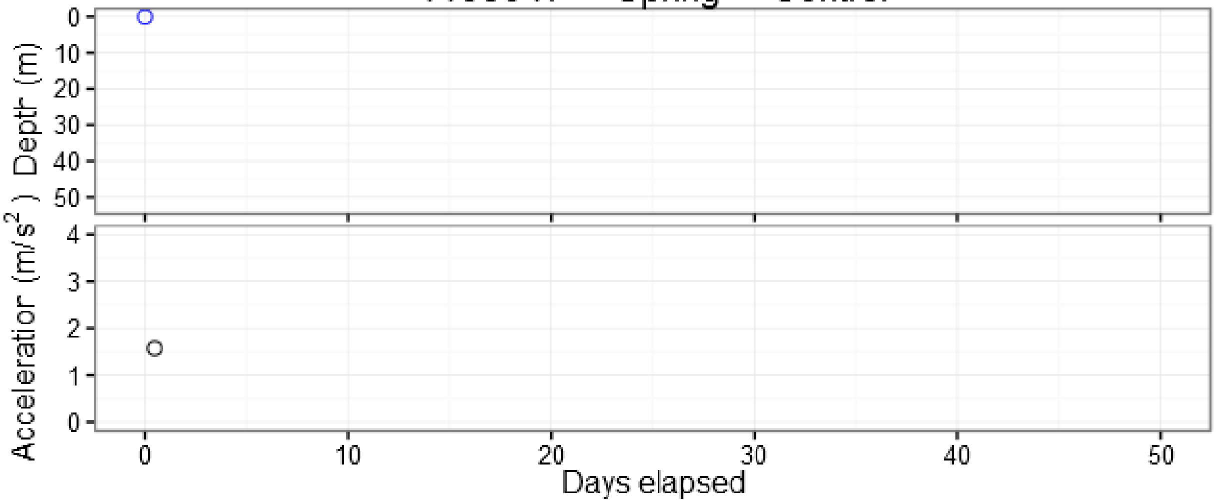

1105039 - Spring - Control

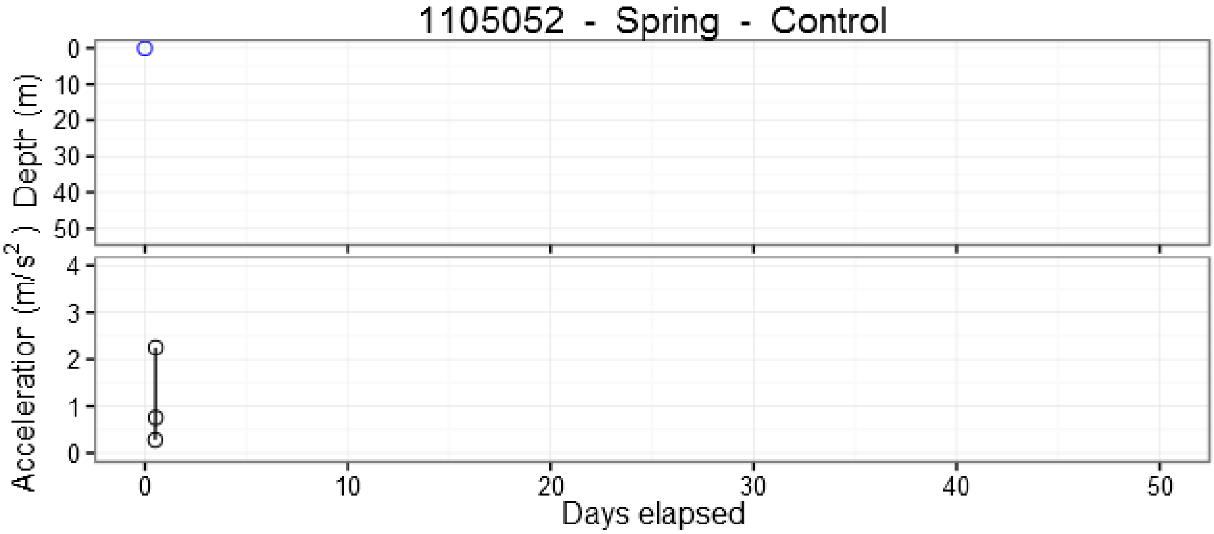

1105040 - Spring - Vent

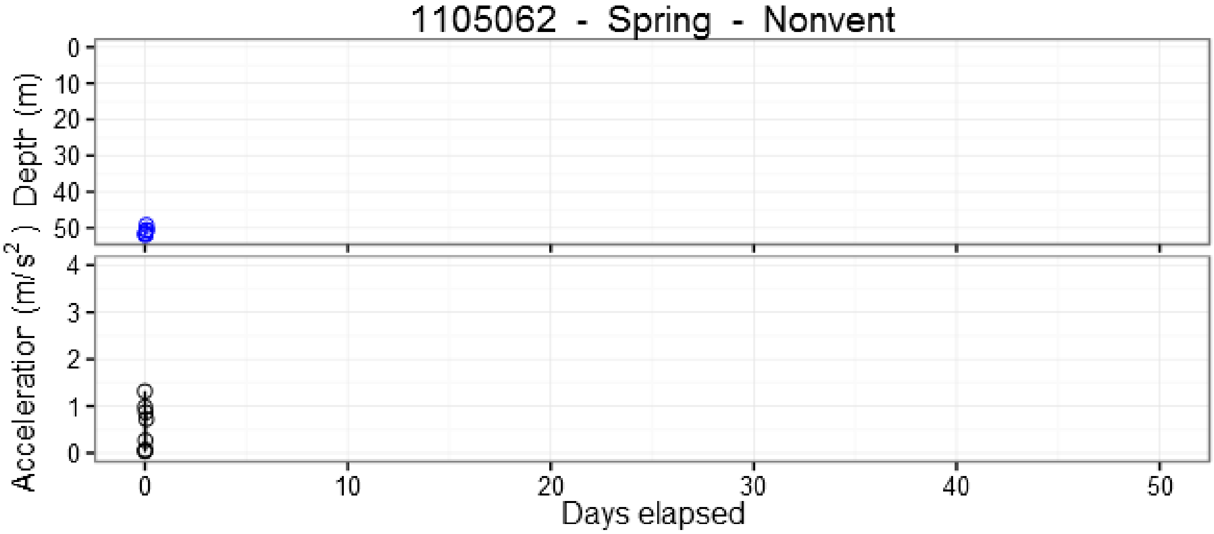

1105044 - Spring - Descend

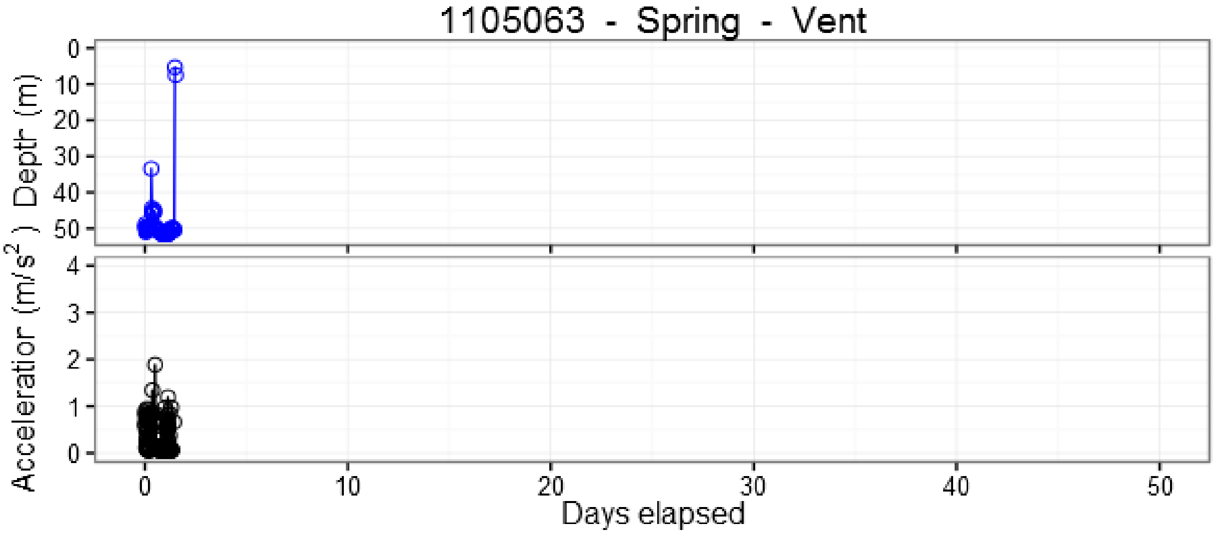

1105045 - Spring - Descend

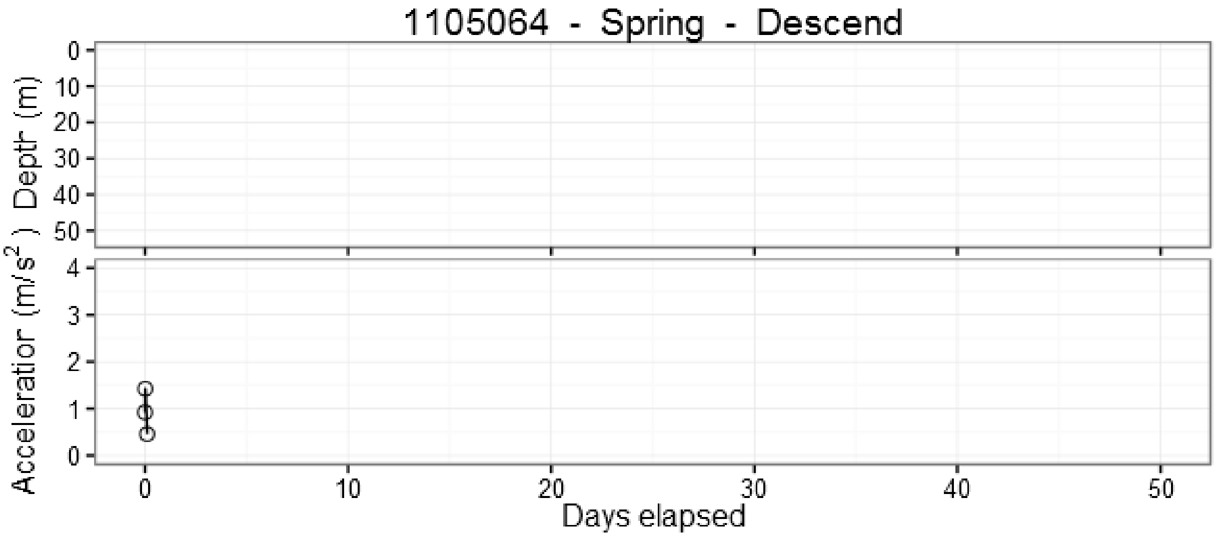

1105046 - Spring - Vent

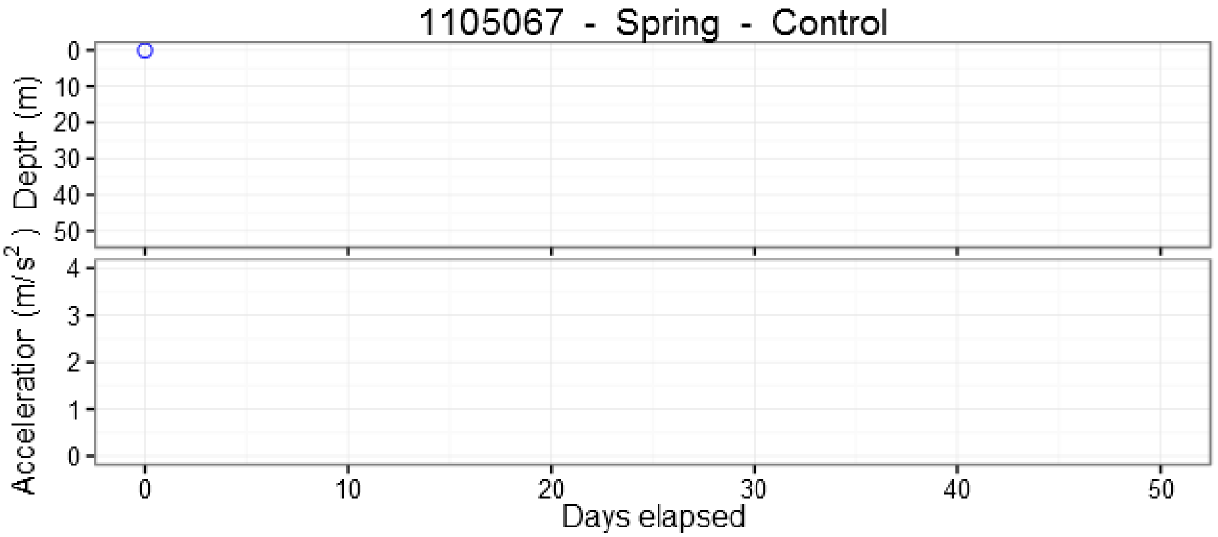

1105047 - Spring - Control


1105052 - Spring - Control
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed


1105062 - Spring - Nonvent
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed


1105063 - Spring - Vent
Depth (m)
0
10
20
30
40
50
Acceleration (m/s^2)
4
3
2
1
0
0
10
20
30
40
50
Days elapsed


1105064 - Spring - Descend


1105067 - Spring - Control