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Recommended Citation

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Changing Oceanic Conditions on The Foraging Patterns of Cassin's Auklets, *Ptychoramphus aleuticus*

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2018 Thesis
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Chapter 1

The Islands of Souls, Fur Seals, Eggs, and a Lighthouse

The Farallon Islands, or the Farallones, are a group of rocky islands and sea stacks 27 miles west of San Francisco. During the last ice age, the Farallones were part of the continent, since the sea surface level was much lower (Chin & Graymer). They used to make up the foothills of California, but now can only be spotted from the mainland on exceptionally clear days. The Farallon Islands are home to thirteen species of breeding seabird, three species of sea lion, two species of seals, and endemic salamander and cricket populations. Additionally, cetaceans and great white sharks often swim past the islands. Since humans first travelled to the islands, they have had many negative, and some positive effects on the wildlife of the Farallon Islands.

The Farallon Islands have a long and rich human history, starting with the Costanoan Indians. They incorporated the islands into their belief system, though they were never able to travel to the islands, as their boats were made for short trips within calm rivers and bays, not for a rough 25-mile trip through the open ocean (White 1995). That the islands could be seen but not reached seemed to add to the mystique of the Farallones, or as the Costanoans called them, the Islands of the Dead (White 1995). The Costanoans believed the souls of their dead travelled to the Farallones to rest. Some believed the souls experienced a peaceful, luxurious afterlife on the Island of the Dead, while others believed it was a type of purgatory (White 1995).

The mystery inspired by the Farallon Islands did not end with the Costanoans, but has carried on to Americans of the 21st century. The jagged, impressive rock formation sticking out of the ocean intrigues many San Franciscans. The Farallon Patrol, the group of volunteers who sail biologists out to the islands, reports having years long waiting lists for crewmembers eager to spend a 14-hour day out on the rough ocean to be able to set foot on the mysterious Farallon Islands for one hour. When shopping for groceries for the Farallones, I was stopped by a worker in the supermarket who told me about how she's been on such a waiting list for years, and how she's always dreamed of going to the Farallones, as she pushed free fruit samples on me and my coworker. It was a very odd experience for two field biologists, being treated as though we were actors in her favorite movie, or astronauts who had been in space. There have even been two murder mystery novels set on the Farallones, *The Secret of the Farallones: A Detective Mark Johnson Mystery* (Labella 2015), and *The Lightkeepers* (Geni 2016). Luckily for those researching the Farallon islands, this excitement has resulted in a well-documented history of the islands.

The first human to document visiting the life-filled Farallon Islands was Sir Francis Drake, an English privateer on the *Golden Hind*, on August 3rd, 1579 (White 1995). Drake and his crew stopped on the islands to fill their ship with seal and seabird meat, then continued exploring the Pacific coast (White 1995). This also doubles as the first time a European set foot in what is now the city of San Francisco, since the islands are in city limits (White 1995). The islands' current name comes from Sebastian Viscaino, a Basque sailor employed by the Spanish government to map the dangerous Pacific coast. In 1603, Viscaino dubbed the seven islands the *farallones*, meaning the steep rocks of the ocean (White 1995). For the next 200 years, the Farallones were seen as something to be avoided, signaling dangerous waters for sailors (White 1995). It was not until Captain James Cook discovered that sea otter pelts from Alaska could fetch an extraordinary price that people considered the rocky Pacific islands anything other than hazards (White 1995). On their way up to Alaska to partake in the sea otter hunt in 1805, Nathan and Jonathan Winship disembarked on the Farallones, and reported that huge numbers of fur seals were living on the islands (White 1995). Within five years, the Farallones became a major hub for fur hunters (White 1995). Though fur seal pelts did not go for as high a price as sea otter pets, fur seals were much easier to hunt and live in large colonies (White 1995). One estimate states that 150,000 fur seal skins were taken from the Farallones in just three years (White 1995). They also went after the elephant seals, as their blubber was said to make even better oil than whale oil (White 1995). By 1885, the elephant seals had been extirpated from California (White 1995).

After the Winship brothers returned to Boston, the Russians and Kashaya Indians settled in Fort Ross in 1820, and took over the Farallones for seals for (White 1995, Istomin 1992). They continued to hunt the decimated fur seal population, while also hunting sea lions and seals for meat and blubber, and seabirds for meat, feathers, and eggs (Istomin 1992). Anywhere from 7 to 100 people lived on Southeast Farallon Island (SEFI) during this time (Istomin 1992). The Russians also often sent out Aleut Indians to work on SEFI as a punishment for breaking their laws (Istomin 1992). However, in 1840, the fur seal and sea otter populations in California had been too far depleted so the Russians left California, and with it, the Farallones (White 1995).

Many important changes took place in the 1850s. Thousands of argonauts colonized San Francisco, and made it into a major seaport (White 1995). However, very few farmers had settled in the area, so San Francisco suffered a shortage of some foods, including eggs (NPR 2016). At the time, hundreds of thousands of common murres nested on the Farallones, and their eggs are twice the size of chicken eggs and apparently just as tasty (White 1995). This led six men to claim the island as their own, and start an egging company based on the Farallones. Also in the 1850s, Congress decided the country was behind on maritime development, and commissioned sixteen lighthouses along the Pacific coast, including one on SEFI (White 1995). The territorial eggers allowed the contractors on the island to build the lighthouse only because they worked for the government (White 1995). To build the lighthouse, they had to lay a road up to the top of the island and bring out a mule to haul the materials up (White 1995).

The egg company built roads, houses, and even a school on the island. Despite an executive order by President Buchanan in 1859 declaring the Farallones to be exclusively used for lighthouse maintenance, the egg company continued to employ 10-30 men at a time to collect as many murre eggs as possible from May to mid July (White 1995). They would go to the murre colonies, and crush all of the eggs on the first day. They would then return two days later to collect the replacement eggs, knowing that they were all freshly laid, and would continue to return every other day for the rest of the season (White 1995). Though common murres only lay one egg at a time, if their egg is destroyed, they can relay. The eggers took full advantage of this, and took multiple eggs from each murre throughout the season. The eggers would also sometimes take Western gull eggs, though they were smaller and easier to break, so they weren't as sought after as the common murre eggs (White 1995). The larger effect on the Western gulls was that the eggers tried to kill as many as they could and crush their eggs. The gulls also fed on murre eggs, and were smart enough to take advantage of the eggers. When an egger would enter a murre colony and scare all the murres off to the water, the gulls would immediately swoop in and seize the unprotected eggs (White 1995). Not only were they limiting the number of eggs eggers could take, but they also attacked the eggers for their eggs.

The egg business was so profitable, that in 1863 an egg war broke out over control of the island (NPR 2016). Rival eggers came to SEFI with rifles and cannons and the egg company fought back, managing to fight off the invaders (NPR 2016). Two men died in this egg war (White 1995). Though they managed to hang on to the island, the eggers afterwards lost a fight with the lightkeepers. The egg company tried to tell the lightkeepers that they could not collect eggs, even for their own use, and assaulted a lightkeeper who tried collecting eggs (White 1995). The lighthouse keepers told the federal government, and a new executive order was signed in 1881, reestablishing that only lighthouse keepers may use the islands, and the eggers were evicted (White 1995). The lightkeepers then launched a black market of selling murre eggs for years to come. They also would catch sea lions to sell their whiskers and genitalia for Chinese medicine, and would often allow trespassers on the island to collect eggs and poach sea lions as well (White 1995). By the end up the 19th century, only 60,000 murres remained on the island, as opposed to the half a million from pre-egging times, and the egging business was no longer profitable (White 1995).

In 1905, the Navy set up a station on SEFI to run a new radio transmitted weather station and marine traffic control center (White 1995). During World War I, 26 marines were sent to protect the naval station, as it was able to contact both submarines and the Hawaiian naval station (White 1995). In 1939, the Farallones came under control of the U.S. Coast Guard, and it has managed island ever since. During WWII, a Farallon Naval Station was built to send encoded messages to passing US warships and airplanes (White 1995). During this time, the Farallon Islands reached 78 residents, and all-time high since the Russians had left (USFWS 2014). The increased human activity had negative effects on the breeding birds of the island. The humans developed all over the island, and imported mules, dogs, and worst of all, cats. Freighters also frequently passed by the islands, which led to multiple oil spills that killed huge numbers of seabirds (White 1995). In 1959, an ornithologist counted fewer than 6,000 breeding murres, somewhere around 1% of the original population size. Luckily for the birds, after the war, the naval station was no longer needed. Additionally, the lighthouse became much more automated, so it required fewer keepers. In 1972, the last lighthouse keeper left the island, though he did not leave it unoccupied (USFWS 2014). In 1968, the Point Reyes Bird Observatory (PRBO, now Point Blue Conservation Science) recognized the scientific and conservation value of the island, and set up permanent residence (USFWS 2014).

Point Reyes Bird Observatory to Point Blue Conservation Science

Point Reyes Bird Observatory (PRBO) was founded in 1965 to survey the diverse assemblage of birds in the area. Point Reyes is a major stopping point on the Pacific flyway, the migratory path that over a billion birds follow every spring and fall. PRBO's original goal was to study these birds, and to spread public awareness. Basically, it was founded as an organization for people who wanted to see large numbers of some extraordinary birds. It only took PRBO three years after their conception to discover the wonders of the Farallones. The Farallon Islands are the breeding grounds of thirteen species of seabirds, including the largest colony of Western gulls in the world, over half of the world's ashy storm petrel population, and the charismatic tufted puffins. Not only are the Farallones a stopping point along the Pacific flyway, but the islands are a stopping place for many lost vagrants—rare bird species—that end up on the wrong side of the continent (Hecocks 2018). This makes the Farallones a very attractive place for birders hoping to see rare birds.

The Fish and Wildlife Service asked PRBO to remain on the Farallones to protect the seabirds once the lighthouse atop SEFI became automated (White 1995). The PRBO biologists had a tough time of protecting the island; fisherman had become used to roaming it at will, even shooting sea lions and birds for sport (White 1995). PRBO had to negotiate with the fishermen to stop their destructive habits, with the Coast Guard residents to get rid of their cats, and even with the US Navy, which had taken to practicing aerial bombing on Middle Farallon Island (White 1995). Slowly, the island started to refill with life under the supervision of PRBO.

PRBO has not only protected the seabirds on the Farallones, but has also collected vast amounts of data on them. Biologists collected data such as what bird species were present on the island, their breeding success, their diets, and any other information they could. Much of the early research on the Farallones focused on determining the life history traits of the species on the Farallones. For example, one of the first studies published on Cassin's auklets of the Farallones, titled "The Natural History of Cassin's aukets (*Ptychoramphus aleuticus*)," details their attendance patterns to the colony, their nocturnal arrival and departure patterns, that they make their nests in burrows, lay one egg at a time, and feed on euphausiids and other zooplankton (Manuwal 1974). Though this is all known information now, much of it was novel in 1974. Once PRBO had collected multiple years of data, biologists started conducting research on how the ecology of the Farallones was changing by looking at factors such as population trends and changes in breeding success (eg. Shultz & Sydeman 1997, Sydeman 1997, Sydeman 1998). Recently, PRBO's database on seabird data has been used to analyze the impacts of climate change.

The seabirds of the Farallon Islands are once again under threat, not from eggers or cats, but from anthropogenic global climate change. In 2005 and 2006, anomalous climate conditions caused all Cassin's auklets to give up on breeding those summers and abandon their eggs on SEFI (Sydeman *et al.* 2006). Not only was this a bad sign for seabirds on the islands, but also for the surrounding waters. Cassin's auklets feed on krill, so their breeding failures can often be attributed to a lack of productivity in the surrounding oceans. In 2013, PRBO changed its name to Point Blue Conservation Science to indicate that they are moving towards a more holistic, environmental approach. They recognized that to save the Cassin’s auklet, they needed to do more than shoot feral cats and keep fishermen off the island; they needed to help restore the entire ecosystem. I worked for Point Blue Conservation Science over the summer of 2018 as part of a team helping to protect the biodiversity of the central California ocean. The main focus of my research is an attempt to understand how the Cassin’s auklet will be affected by the changes that are occurring in the Pacific Ocean.

Chapter 2

Abstract

Cassin's auklet (*Ptychoramphus aleuticus*) reproductive success has been monitored on Southeast Farallon Island (SEFI) for the past 45 years. Their productivity has varied with oceanic conditions. The purpose of this study is to connect how oceanic conditions affect Cassin's auklet foraging behaviors. The California Current System (CCS) can normally maintain high plankton productivity, and thus high seabird productivity, because of coastal upwelling. I hypothesized that lower upwelling and/or higher sea surface temperatures (SSTs) lead Cassin's auklets to spend more time on intensive foraging behaviors such as flying and diving, and have less time to spend resting. I also hypothesized that they would dive more, dive deeper, and spend more time underwater in years of high SST and/or low upwelling. We deployed time depth recorders (TDRs) on 85 Cassin's auklets on SEFI from 2008-2017 for a total of 268 foraging trips. We programmed the TDRs to record temperature and pressure every 5 seconds, and every 0.5 seconds when diving. I used the Pacific Fisheries Environmental Laboratory derived upwelling index (UI) from three months prior to the early chick-rearing season, and SST measured from SEFI during the days the TDRs were deployed. UI from three months prior and SST were not correlated. I found that in years with higher SSTs and in years with less upwelling, the Cassin's auklets made deeper dives and stayed underwater longer. Neither higher SSTs nor lower UIs significantly affected the amount of time the auklets spent flying, diving, or resting. These results show that the physical conditions that drive the development of the California current food web influence they diving behavior of top predators.

Introduction

Our oceans are changing. Not only are the temperatures and surface levels rising, but the circulation, chemistry, and species distribution are being altered as well (Harley *et al.* 2006). However, the ocean's immense volume and inaccessibility can make oceanic conditions extremely hard to monitor. To increase our understanding of ocean conditions, we use seabirds to provide insights into marine ecosystems (eg. Cairns 1988, Piatt & Sydeman 2007, Diamond & Devlin 2003).

Since seabirds are ground nesting and often very conspicuous, we can monitor them more easily than most marine species (Cairns 1988, Piatt & Sydeman 2007). Since the 1980s, biologists have used seabirds as indicators of local marine food supply (Cairns 1988, Montevecchi 1993). A decrease in sandeels (*Ammodytes* spp) in the waters around the British Isles has caused Black-legged kittiwake (*Rissa tridactyla*), European shag (*Phalacrocorax aristotelis*), arctic skua (*Stercorarius parasiticus*), arctic tern (*Sterna paradisaea*), and little tern (*Sternula albifrons*) populations on the British Isles to decrease (Mitchell *et al.* 2011). In years with poor Atlantic herring supply (*Clupea harengus*), up to 60% of reproductively mature shags (*Clupea harengus*) on the Isle of May in Scotland do not even attempt to breed (Aebischer & Wanless 1992). Aebischer *et al.* (1990) were the first to suggest seabirds could be used not only as indicators of fish stock, but also as indicators of climate change when they linked kittiwake gull (*Rissa tridactyla*) productivity to variations in weather conditions. Since then, many studies have analyzed seabird success to gain understanding into how climate change is affecting the marine ecosystem (eg. Sydeman *et al.* 2006, Diamond & Devlin 2003, Jones *et al.* 2002).

There is no one ideal way to measure seabird success, but often use adult survival, breeding success, chick growth, colony attendance, and activity budgets (Cairns 1988). This study will be examining activity budgets of Cassin's auklets as marine ecosystem indicators. The Cassin's auklet (*Ptychoramphus aleuticus*) is a small, zooplanktivorous Pacific seabird. The Cassin's auklet is considered a sentinel species, meaning they can be used as an indicator of the health of their ecosystem (Sydeman *et al.* 2006, Bertram *et al.* 2017, Wolf *et al.* 2010). Cassin's auklets' survival and productivity are highly susceptible to changing oceanic conditions, such as

El Niño Southern Oscillation (ENSO) events, sea surface temperature (SST) and upwelling (Hyrenbach & Veit 2003, Lee *et. al* 2007, Wolf *et al.* 2010). Trends in Cassin's auklet survival and productivity are much easier to study than most marine species' so they are used as indicators of other marine species. Roth *et al.* (2007) discovered that Cassin's auklets' breeding success and survival in response to changes in oceanic conditions co-vary with those of Chinook salmon (*Oncorhynchus tshawytscha*), meaning that the success of the difficult to monitor Chinook salmon can be predicted by that of the Cassin's auklet.

Cassin's auklets are highly susceptible to changing ocean conditions because they are only two trophic levels above primary production (Wolf *et al.* 2010). They feed mainly on euphausiids (krill), specifically *Euphausia pacifica* and *Thysanoessa spinifera*, although they will switch to alternative zooplankton such as mysids in years where krill are scarce (Manugian *et al.* 2015). Krill and mysids feed directly on phytoplankton, so the Cassin's auklet diet depends on the quantity of primary production. As in most sea surface level ecosystems, primary productivity in the California Current System (CCS) is mainly nutrient limited. In stable ocean columns, the surface is nutrient deficient because phytoplankton use the nutrients to photosynthesize. However, deeper in the water column, most of the nutrients are unused since there is not enough light for phytoplankton to photosynthesize. Productive ecosystems need water column mixing in order to replenish the sea surface's nutrients. Because of coastal upwelling, the CCS is a highly productive ecosystem, providing over 20 percent of the world's commercial fish catch despite making up only 1 percent of the world's ocean (Dorman 2015). Upwelling in the CCS happens when the strong winds present through the spring and summer push the currents off the shore, causing cold, nutrient rich water to be drawn up from the depths to replenish the coastal water. These nutrients allow for more photosynthesis, which sustains the zooplankton, and consequently the Cassin's auklet.

However, as the climate changes, the frequency of anomalous events such as ENSO events, which cause poor upwelling conditions, has increased (Timmerman *et al.* 1999, Barber & Chavez 1983). ENSO events cause a lessening of upwelling favorable winds in the CCS, which in turn create a more stable water column, and decrease primary production. The upwelling favorable winds that do occasionally occur in these years are only able to bring warm water to the surface since the water column is deeper than usual. In 2005, a combination of a weak El Niño and anonymously late atmospheric blocking caused such a high krill mortality in the CCS that Cassin's auklets on SEFI had 0 productivity for the season, meaning they did not fledge a single chick (Dorman 2015, Sydeman *et al.* 2006). Cassin's auklets need to consume 67% of their body weight in euphausiids daily while chick rearing, and as shown in 2005, if there are not enough euphausiids to meet that requirement, they will abandon their eggs to save energy and increase their own chances at survival (Hodum *et al.* 1998).

When their main food sources are less abundant, Cassin's auklets will need to change their foraging habits. Common murres (*Uria aalge*; also referred to as common guillemots) are able to maintain breeding success in years of poor food supply partially because they have many prey options, a luxury the Cassin's auklet does not have (Burger & Piatt 1990). In the Northern Atlantic, if capelin, the common murre's main prey, is scarce, they catch more adult sandlance instead (Burger & Piatt 1990), whereas the Cassin's auklet feeds exclusively on zooplankton, so they are less able switch prey. Though they do not prey switch to the same extent as common murres, Cassin's auklets do consume more *E. pacifia* when there is a lot of upwelling, and can switch almost completely to mysids in years where euphausiids are scarce (Abraham & Sydeman 2006, Manugian *et al.* 2015).

Common murres have also been found to have flexible time budgets, so when food is scarce, they spend more time foraging to catch enough food for their chicks (Harding *et al.* 2007, Uttley *et al.* 1994, Burger & Piatt 1990). In years of poor food availability, the adults spend significantly less time resting at the colony, and twice as long on foraging trips than in years with high food availability (Uttley *et al.* 1994). Additionally, Murres can fly 35% further from their colony to forage in years with poor food availability (Burke & Montevecchi 2009). However, very little research has been done on whether Cassin's auklets have flexible time budgets. The Cassin's auklets breeding on Triangle Island, 30 miles from Vancouver Island, British Columbia, fly further when their preferred prey is further from the colony (Bertram *et al.* 2017). This suggests that Cassin's auklets may budget more time for flying in years with less prey availability.

Some diving seabirds such as king penguins and thick-billed murres will dive to depths where they need to switch from aerobic to anaerobic respiration, meaning they do not use as much oxygen, but build up lactic acid (Kooyman *et al.* 1992, Croll *et al.* 1992). Rhinocerous auklets, however, have a linear relationship between their time underwater and time before dives to avoid anaerobic respiration (Burger *et al.* 1993). This means they were taking in enough oxygen to handle the amount of time spent underwater aerobically, without switching over to anaerobic respiration. Because they dive aerobically, rhinoceros auklets are able to spend 80% of their diving bouts underwater, which is not achievable for birds who use anaerobic respiration when diving, and need to spend more time on the surface recovering (Burger *et al.* 1993). There is a tradeoff between diving depth and time spent diving that some species make, while others do not (Burger *et al.* 1993). If Cassin's auklets need to make deeper dives in order to catch enough prey, they may need to switch to anaerobic dives. This would take a greater physical toll on the Cassin's auklets than aerobic dives do.

Past studies have been limited in their understandings of seabird activity when they are away from the colony. Time spent on foraging trips could be estimated from when the birds left their nests to when they returned, but this gives no information about what they do when not on their nest. Researches would need to conduct intensive research cruises to collect data on Cassin's auklets outside of the colony. In some cases, they would shoot and collect Cassin's auklets they came across to examine their stomach contents (Ainley *et al.* 1996). The Cassin's auklets nocturnal activity makes them difficult to directly monitor even when they are in the colony. Manuwal (1974) describes putting toothpicks at the entrance of Cassin's auklets' burrows, then checking whether the toothpicks had been knocked over at different times throughout the night in order to estimate when the auklets returned to their nests. New technology can be used to better understand how Cassin's auklets spend their time.

Warmer waters and less upwelling in the California Current System decreases the biomass of zooplankton, which causes Cassin's auklets to spend more effort foraging. In this study, I tested the hypothesis that climate change increases foraging requirements for Cassin's auklets by testing the following predictions:

1. Time spent flying and diving increase with increasing SST and decreasing upwelling index (UI)
2. Time spent resting on the water decreasing with increasing SST and decreasing UI
3. Number of dives per diving bout increases with increasing SST and decreasing UI
4. Diving depth increases with increasing SST and decreasing UI

Methods

I worked on the Southeast Farallon Island (SEFI) for three months during the 2018 seabird breeding season. The SEFI is 27 miles west of San Francisco and 96 acres, and all of the Farallones together are 211 acres. PRBO has been monitoring the breeding success of Cassin's auklets on SEFI since 1973, and their foraging patterns using time depth recorders since 2008.

Tracking Cassin's Auklet Productivity

Point Blue Conservation Science (PRBO) uses artificial Cassin's auklet nest boxes on SEFI to make extracting and observing the birds easier. The boxes have a tube for the bird to enter and exit, and a wood door on the roof for biologists to look in and extract birds from. Each box also has a wood shade on top to keep the box cool on sunny days. To check the boxes, I knelt in front of them with my knee covering the tube so the adults could not exit. We wanted to keep the auklets in their nest boxes during the day so they can incubate their eggs or chicks, and because they are highly susceptible to predation by Western gulls (*Larus occidentalis*) during the day. I removed the shades, then slowly lifted open the lids of the boxes and peered inside.

In the beginning of the season, we, the PRBO biologists and interns, extracted every adult found in the boxes to read their band and identify them, or to band them if unbanded. If the boxes had one or two known age birds nesting in them, we classified them as known age boxes. We followed these boxes throughout the season, recording egg lay date, hatch date, and each chick's fledge date. When chicks were present, we weighed and recorded the feathering status of the chicks every 5 days until they fledged. Feathering statuses were determined by the status of the pinfeathers on the undersides of the wings. After the chicks fledged, we continued visiting each box every 5 days to check for second broods. If there was a second brood, we repeated the process.

Deploying and Recovering TDRs

We used Time Depth Recorders (G5, CEFAS Technology Limited, Lowestoft, Suffolk, United Kingdom) for the past 11 years to track the activities of Cassin's auklets. The Time Depth Recorders (TDRs) weigh 2.7g in the air and 1.3g in the water and measure 31mm long by 8mm wide. The average Cassin's auklets weighs about 175g and is 230 mm long, so a TDR adds about 1.5 percent to the weight of the bird and spans 13.5 percent of its length. We programmed the TDRs to record both the temperature (°C) and pressure every 5 seconds for 72 hours, starting at midnight on the night they were deployed. When the device registered that the bird was diving due to an increase in pressure, it then took measurements every 0.5 seconds.

We deployed the TDRs to Cassin's auklet known-age adults with chicks between the ages of 1 and 20 days old, since small chicks require the greatest amount of food from their parents. We deployed the TDRs around 23:00, when most auklets had returned to the colony for the night. We extracted the known age Cassin's auklets from their nest boxes, collected diet samples in Whirl-packs if they had any food to regurgitate, and weighed them and their chicks. To deploy the TDRs, we applied cyanoacrylate glue to the TDR, then placed the TDR on the ventral side of the auklet. We also glued the surrounding feathers to the TDR in order to make the device as secure and hydrodynamic as possible. We then returned the auklets to their nest boxes.

Three nights after deploying the TDRs, we returned to the nest boxes after 23:00 to recover the TDRs. If the TDR bird was present, we extracted it from its nest box, and collected diet samples if possible. We then pried the TDRs off of the belly of the bird, being careful to leave all feathers intact. We weighed the adult and its chick, then returned them to their nest box. We repeated the process at midnight that night and 04:00 the next morning for the birds that were not present the first time. Some Cassin's auklets remain at sea overnight, so for birds that did not return the first night, we returned the following three nights at 22:30, 24:00, and 04:00, or until we recovered the TDRs. After three nights, if we still had not recovered the TDRs, we assumed the TDR adult had abandoned its nest, and we stopped checking that nest box in order to stop disturbing the mate and chick.

Processing the TDR Data

Using the python script that processed the TDR data, I identified that an auklet was in the colony if the TDR registered a high temperature and low pressure. I classified the bird as flying if the TDR registered a mid temperature and low pressure, and resting on the water if the TDR registered a low temperature and low pressure. Once the auklets started diving and the pressure increased, the TDR went into fastlog mode, where it took measurements every 0.5 seconds. The python program calculated how much time each bird spent in the colony, flying, resting on the water, and diving.

I also calculated how deep each dive was based on the maximum pressure. I calculated the amount of time each auklet spent at the bottom of each dive by calculating how long the bird was at the maximum depth for each dive. I found the length in seconds of each dive by calculating how long the pressure was elevated for. I also calculated the post dive interval (PDI) for each dive by calculating how long the pressure remained at 0 after every dive, representing how long the birds rested after each dive.

Statistical Methods

I only used the data from foraging trips from first broods that occurred in May and in the first half of June from 2008 to 2017 to avoid any biases of throughout season foraging differences. I calculated SST in two different ways: the SST at each bird's foraging locations, and the SST at SEFI. For the SST of where each bird foraged, I took the maximum temperature from each dive, as measured by the TDRs, and averaged those temperatures for each bird. This resulted in a different local SST for each of the birds. I calculated the Farallon SST by averaging the SSTs taken from SEFI for the three days the TDR was deployed for each Cassin's auklet. This resulted in only one Farallon SST per year since all TDRs were deployed on the same night, except in 2015, when they were deployed in two waves.

I used each bird as one data point. I took the proportion of time each bird spent flying, resting on the water, and diving. I averaged the maximum depths of every dive per bird for the average dive depth of each bird. I did the same for time spent underwater per dive, and the number of dives per bout. Finally, I averaged the time spent on each foraging trip per bird to determine each bird's average trip duration.

I tested whether the age of the chicks was a predictor of foraging variables using a one-way analysis of variance (ANOVA). I tested whether the amount of time Cassin's auklets spend flying, diving, and resting on the water differ by year using a one-way ANOVA. I then ran linear regression for each foraging variable, to see how they varied with each measurement of SST.

To quantify the amount of upwelling, I used the Pacific Fisheries Environmental Laboratory (PFEL) derived daily UI from 36°N, 122°W, which was the closest point to the Farallones (37.7°N, 123°W). I calculated three UIs for each TDR deployment—a one-month lag, where I averaged the UI from each day from the month leading up to the deployment data; a two-month lag, where I averaged the UI the 30-60 days before deployment; and a three-month lag, where I averaged the UI from the 60-90 days before deployment. I did this because many studies have reported time-lags in the effects of upwelling on zooplankton in the CCS (Manugian *et al.* 2015, Abraham & Sydeman 2004, Abraham & Sydeman 2006). I then ran linear regression for each foraging variable, to see how they varied with each time-lag of UI.

Results

We successfully collected and downloaded data from 132 TDRs from 2008 to 2017. I only used data from the TDRs deployed on first broods to lessen the effects of time of breeding season. This left me with 85 samples, with the fewest number of samples per year being 3 in 2010, and the most at 19 in 2015 (Table 1). Each sample gave me 3-5 days of data, many including multiple foraging trips, for a total of 268 foraging trips (Table 1, eg. Fig 1).

Table 1. The number of TDRs collected and the total number of foraging trips per year.

	2008	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**Total**
TDRs	10	8	3	9	6	7	9	19	7	7	85
Foraging Trips	22	23	9	30	16	23	27	53	17	16	268

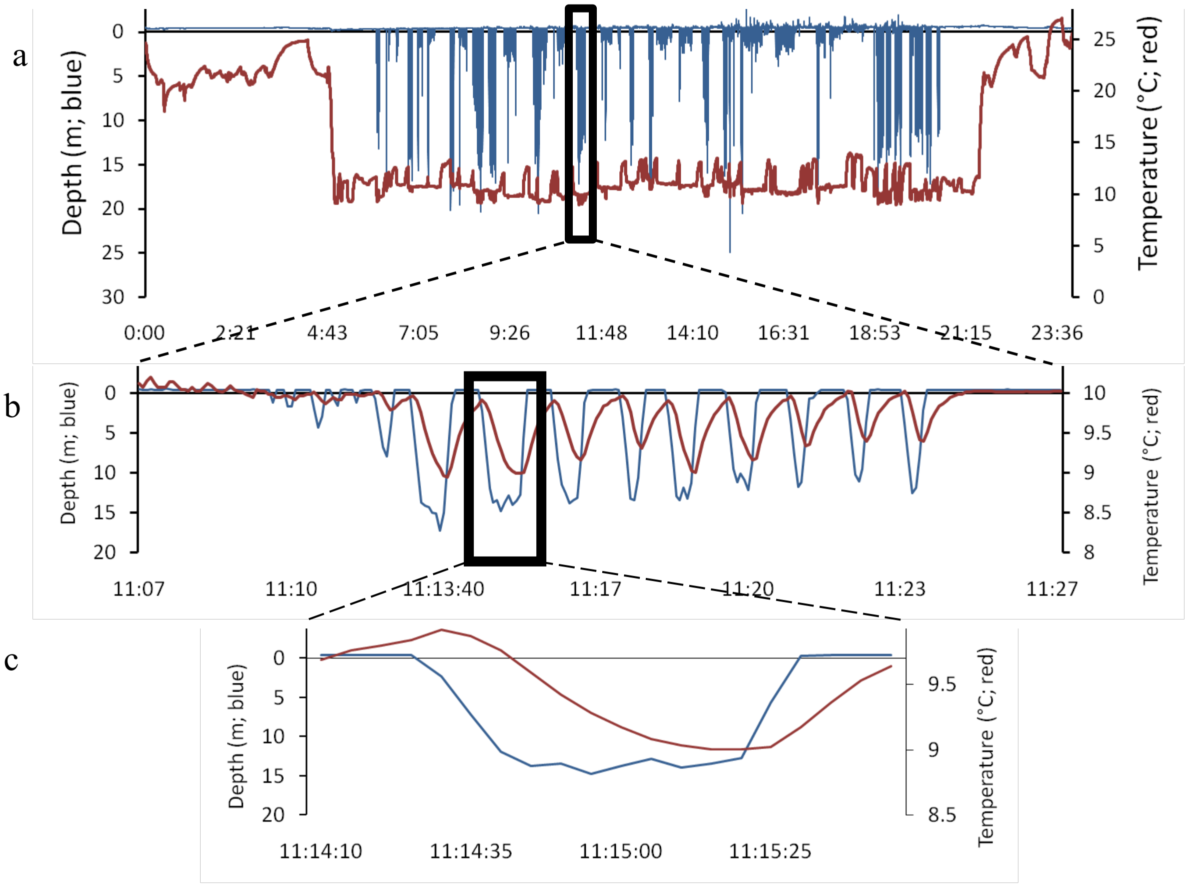

Figure 1. The temperatures (red) and depth (blue) during a) a foraging trip, b) a diving bout, and c) a single dive of a 2008 SEFI Cassin's auklet. Figures made by Dr. Nina Karnovsky.

The average SSTs from where each bird foraged differed significantly by year ($p < 0.001$, Fig 1). The lowest average foraging temperature was in 2008 at 8.31°C, and the highest temperature in 2017 at 13.03°C. The average SST from the days the TDRs were recording, as measured from SEFI, were 9.53°C in 2008 and 11.3°C in 2017. SST as measured from SEFI and from the TDRs were positively correlated, though still dissimilar ($r^2= 0.376$, $p < 0.001$, slope= 0.746, Fig 2).

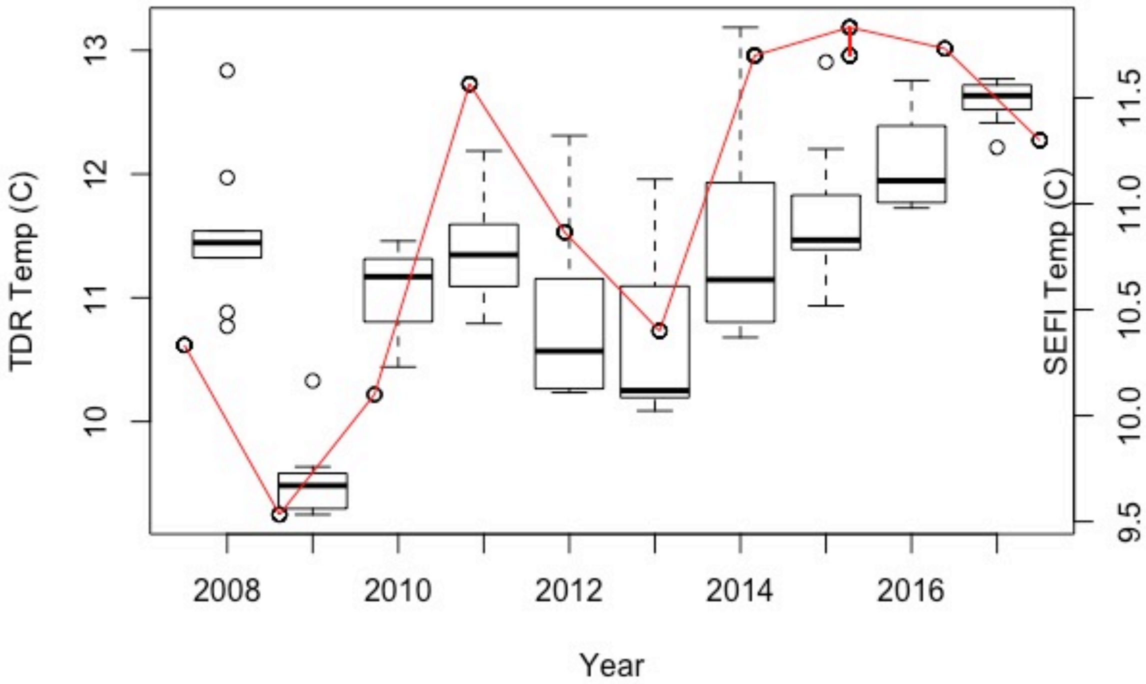

Figure 1. The average temperature of where each bird foraged, as measured by the TDRs, by year, with the SST measured from SEFI overlaid in red. There are two SEFI temperatures for 2015 as the TDRs were deployed in two waves that year.

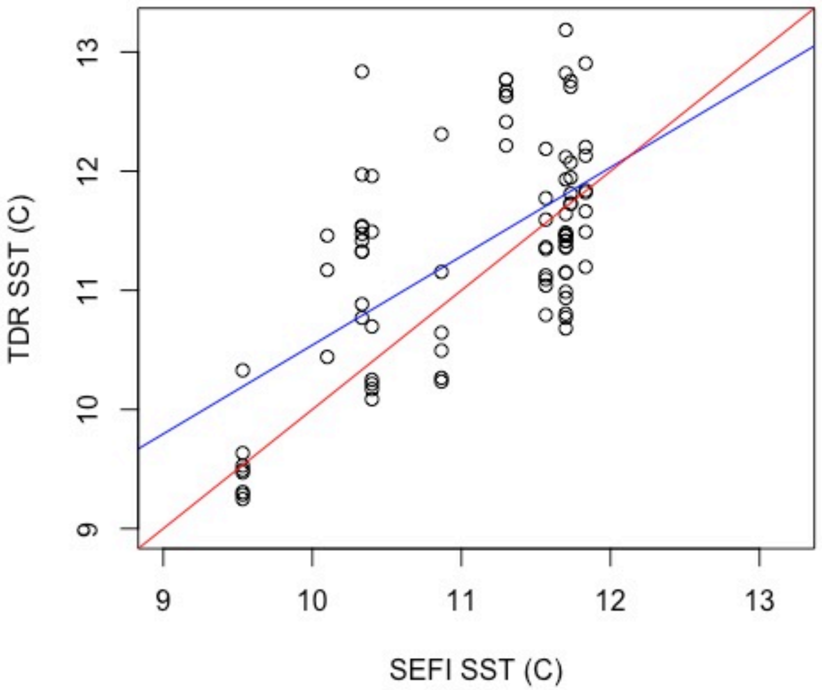

Figure 2. The average temperature of where each auklet foraged, as measured by the TDRs, by the SST as measured from SEFI. The blue line is the line of best fit, the red line has a slope of 1 and intercept of 0, to represent if the two measurements of SST were the same.

The average amount of time each bird spent flying differed significantly by year (p = 0.002, Fig 3a), though amount of time spent resting and diving did not (p = 0.107, Fig 3b; p = 0.675, Fig 3c, respectively). However, the program was unable to detect all times the auklets were flying, and thus underestimated the amount of time spent flying. The percentage of time spent flying should be used as an indicator of time spent flying, not the actual value. The average trip durations also did not significantly differ by year (p = 0.508, Fig 3d), and the shortest trip durations were still always longer than the amount of daylight. The average maximum diving depth did differ significantly by year (p = 0.006, Fig 3e), though the number of dives per diving bout did not (p = 0.793 Fig 3f). The age of the Cassin's auklets chicks was not a significant predictor of any of the foraging variables.

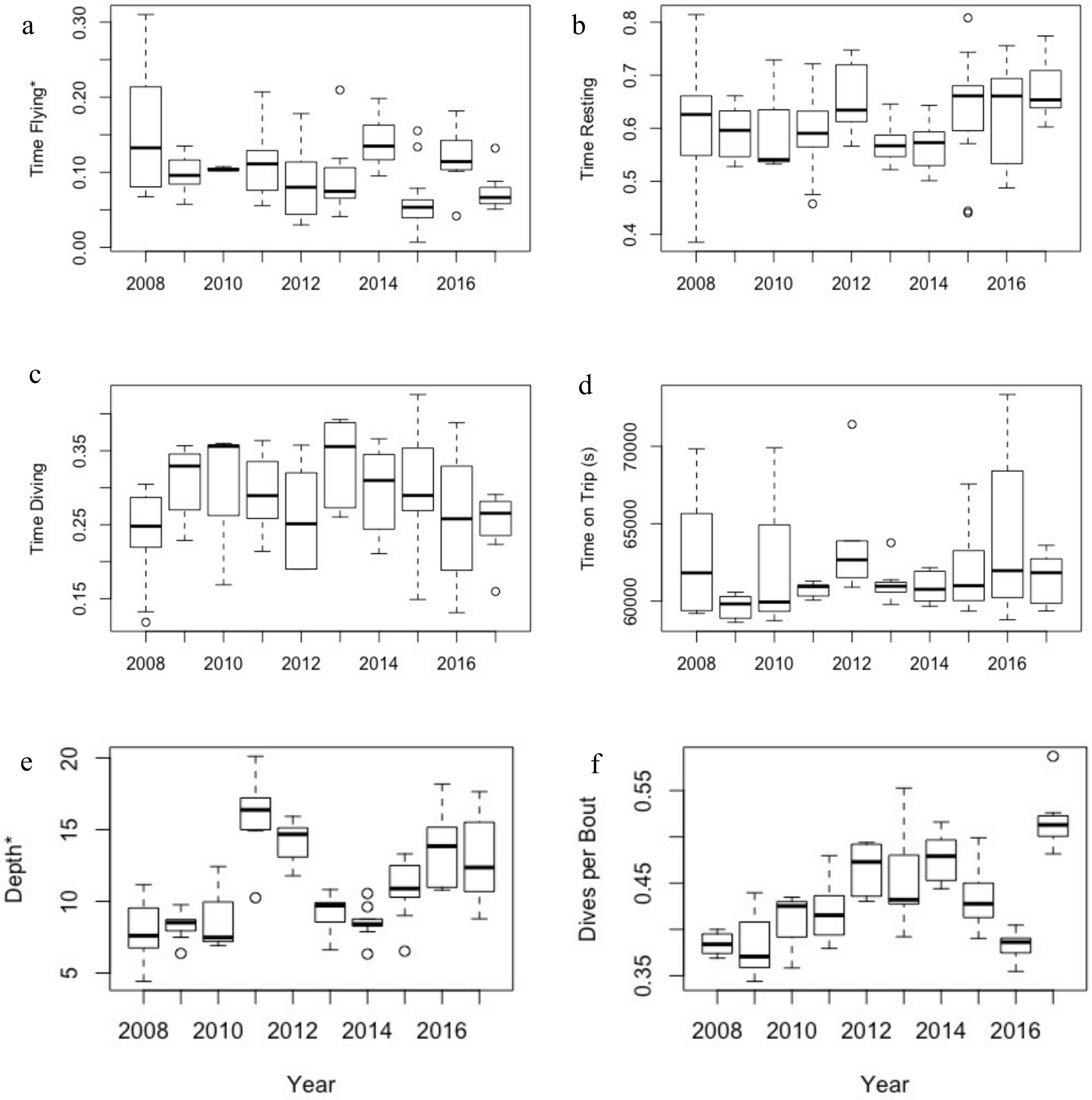

Figure 3. The different foraging variables by year, a) the proportion of time the auklets spent flying, b) the proportion of time spent resting, c) the proportion of time spent diving, d) the trip durations, e) each auklet's average dive depth, and f) the average time spent at the maximum depth of each dive. The stars on the y-axis labels represent significant correlations.

The percentage of time the Cassin's auklets spent diving was significantly negatively correlated with the percentage of time they spent resting on the water ($r^2 = 0.595$, $p < 0.001$, slope= -0.940), meaning that as the auklets spent more time diving, they spent less time resting (Fig 4a). However, the number of dives per diving bout and the time spent recovering after the diving bout were significantly positively correlated ($r^2 = 0.32$, $p<0.001$, slope= 35.954 seconds/ dive, Fig 4b).

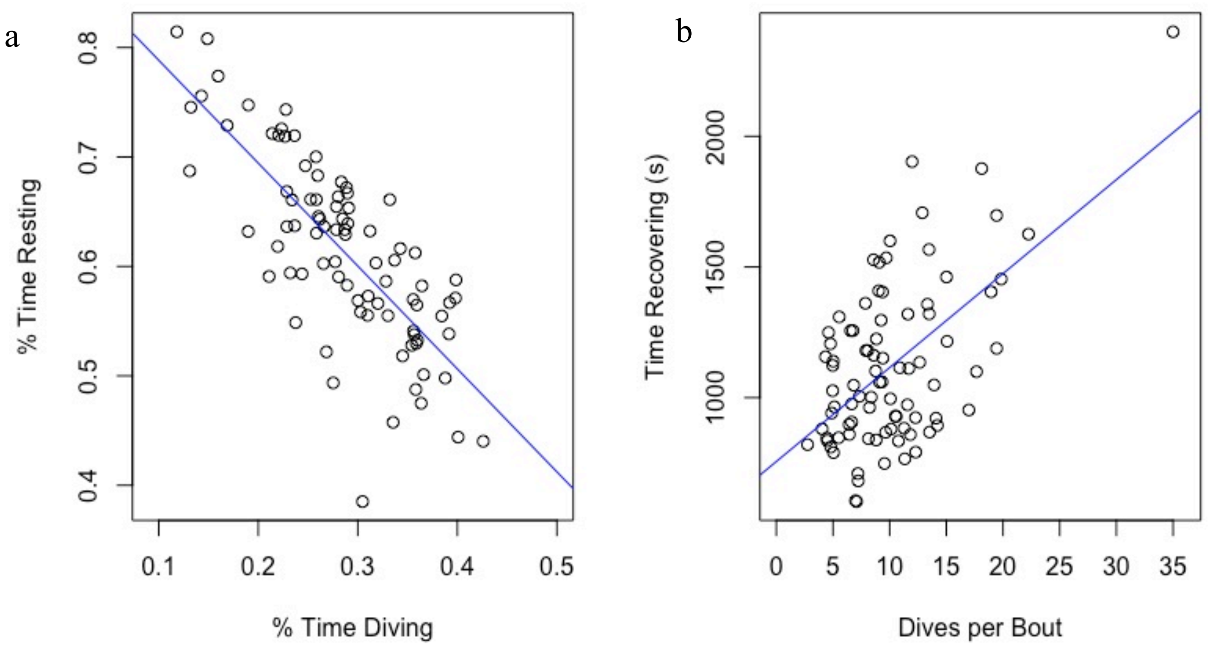

Figure 4. The relationships between time spent resting and diving as shown by a) the percentage of time each auklet spent resting by the percentage of time they spent diving, and b) the average amount of time each auklet spent recovering after diving bouts by the average number of dives they did per bout. The blue lines are the lines of best fit.

SST measured by the TDRs was not significantly correlated with the amount of time spent flying, diving, or resting (Fig 5a-c). It was a slight predictor of both dive depth ($r^2 = 0.081$, p= 0.008, slope= 1.046 m/°C, Fig 5d) and time spent underwater per dive ($r^2 = 0.147$, $p < 0.001$, slope= 4.663 s/°C, Fig 5e). It was very slightly negatively correlated with the number of dives per bout (r^2= 0.0643, p= 0.019, slope= -1.369 dives/°C Fig 5f). Similarly, SST from SEFI was not a predictor of time spent flying, diving, or resting (Fig 6a-c), but was significantly positively correlated with depth (r^2= 0.18, $p < 0.001$, slope= 1.046 m/°C, Fig 6d) and time underwater per dive (r^2= 0.292, $p < 0.001$, slope= 4.663 s/°C, Fig 6e and Fig 7), though it was not correlated with the number of dives per bout (Fig 6f).

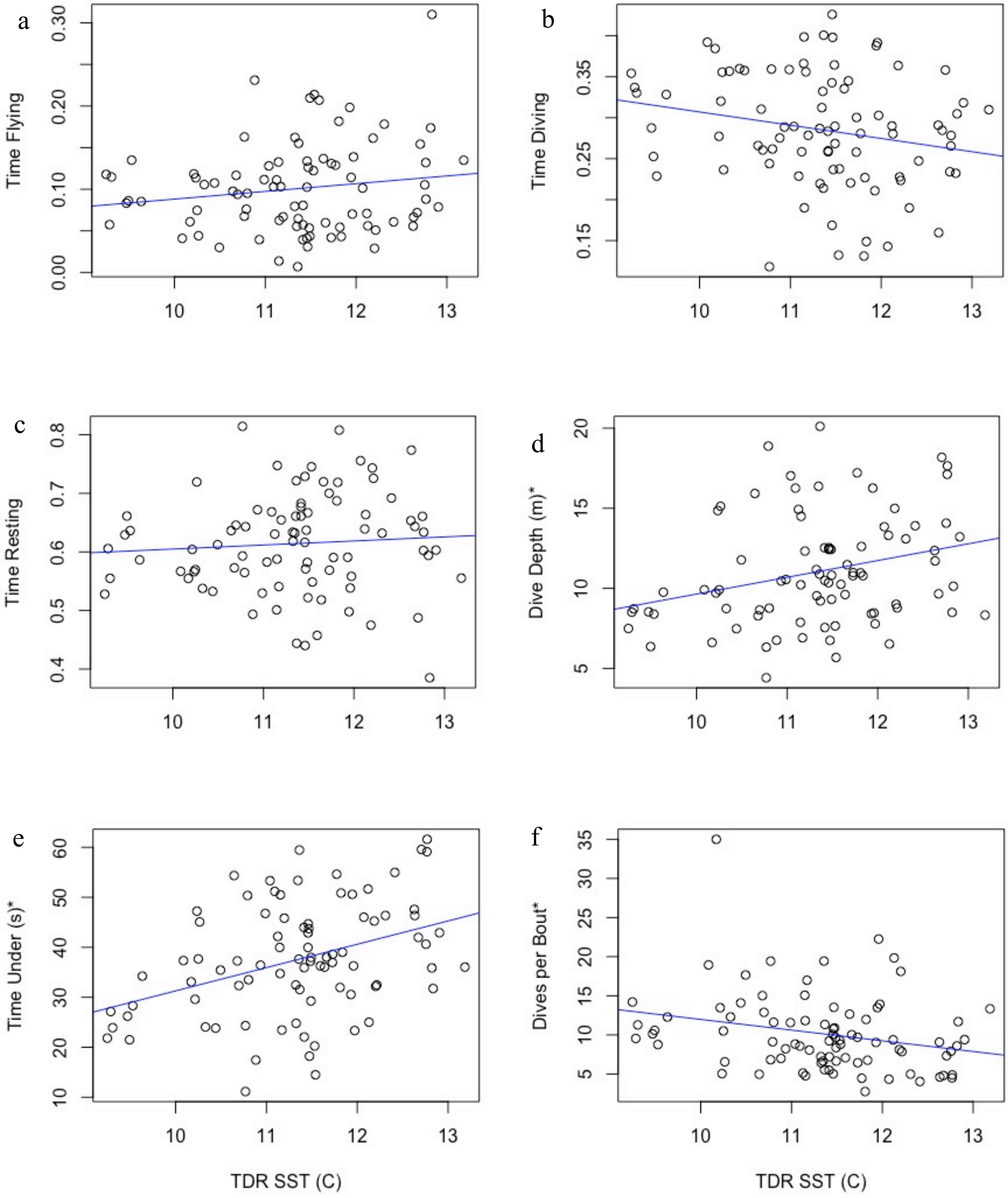

Figure 5. The different foraging variables by the SST of the foraging locations as measured by the TDRs, the proportion of time each auklet spent a) flying, b) diving, c) resting, d) the average maximum dive depth of each auklet, e) the average time underwater for each dive, and e) the average number of dives per bout by year. The blue lines are the lines of best fit, and the stars on the y-axes denote significant correlations.

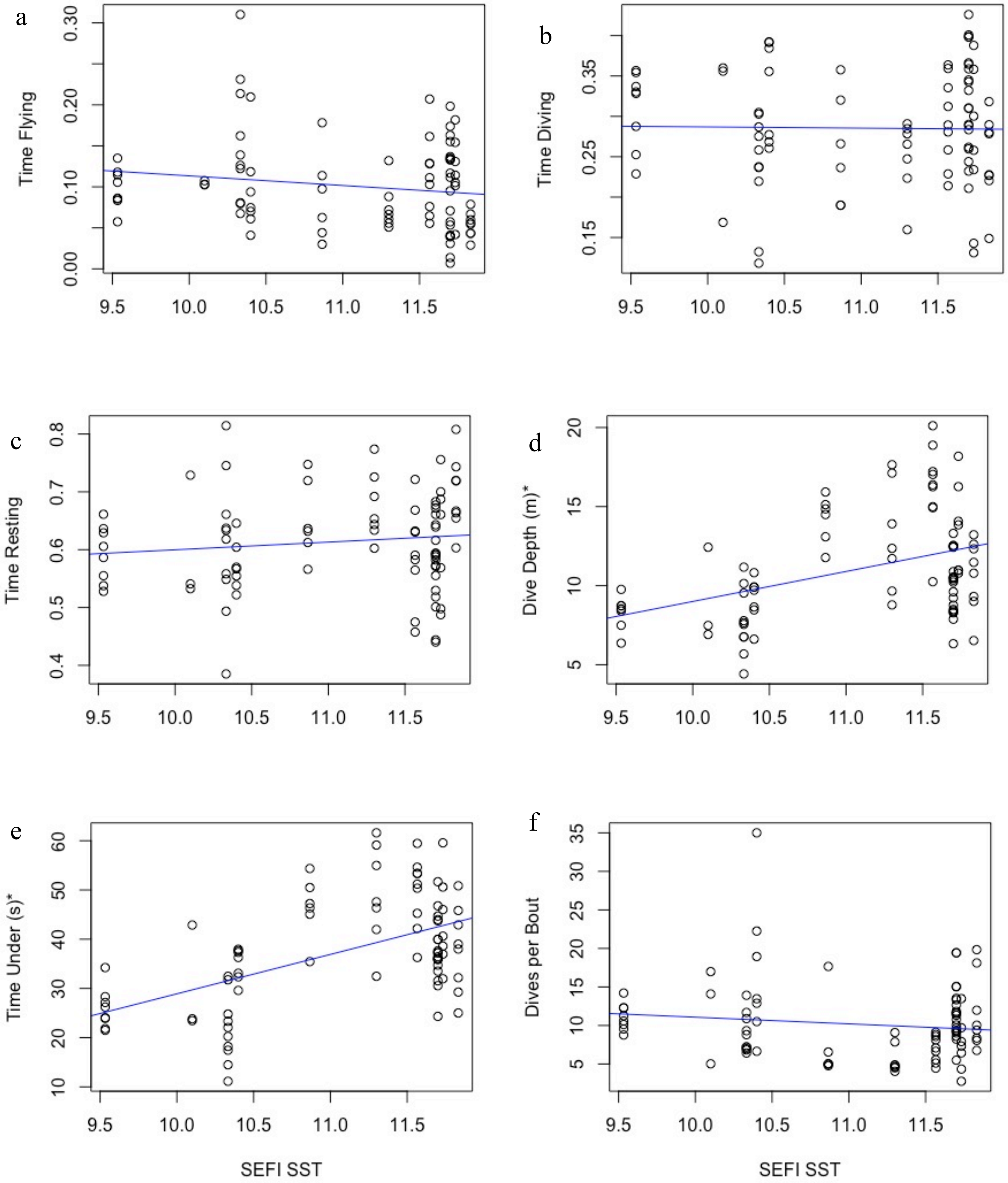

Figure 6. The different foraging variables by the SST as measured from SEFI, the proportion of time each auklet spent a) flying, b) diving, c) resting, d) the average maximum dive depth of each auklet, e) the average time underwater for each dive, and e) the average number of dives per bout by year. The blue lines are the lines of best fit, and the stars on the y-axes denote significant correlations.

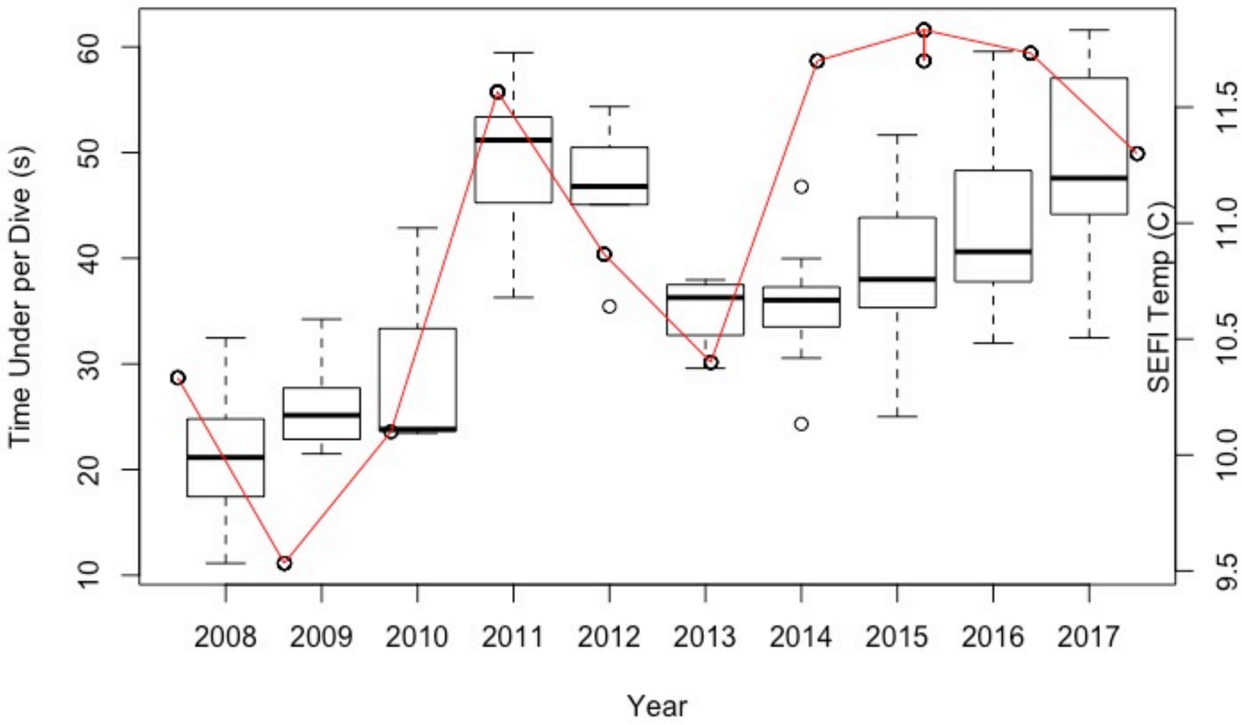

Figure 7. The average amount of time each auklet spent underwater per dive by year, with the SST measured from SEFI overlaid in red. There are two temperatures for 2015 as the TDRs were deployed in two waves that year.

I calculated the average daily UI with a one-month lag, a two-month lag, and a three-month lag, with the PFEL derived daily UI from 36°N, 122°W as described in the statistical methods. Neither the one-month nor the two-month UI indices were predictors of the amount of time the auklets spent flying, diving, or resting. The three-month UI was a very slightly negatively correlated with the amount of time spent diving (r^2= 0.045, p= 0.052, slope= -0.0004, Fig 8). The time spent underwater per dive and the one-month lagged UI were very slightly positively correlated, though the relationship is not significant (r^2= 0.025, p= 0.147, slope= 0.053, Fig 9a). Conversely, the time spent underwater per dive was slightly *negatively* correlated with two-month lagged UI (r^2= 0.029, p= 0.12, slope= -0.089, Fig 9b), and significantly negatively correlated with three-month lagged UI (r^2= 0.147, p< 0.001, slope= -0.119, Fig 9c). Similarly, dive depth was not correlated with one-month lagged UI (Fig 10a), was slightly negatively correlated with two-month lagged UI (r^2= 0.045, p= 0.051, slope= -0.034, Fig 10b), and was significantly negatively correlated with three-month lagged UI (r^2= 0.208, p< 0.001, slope= -0.043, Fig 10c).

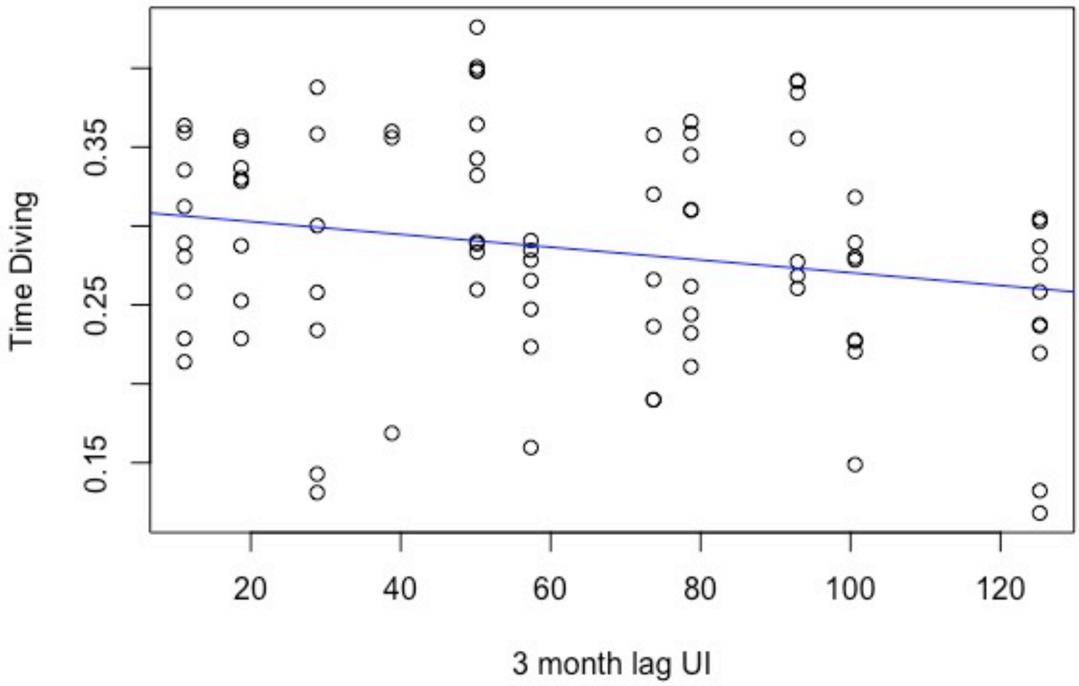

Figure 8. The percent of time each auklet spent diving by the three-month lagged UI. The blue line is the line of best fit.

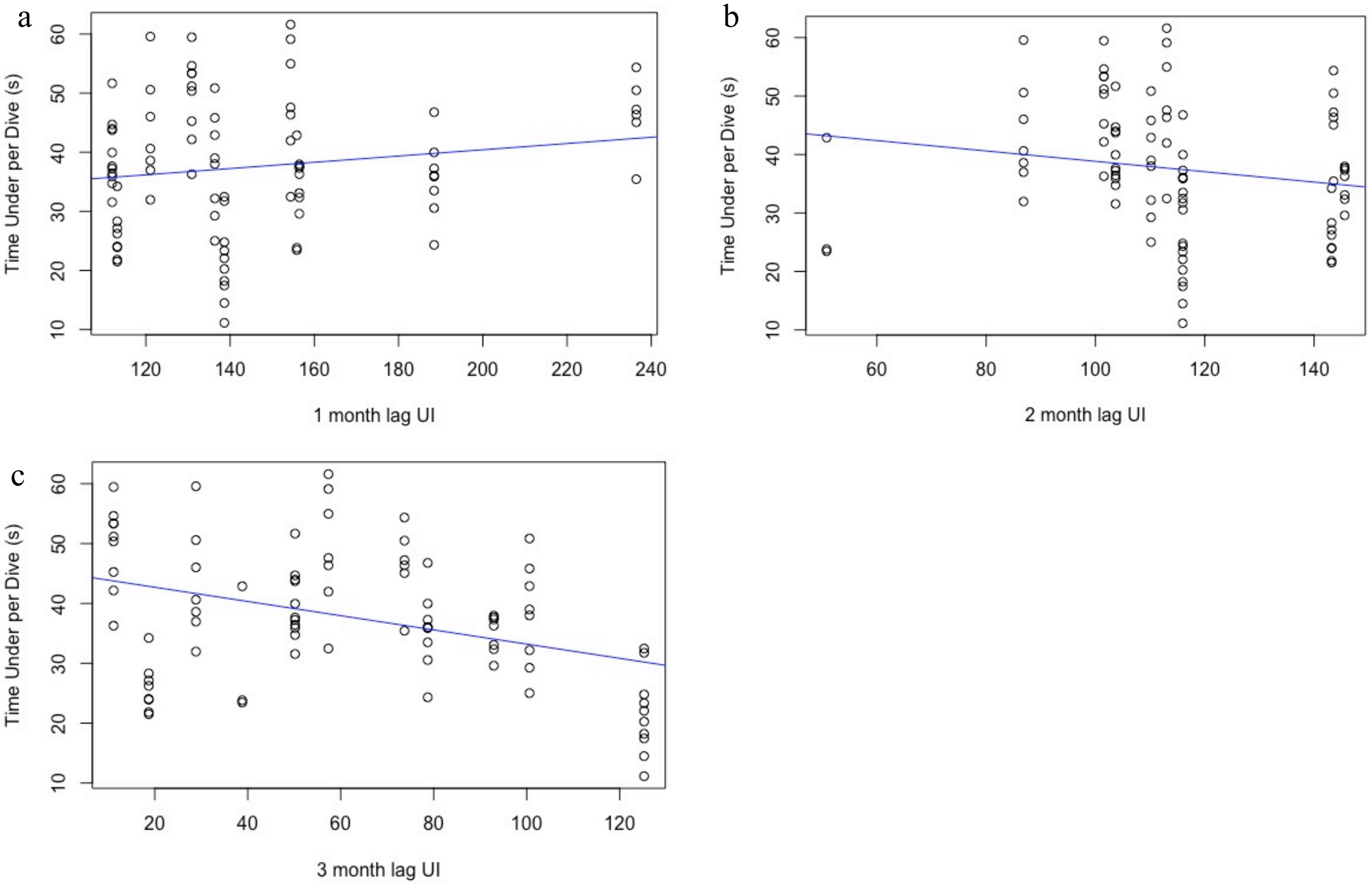

Figure 9. The average amount of time each Cassin's auklet spent underwater per dive by the a) one-month lag UI, b) two-month lag UI, and c) 3 month-lag UI. The blue lines are the lines of best fit.

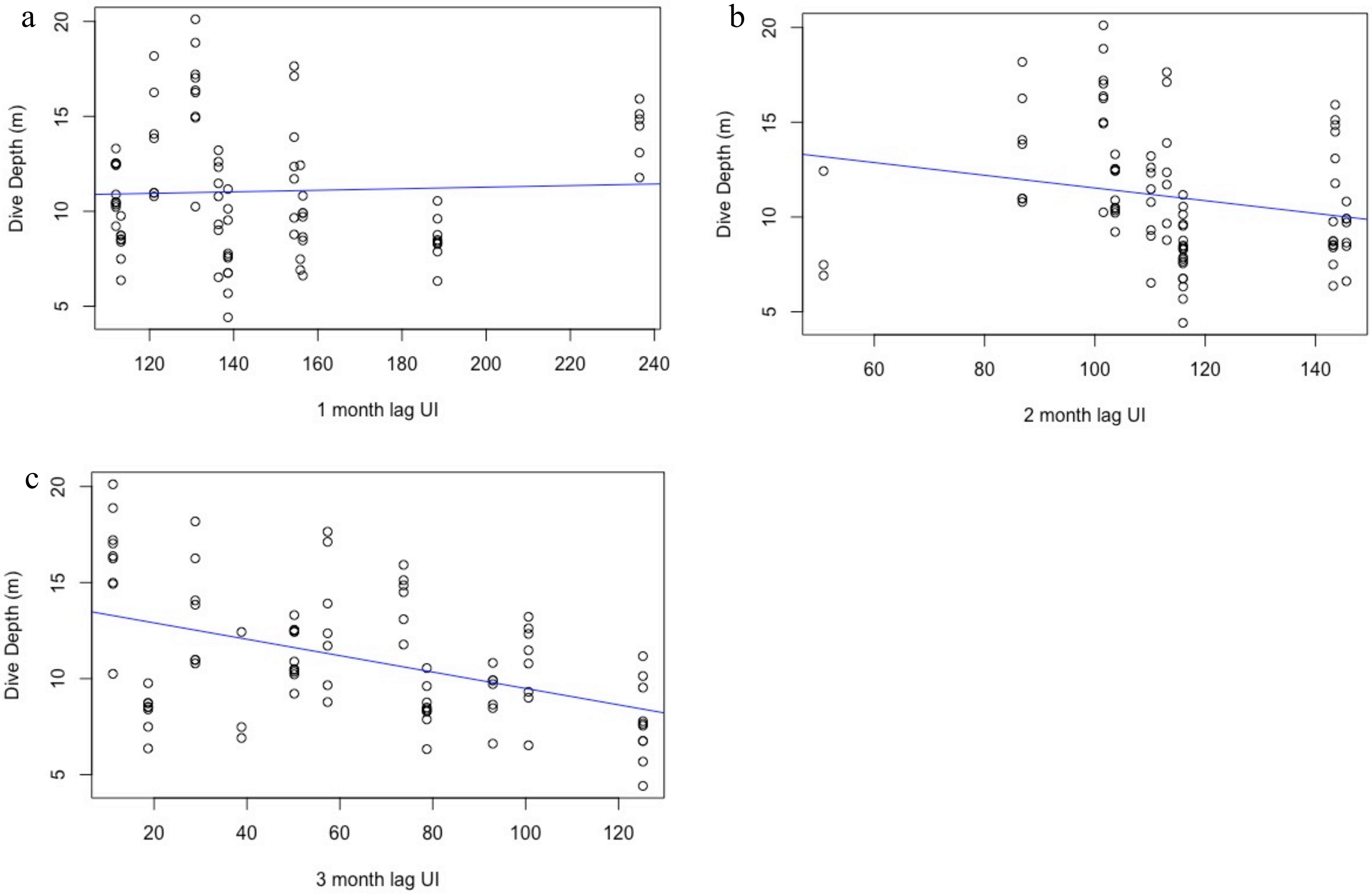

Figure 10. The average depth each Cassin’s auklet dove to by the a) one-month lag UI, b) two-month lag UI, and c) 3 month-lag UI. The blue lines are the lines of best fit.

Discussion

I found that Cassin's auklets on SEFI are able to change some aspects of their foraging habits from year to year. From 2008 to 2017, the percentage of time the auklets spent flying during their foraging trips differed by year, as well as how deep they dove, and how long they spent underwater per dive. Some of these changes occurred with the changing ocean conditions; SST and UI are both predictors of the depths the auklets dove to and how long they spent underwater per dive, though they were not predictors of the amount of time they spent flying. Overall, the climate variables I observed are related to changing diving behavior in Cassin's auklets, but not the time spent on foraging trips, flying, or resting.

Both the SEFI SST and the TDR-measured SSTs were significant predictors of how deep the auklets dove and how long they spent underwater per dive, and in the case of the TDR-measured SST, how many dives they did per bout. I found that UIs from two to three months before the TDRs were deployed were the best predictors of Cassin's auklets diving variables. When I analyzed the average UI from the one month leading up to the deployments, it appeared that UI was not correlated with diving depth and indicated a decrease in time underwater. However, with a three-month lag, higher UIs clearly indicated shallower diving depths and less time underwater per dive. The three-month lagged UI was also very slightly correlated with the percent time spent diving, making it the only climate variable that is a predictor of the amount of time Cassin's auklets spent diving. The three month lagged UI was definitely the best predictor of Cassin's auklets diving behavior, indicating that there may be an approximately three-month lag between UI and the availability of zooplankton in the CCS. This corroborates the findings of Manugian *et al.* (2015), who also analyzed the relationships between different upwelling lags and euphausiid populations in the CCS, and found that the UI from 90 days prior was the best predictor of euphausiid abundance.

The foraging trip durations of Cassin's auklets on SEFI did not change from year to year. Cassin's auklets are limited in their ability to alter their foraging time budgets for two reasons. Firstly, they are diurnal; since they are visual foragers, they are only able to forage during the day. Secondly, the Western gulls on SEFI predate the Cassin's auklets if they are out of their burrows during the day, so the auklets must leave the colony before the sun rises and return after the sun sets to avoid predation (Manuwal 1974). This leaves Cassin's auklets much less flexibility in their foraging trip durations than other alcids, such as the common murre, who are able to fly in and out of the colony during the day since they are much larger than Cassin's auklets and are thus not predated on by gulls. Common murres have been found to increase the amount of time they spend on foraging trips (Uttley *et al.* 1994), which Cassin's auklets are unable to do. As expected, I found that Cassin's auklets do not adjust their foraging trip durations from year to year.

The lack of correlation between UI and time spent flying by Cassin's auklet is surprising since upwelling has been linked to differences in Cassin's auklets' foraging locations. The amount and timing of upwelling, along with the depth of the water column, determine the amount of primary production that takes place in the CCS, and thus the amount of zooplankton available for Cassin's auklets. Prior studies have shown that Cassin's auklets change their foraging locations based on prey availability (Manugian *et al.* 2015, Bertram *et al.* 2017). Manugian *et al.* (2015) found that Cassin's auklets switched from feeding on the krill species *E. pacifia* and *T. spinifera* along the shelf break near the Farallones to feeding on mysids in the Cordell Bank, North of Point Reyes in years of poor upwelling. My findings that Cassin's auklets do not spend more time flying in years of poor upwelling indicates that the auklets either did not vary their foraging locations because of zooplankton abundance, or that their different foraging locations were similar distances from SEFI.

As the number of dives per bout increased, the time spent recovering increased, but as the percent time each bird spent diving increased, the percent time they spent resting decreased. The relationship between time spent resting and diving had a slope of -0.94, meaning there was almost a one-for-one tradeoff. For each additional dive per bout, the birds rested an additional 35 seconds, though the average time spent per dive was 37.6 seconds, indicating that they are still spending less time resting per dive with more dives per bout.

While the auklets studied did not change the amount of time they spent resting on the surface from year to year, or in response to SST or UI, different individuals did spend varying amounts of time resting, at the expense of the time they spent diving. Perhaps some Cassin's auklets are simply more efficient foragers, so they can spend more time resting while still catching enough food, while others must spend more time diving to catch the same amount of food. The lack of variation from year to year suggests that time spent resting is not an indicator of ocean productivity. Cassin's auklets may be able to rest more in high productivity years because catching zooplankton is easier, so they have more discretionary time, while in years of low productivity, they may need to rest more because they are spending more energy foraging. While the reasons they rest may differ, the amount of time they spend resting does not differ by year.

Since three-month lagged UI and the SST from the foraging days were not correlated, it is unclear how much SST played a role in krill abundance. However, increasing SST was still correlated with deeper dives and longer dives of Cassin's auklets. This could indicate that SST affects the abundance of zooplankton in the short-term, or that it affects the depth of the zooplankton. If SST only affects the depth of zooplankton, there may still be enough food available for Cassin's auklets at higher SSTs, but they need to dive to deeper depths to obtain it. This differs from the three-month lagged UI, in that UI has been shown to affect zooplankton abundance (Manugian *et al.* 2015). Instead of being able to make shallow dives and catch enough zooplankton, they must dive deeper to reach the less accessible zooplankton in years of low UI. Thus, the shallowest auklet dives occur when there is a low SST and high UI, as this most likely means that there is a high abundance of zooplankton at shallow depths, and the deepest dives when there is high SST and low UI, as that is when there are the fewest zooplankton, and they are at deeper depths.

SSTs in the CCS are increasing (eg. Zaba & Rudnick 2016, Di Lorenzo *et al.* 2005). Future upwelling trends are uncertain, but there will be an increase in ENSO events, which cause poor upwelling conditions (Timmerman *et al.* 1999, Barber & Chavez 1983). In future years of poor upwelling conditions and high SSTs, Cassin's auklets will need to dive deeper and spend longer underwater per dive than they normally would. This could force the auklets to make anaerobic dives, which are much more physically demanding than their usual aerobic dives. Additionally, Oswald and Arnold (2012) identified small, highly active seabirds, such as Cassin's auklets, as one of the most susceptible to heat stress in warm years while at sea. The higher temperatures could make the exertions needed to complete deep dives too much for Cassin's auklets, and render them unable to obtain the deeper zooplankton. Oswald and Arnold (2012) also found that other species could be even more affected; small aerial hunters, who spend most of their foraging time flying, such as terns (family *Laridae*) and shearwaters (family *Procillariidae*), are more likely to overheat since they are not experiencing the conductive heat loss that comes from sitting on the water. Many seabird species could be at risk of overheating if they are forced to make deeper, more strenuous dives, like the Cassin's auklet, in years of poor upwelling and warmer SSTs.

It has been well established that upwelling drives primary production in the CCS, which in turn drives zooplankton abundance (Smith 1983, Barber *et al.* 1971, Dorman 2015). There has also been research done to study the effects of zooplankton abundance on the foraging patterns of seabirds (Manugian *et al.* 2015). This study is the first to connect how changes in upwelling affect the foraging patterns of seabirds. This is important because it means that we can use seabird diving patterns as insights into the ocean's productivity.

Acknowledgements

I would like to first and foremost thank Dr. Nina Karnovsky for all of her guidance throughout the entire process, as well as Drs. Marc Los Huertos and Char Miller for reading my thesis. I would also like to thank Dr. Andre Cavalcanti for his TDR processing Python code. Thank you to everyone at Point Blue Conservation Science for the amazing experience of working on the Farallones, especially seabird biologists Pete Warzybok and Mike Johns, as well as all of my fellow interns.

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