PLATTE RIVER RECOVERY IMPLEMENTATION PROGRAM

Data Synthesis Compilation

Weight of Evidence Approach to Assessing Relationships between Flow and Interior Least Tern Forage Fish Abundance, Foraging Behavior, Productivity, and Dietary Requirements

PLATTE RIVER
RECOVERY IMPLEMENTATION PROGRAM

Prepared by staff of the Executive Director's Office for the Governance Committee of the Platte River Recovery Implementation Program

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REVIEW DRAFT

PREFACE

This document was prepared by the Executive Director's Office (EDO) of the Platte River Recovery Implementation Program ("Program" or "PRRIP"). The information and analyses presented herein are focused solely on informing the use of Program water and fiscal resources to achieve one of the Program's management objectives: increasing production of interior least tern from the Associated Habitat Reach (AHR) along the central Platte River in Nebraska. The Program has invested eight years in implementation of an adaptive management program to reduce uncertainties about proposed management strategies and learn about species responses to management actions. During that time, the Program has implemented management actions, collected a large body of species response data, and developed modeling and analysis tools to aid in data interpretation and synthesis.

Implementation of the Program's AMP has proceeded with the understanding that management uncertainties, expressed as hypotheses, encompass complex ecological responses to limited treatments that occur within a larger ecosystem that cannot be controlled by the Program. The lack of experimental control and complexity of response precludes the sort of controlled experimental setting necessary to cleanly follow the strong inference path of testing alternative hypotheses by devising crucial experiments (Platt 1964). Instead, adaptive management in the Platte River ecosystem must rely on a combination of monitoring species response to management treatments, predictive modeling, and retrospective analyses (Walters 1997). The Program has pursued all three of these approaches, producing multiple lines of evidence across a range of spatial and temporal scales.

This document is compilation of six sections with unique objectives and analyses that generally are separate and distinct lines of evidence for testing Program hypotheses and answering the associated Big Question. Section 1 was developed to provide background and context to the discussions in the subsequent sections. Section 1 contains: 1) the means by which the Program addresses scientific uncertainties; 2) a brief summary of least tern life history and occurrence in the central Platte River; and 3) relevant data used to address Program uncertainties herein.

Sections 2–4 of this document report analytical methods and results of using the Districts' forage fish sampling data, the Program's foraging ecology data, the Program's productivity data, and flow data collected at United States Geological Survey gaging stations to test three inferred relationships in the hypotheses including: 1) forage fish abundance is related to flow in open channel habitat; 2) foraging behavior and success in open channel habitat is related to forage fish abundance, flow, or both; and 3) given a relationship between forage fish abundance and flow, least tern productivity is related to flow and thus forage fish abundance. We also used the Districts' forage fish data and a review of literature to develop a bioenergetics approach to estimate numbers of least tern family units the AHR could support at various flows in section 5. Finally, in section 6 we summarize all findings related to our weight of evidence approach for testing a Program priority hypothesis and an associated sub-hypothesis.

REVIEW DRAFT

SECTION 1 – Forage Fish Uncertainties and Data Sources

Approach to Addressing Program Uncertainties

The Platte River Recovery Implementation Program (Program) is responsible for implementing certain aspects of the endangered interior least tern (*Sternula antillarum athalassos*; hereafter, least tern) and threatened piping plover (*Charadrius melodus*) recovery plans. More specifically, one of the Program's Adaptive Management Plan (AMP) management objectives is to increase productivity of the least tern and piping plover from the Associated Habitat Reach (AHR) of the Platte River in central Nebraska. This ninety-mile reach extends from Lexington, NE downstream to Chapman, NE and includes the Platte River channel and off-channel habitats within three and one half miles of the river (Figure 1).

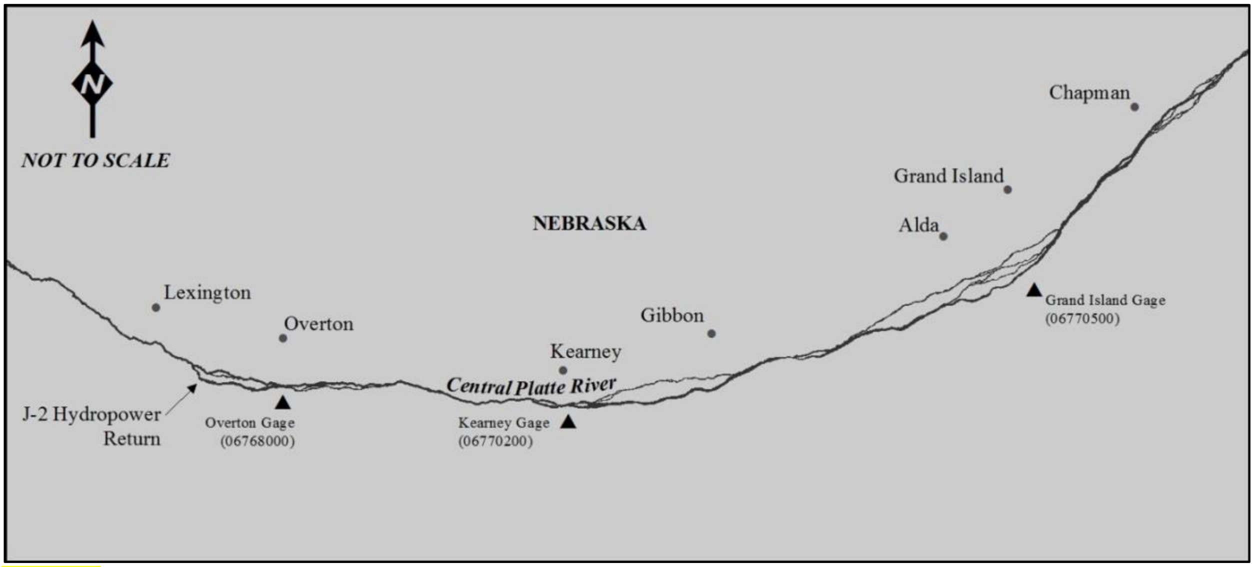


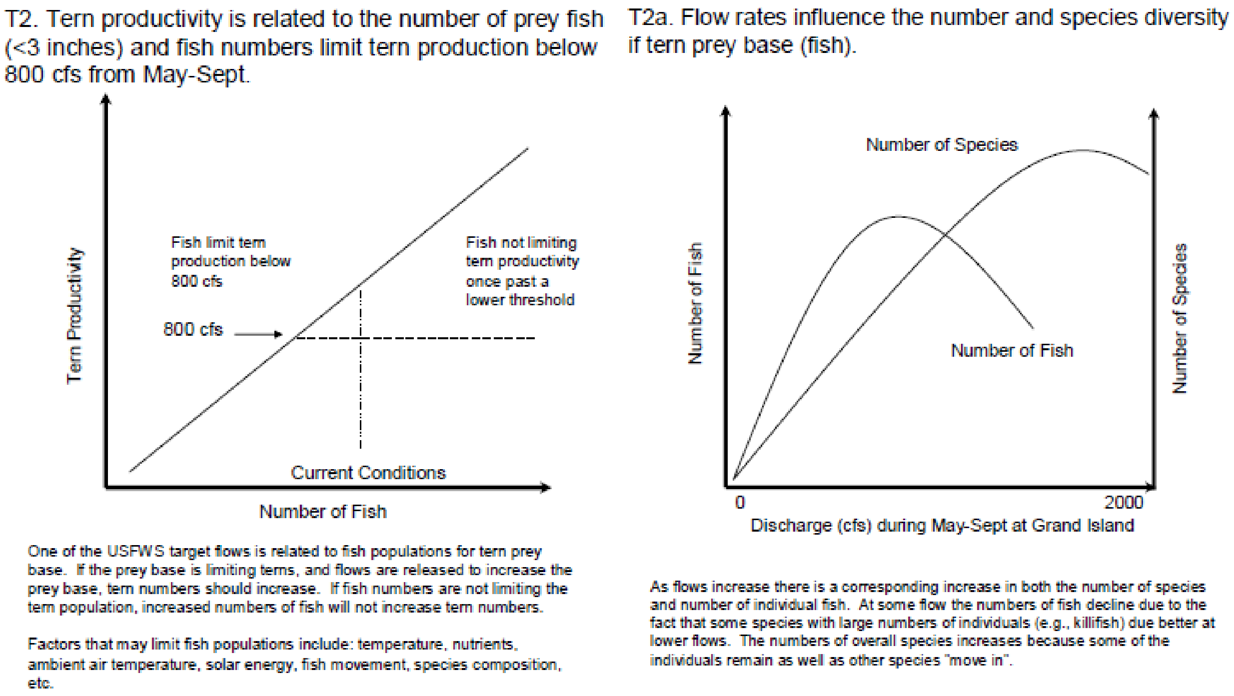
Figure 1. Associated Habitat Reach (AHR) of the central Platte River extending from Lexington downstream to Chapman, Nebraska.

The Program addresses key scientific and technical uncertainties through application of adaptive management. The Program's AMP provides a systematic process to test hypotheses and apply information learned to improve management (Smith 2011). The Program defines adaptive management as "a series of scientifically driven management actions (within policy and resource constraints) that use the monitoring and research results provided by the Integrated Monitoring and Research Plan to test priority hypotheses related to management decisions and actions and apply the resulting information to improve management" (Program 2006). During the negotiation and development phases of the Program, Program participants developed conceptual models to provide a visual framework of the hypothesized understandings of central Platte River processes relative to the target species, including least tern (Smith 2011). A hierarchy of broad and priority hypotheses, management strategies and actions, implementation activities, monitoring protocol development, and data evaluation detailed in the AMP are an extension of the relationships identified in the conceptual models. Based on the objectives and intent of Program broad and priority hypotheses, the Program developed a set of 11 "Big Questions" to summarize a large amount of data into a straight-forward, well-focused, and easy to understand format to assist the Program's Governance Committee in decision making (Program 2013).

Several of the Program's priority hypotheses are focused on relationships between productivity of least terns on the central Platte River and management actions. Among other things, variation in productivity of least terns on the central Platte River has been attributed to several factors including predation events, changes in the amount of natural and manmade nesting habitat, alterations in flow patterns, and abundance of prey fish (Wilson et al. 1993, National Research Council 2004, U.S. Department of the Interior et al. 2006, Jenniges and Plettner 2008).

Within the Great Plains, abundance and diversity of fish occurring in streams has been shown to decrease with groundwater extractions and flow alterations especially when desiccation events occur due to prolonged periods of zero flow (Falke et al. 2011, Perkin et al. 2014). The Program's Biological Opinion includes a USFWS Target Flow of 800 – 1,200 cfs from 11 May – 15 September. One of several purposes for the flow target is to maintain flows in the central Platte River to increase forage fish abundance and diversity to increase productivity of least terns within the AHR (USFWS 2006). It is important to note, however, that this flow target was based on decreasing water temperatures and thus increasing the abundance and diversity of all guilds of fish within the central Platte River, not solely the guilds that include forage fish species for least terns. The Biological Opinion states "no flow (i.e., a dry channel) or very low flow conditions would affect forage fish and, thus, least terns if such a flow event occurred during the nesting season." (USFWS 2006). This assertion is articulated in Priority Hypothesis T2 and sub-hypothesis T2a (Figure 2) in the Program's AMP (Program 2006) that state:

> T2 – Tern productivity is related to the number of prey fish (<3 inches) and fish numbers limit tern production below 800 cfs from May–September.
>
> T2a – Flow rates influence the number and species diversity in tern prey base (fish).



T2. Tern productivity is related to the number of prey fish (<3 inches) and fish numbers limit tern production below 800 cfs from May-Sept.

T2a. Flow rates influence the number and species diversity if tern prey base (fish).

One of the USFWS target flows is related to fish populations for tern prey base. If the prey base is limiting terns, and flows are released to increase the prey base, tern numbers should increase. If fish numbers are not limiting the tern population, increased numbers of fish will not increase tern numbers.

Factors that may limit fish populations include: temperature, nutrients, ambient air temperature, solar energy, fish movement, species composition, etc.

As flows increase there is a corresponding increase in both the number of species and number of individual fish. At some flow the numbers of fish decline due to the fact that some species with large numbers of individuals (e.g., killifish) due better at lower flows. The numbers of overall species increases because some of the individuals remain as well as other species "move in".

Figure 2. Hypothesized relationships between forage fish abundance and least tern productivity (T2; left) and flow and fish abundance and diversity (T2a; right).

The Big Question associated with these hypotheses states: "Does forage availability limit tern […] productivity on the central Platte River?" This question is used to direct a weight of evidence approach to synthesize multiple lines of evidence to assess what the Program has learned about the relationship between forage fish abundance and least tern productivity. This synthesis document is the result of that approach and will be used by the Program to assess the Big Question and its impact on Program decision-making.

Least Tern Life History

The least tern was listed as endangered on June 27, 1985 (USFWS 1990); however, a recently completed five-year review recommends delisting least terns due to recovery (USFWS 2013). The USFWS is now in the process of putting in place the necessary monitoring plans, conservation agreements, and population models in hopes of moving forward with a proposed delisting in the near future. The breeding range for least terns spans from Montana to Texas and from Eastern New Mexico and Colorado to Indiana and Louisiana (USFWS 1990). Least terns are a colonial nesting bird that mobs predators or other intruders by dive-bombing and defecating on them. The species breeds and nests on barren to sparsely vegetated riverine sandbars, sand and gravel pits, lake and reservoir shorelines, rooftops, ash pits, and salt flats from late April to early August. The central Platte River Valley in Nebraska, USA supports a small population of least terns that typically utilize manmade river sandbars and off-channel habitats (i.e., sandpits) that are managed specifically for nesting; however, a small proportion (<10%) have nested on unmanaged sandbars and sandpit sites (Jenniges and Plettner 2008, Baasch 2014). Least terns usually lay two to three eggs in a shallow scrape and may renest if their nest is destroyed (USFWS 1990). The incubation and brood rearing period for nests and chicks generally lasts from 38 to 50 days. Although the persistence of least terns along the central Platte River has been dependent on manmade habitat for nesting, this piscivorous species relies heavily on the river for foraging (Wilson et al. 1993, Sherfy 2012).

During the nesting and brood rearing season, least tern forage on small fish (<7.6 cm; 3 in) they capture by diving into shallow riverine habitats and freshwater ponds. However, least terns forage most intensively and successfully in the river channel (Wilson et al. 1993, Sherfy et al. 2012). Least terns are a semi-altricial species and thus chicks are not capable of foraging on their own so only a single brood is raised each year as adults must continue to feed offspring for several weeks after fledging. Based on sampling data, the predominant species of forage fish available for least terns included red shiner (*Cyprinella lutrensis*), sand shiner (*Notropis stramineus*), bigmouth shiner (*Notropis dorsalis*), brassy minnow (*Hybognathus hankinsoni*), mosquitofish (*Gambusia affinis*), plains killifish (*Fundulus zebrinus*) and unidentifiable young-of-the-year fish species (Program 2013). These six species and unidentifiable young-of-the-year fish accounted for >75% of all fish captured in each sample. Similarly, Wilson et al. (1993) reported 79% of identifiable fish that were captured and carried to a nest by least terns were cyprinid species. As such, we limited our definition of forage fish to these six species and unidentifiable young of the year fish.

Least tern observations in the AHR prior to systematic monitoring

Historical records of least tern occurrence in Nebraska were compiled by Ducey (1985, 2000) and Pitts (1988). The first recorded observation of least terns in what is now Nebraska was made near the mouth of the Platte River in 1804 by the Lewis and Clark expedition as they traveled up the Missouri River. The next recorded observations were made by Duke Paul Wilhelm at the mouth of the Platte River in 1823. Subsequent observations in the 19th century include the Loup River in 1857, the North Platte River in Keith County in 1859, and on the banks of a wetland basin near York, Nebraska in 1896 and 1897 (Ducey 2000, Pitts 1985). Least terns were next observed nesting on the South Platte River near the city of North Platte in 1926-1929 with 57 nests recorded as well as documentation of foraging movements to the North Platte River and sand pit lakes when the South Platte River went dry (Tout 1947).

The next recorded least tern observation on the Platte River occurred near Columbus in 1941, the same year that Lake McConaughy, the largest reservoir in the basin, was completed. Ten nests were observed on river sandbars (Shoemaker 1941). The first recorded least tern observations in the Program's AHR occurred in 1942 when a colony was discovered nesting on the river near Lexington, Nebraska by Dr. Ray S. Wycoff. Dr. Wycoff studied the colony for 17 years and observed nesting on a low sandbar in the channel, high in-channel island created by sand mining, and at adjacent sandpits (Wycoff 1960). In 1943, a single nest was observed on a swimming lake beach near Plattsmouth (Heineman 1944). In 1948 and 1949 least tern were again observed nesting on the South Platte River (Benckeser 1948, Audubon Field Notes).

Pitts (1988) compiled records from the Proceedings of the Nebraska Ornithologists Union, Wilson Bulletin, and Nebraska Bird Review and other sources to identify annual adult and nest sightings by county for the period of 1804-1984. Records of adult and nest sightings in the AHR began with Dr. Wycoff's observations which account for the majority of AHR records. Other observations prior to the first systematic survey results for the AHR in 1979 include one mid-reach adult observation in 1960 and observations of adult birds in the downstream portion of the reach in 1953, 1954, 1957, 1959, and 1973.

Systematic monitoring of least tern in the AHR

Intermittent systematic monitoring of least tern occurrence and productivity has been conducted in the AHR since 1979 with variable degrees of monitoring effort expended every year after 1982 (Pitts 1988, Lingle 2004, Baasch 2010, 2012, 2014). Since 2001, efforts have included systematic monitoring of least tern habitat use and productivity within the AHR. Since 1979, a total of 1,946 least tern nests have been documented in the AHR (Table 1; Figure 3). Of all nests documented in the AHR, 89.1% of least tern nests occurred on off-channel sandpit habitat. Approximately 3.1% of least tern nests occurred on natural sandbars; the remaining in-channel nests were observed on islands that were mechanically created and maintained as nesting habitat.

Table 1. Central Platte River nest incidence by habitat type, 1979-2013.

Habitat Type	**Interior Least Tern**	
	Count	**Percent**
Sandpit	1,733	89.1%
Natural Sandbar	61	3.1%
Constructed or Managed Sandbars	152	7.8%
Total	**1,946**	**100.0%**

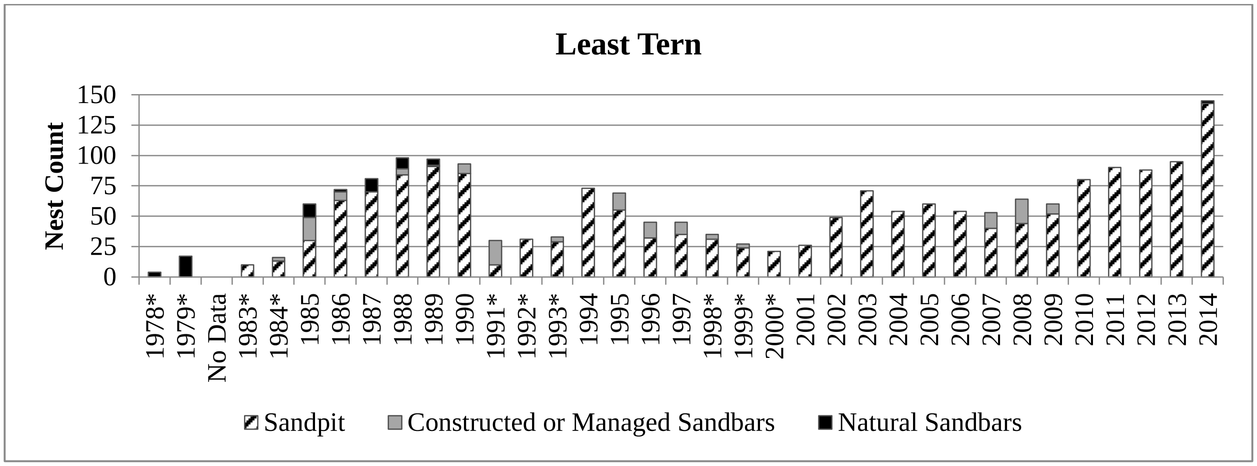


Figure 3. Central Plate River least tern nest incidence by year and habitat type, 1978-2013. Asterisks indicate periods when monitoring effort changed substantially.

Least tern productivity data

Least tern nests and broods were monitored at least twice weekly from 2001–2014 where nesting occurred within the AHR (Figure 4; Program 2011). These data contain, among many other variables, the number of eggs that hatched, date nests hatched, fate of broods (fledged, failed, unknown), date the brood's fate was determined, and the number of successful fledglings in each brood. The fate of the brood was recorded as "fledged" if one or more chicks from each brood were observed approximately 21 days after hatching or when sustained flight was observed if <21 days. A fate of "failed" was recorded if no chicks were observed as fledglings or if mortality was confirmed. A fate of “unknown” was assigned to broods when chicks were observed within a few days of the fledging age (i.e., 21 days after hatching), but no fledglings were actually observed.

Monitoring Forage Fish Abundance in the AHR

On January 25, 1999 the Central Nebraska Public Power and Irrigation District (CNPPID) and the Nebraska Public Power District (NPPD; known collectively as the Districts) filed a plan with the Federal Energy Regulatory Commission to, among other things, monitor least tern productivity and forage availability for least terns at habitat areas managed by the Districts. The objective of the forage fish monitoring program was to monitor the abundance of forage fish for least terns and evaluate fish species diversity on or near areas owned or managed by the Districts. As such, forage fish abundance and diversity were sampled periodically from 1999–2014 using the Districts’ forage fish monitoring protocol. Four sampling sites were established based on their close proximity to areas managed as least tern nesting habitat in 1999. A fifth sampling location near Alda, Nebraska was added in 2003 (Figure 4). Forage fish sampling generally occurred during the latter portion of the least tern nesting season in 1999, 2003, 2005, and 2007–2010. In any given year, data collection generally occurred over a few consecutive days (range of 2–7 days); however, the date sampling was initiated ranged from 23 June to 13 August.

Each area sampled included a 200 m (219 yd) reach of river with areas classified as open channel habitat which was defined as the flowing portion of the active channel area >23 m (25 yd) wide. Open channel areas were sampled using 0.3 cm (1/8-inch) mesh seines to enclose an area 7.5 m by 15 m (112.5 m^2; 8.2 yd by 16.4 yd; 134.5 yd^2). At each site, five to ten samples were obtained; total number of samples at each site depended on the available channel area. The location of sampling at each site was chosen to be representative of open channel areas. Sampling at a site did not occur if flows were too high or water was not present. A total of 237 samples were obtained to document fish abundance and diversity during the study period 1999–2010.

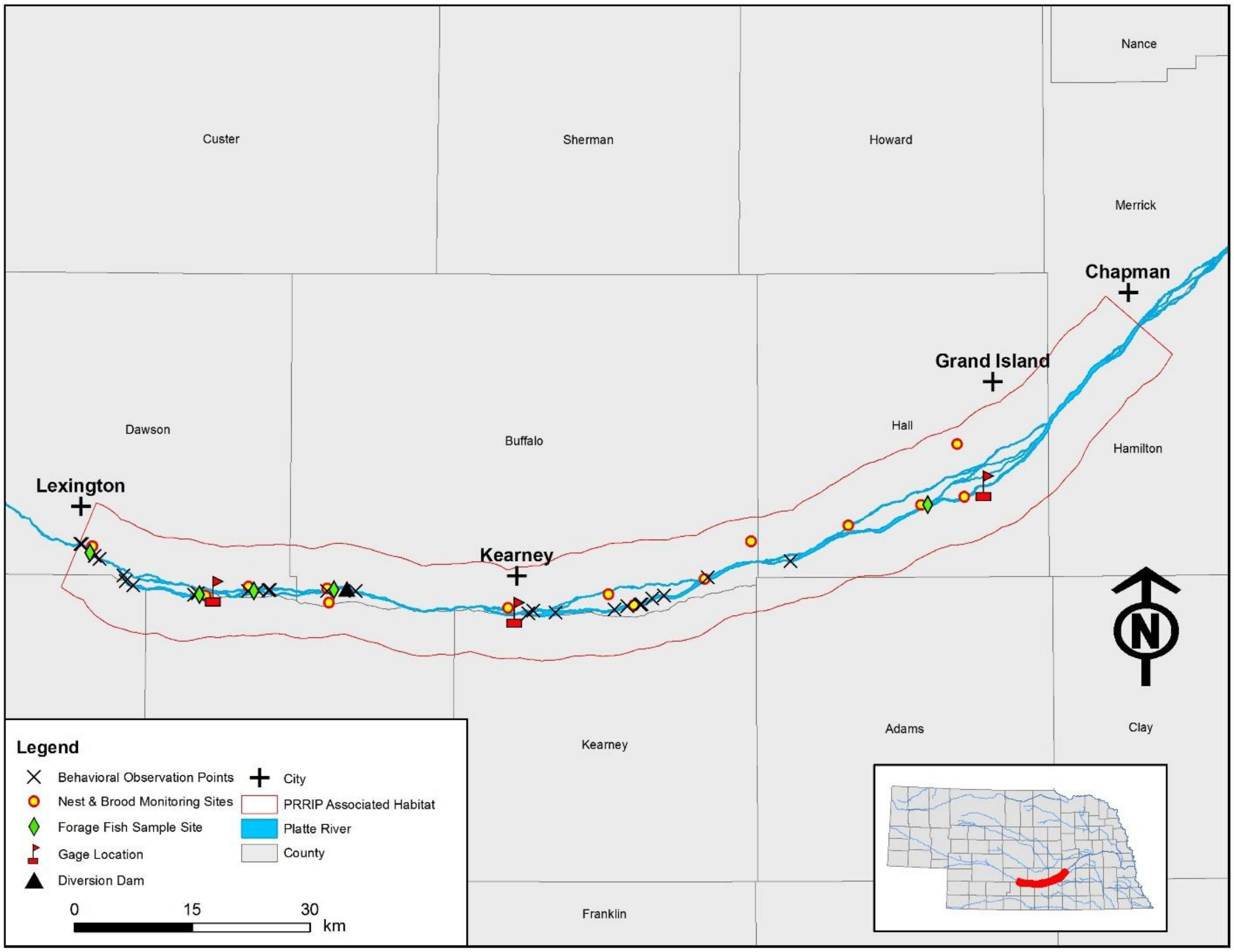


Figure 4. Study area (Associated Habitat Reach) showing data collection sites and other important features.

All captured fish were counted and identified to species or were classified as young-of-the-year if they were too small to identify. We limited our analysis to fish species and age classes generally of an appropriate size (<7.6 cm; 3 in) for least tern forage. The species included in our analysis were: red shiner (*Cyprinella lutrensis*), sand shiner (*Notropis stramineus*), bigmouth shiner (*Notropis dorsalis*), brassy minnow (*Hybognathus hankinsoni*), mosquitofish (*Gambusia affinis*), plains killifish (*Fundulus zebrinus*) and unidentifiable young-of-the-year fish species (Program 2013). These six species and unidentifiable young-of-the-year fish accounted for >75% of all fish captured in each sample.

Monitoring Foraging Habits of Least Terns in the AHR

In 2009 the Program implemented a foraging habits study to document foraging activity of least terns along the central Platte River valley (Sherfy et al. 2012). The purposes of the foraging habits study was to help determine if prey base availability limits reproductive success of least terns on the central Platte River and to attempt to isolate the effects of foraging habits on productivity from other influences such as predation and human disturbance. Sherfy et al. (2012) recorded behavioral observations of least terns at sandpits and riverine sites. During the months of June–August (2009–2010) least tern behavior was observed during 378 sessions (358 hours) conducted opportunistically or during three 4-hour periods between sunrise and sunset (0600–1000, 1200–1600, and 1700–2100 h). The majority of observation sessions (*n*=306) and time (310 hours) occurred at sandpits or at Nebraska Public Power District's Kearney Canal Diversion (Figure 1). The remainder of the sessions (*n*=72) and time (48 hours) focused on two sandbar colony sites and open river channel (hereafter, river channel sessions). We used only river channel sessions in our analysis because we were interested in how foraging behavior is influenced by flow and fish abundance in open river channel habitat and not at sandpits or a division structure. Behaviors were observed using binoculars or spotting scopes from ground blinds at sandpits, river banks and sandbars, canoes, and an airboat. Many behavioral types were reported including three directly related to least tern foraging: 1) successful plunges; 2) unsuccessful plunges (including dives that do not end in a plunge into the water) and; 3) plunges for which the capture success was unknown. From this we constructed a data set to record the date, location, length of the session (to the nearest minute), total number of successful plunges, unsuccessful plunges, and plunges with unknown success. See Sherfy et al. (2012) for more details.

It is important to note that data collected by Sherfy et al. (2012) was the result of two different study designs. The first design involved systematic observations taken by going to a location and making observations (e.g., observations from the blind) while the second design involved opportunistic observations (e.g., from an airboat after observing least terns in a given area). Clearly, the opportunistic observations were likely to have higher rates of plunging because observations were conditional on least terns being present. Due to small sample size, we choose not to analyze both types separately, that is, we analyzed both types of observation as if they were interchangeable.

Central Platte River Flow Data

We obtained mean daily flow (m^3s^{-1} and ft^3s^{-1}) records from U.S. Geological Survey gaging stations on the Platte river near the cities of Overton (06768000), Kearney (06770200) and Grand Island, Nebraska (06770500) from May 1999 to August 2010. Our analyses of the forage fish data used mean daily flow records on the date of sampling from the nearest gaging station as a covariate.

Synthesizing Data

Subsequent sections of this document report the results of using the Districts' forage fish sampling data (CNPPID and NPPD 2013), the Program's foraging ecology data (Sherfy et. al. 2012), the Program's productivity data (Baasch 2014), and flow data collected at United States Geological Survey (USGS) gaging stations to test three inferred relationships in the hypotheses including: 1) forage fish abundance is related to flow in open channel habitat (Districts' forage sampling data and flow records); 2) foraging behavior and success in open channel habitat is related to forage fish abundance, flow, or both (Districts' forage sampling data, Program's foraging ecology data, and flow records); and 3) given a relationship between forage fish abundance and flow, least tern productivity is related to flow and thus forage fish abundance (Program's tern and plover monitoring data and flow records). We also used the Districts' forage fish data and a review of literature to develop a bioenergetics approach to estimate numbers of least tern family units (assuming 2 adults and 3 chicks) the AHR could support at various flows (forage fish data and literature review).

SECTION 2 – Relationship between Forage Fish Abundance and Flow

Priority hypothesis T2 in the Program's Adaptive Management Plan (AMP) deals with concerns over the relationship between least tern productivity on the central Platte River and the availability of forage fish in the river (Program 2006). A sub-hypothesis (T2a) postulates a non-linear relationship between the number and diversity of fish and river discharge (Program 2006). As such, the Big Question associated with this hypothesis states: "Does forage availability limit tern […] productivity on the central Platte River." To provide a line evidence for answering the Big Question and assessing this premise, we used forage fish sampling data collected by the Districts (CNPPID and NPPD 2013) and flow records from USGS gaging stations to determine impacts of river discharge and other factors on forage fish availability. We use these results to begin to build empirical evidence to test the forage fish-related hypotheses in the AMP.

Forage fish model

Our first assumption regarding the priority hypothesis was that flow was related to forage fish abundance in open channel habitat. Therefore we developed a regression model to establish a relationship between flows and forage fish abundance in open channel habitat as follows. Let x_i correspond to the observed catch in the i^{th} seine, for $i = 1,2,\ldots,237$. We let this count have a negative binomial distribution with mean μ_i and dispersion ϕ:

$$x_i \sim Negative\ Binomial(\mu_i, \phi). \tag{3.1}$$

Under this parameterization, the expected value of x_i is μ_i and the variance of x_i is $\mu_i + \phi\mu_i^2$. We assumed the log of the expected catch per seine depends linearly on flow:

$$\log(\mu_i) = \beta_1 + \beta_2 f_i, \tag{3.2}$$

where β_1 is the log expected catch per seine at a flow of 0.0 m^3s^{-1} (0.0ft $^3s^{-1}$) and β_2 is the coefficient that determines how the expected catch per seine depends on the mean daily flow at the nearest gaging station to site *i* on the day of seining (f_i). Since each seine sampled an area of 112.5 m^2 (134.5 yd^2) we reported quantities of interest per m^2 (e.g., $\mu_i/112.5\ m^2$).

To assess the fit of our model, we present posterior predictive model checks. Posterior predictive checks, show agreement (or discrepancy) between the fitted model and the observed data and can be used to asses model adequacy (Gelman *et al.* 2013).

Results

We found expected forage fish densities ($\mu_i/112.5\ m^2$) decreased as flow increased (Figure 5). The number of fish caught per seine was highly variable; however, the negative binomial distribution appears to capture this variability as the posterior median of ϕ was relatively large. Because of the variability in the seining data, our predicted fish densities were also highly variable (Figure 6). The posterior predictive distribution shows agreement between the fitted model and the observed data (Figure 6). This suggests our forage fish model with the single flow covariate is adequate.

Discussion

Previous investigations of tern foraging behavior, as well as observations of least terns foraging on the central Platte River, generally indicate a selection for foraging in open channel habitat provided by the river (Wilson *et al.* 1993; Tibbs & Galat 1998; Sherfy *et al.* 2012). Because of least tern foraging behavior and the proximity of our five sampled sites to areas with the highest nesting densities in the AHR, we expect the sampling design was representative of the open channel habitat readily available to least terns at areas managed as nesting habitat. We note, however, the sampling design was not a random set of sites (or similar design) within the AHR that would lead to broader inference. Because of this, our results should not be extrapolated to the entire AHR. That is, our results cannot be used to determine the relationship between forage fish abundance and species diversity and discharge metrics across the entire AHR (see Section 6).

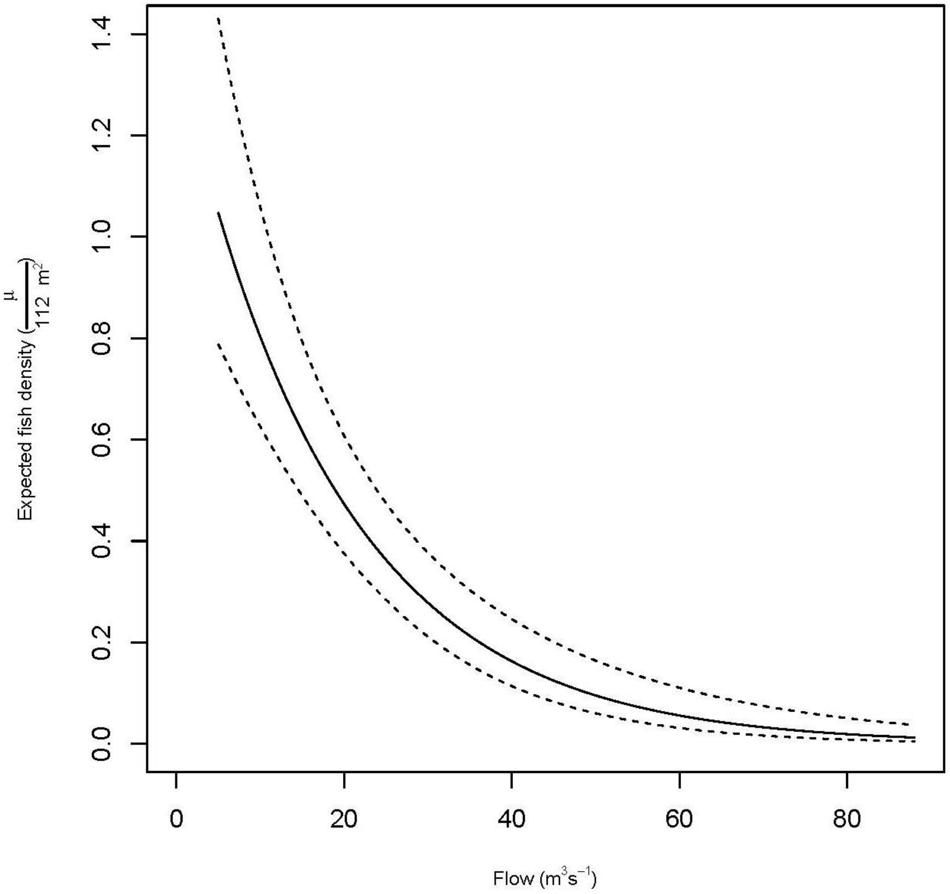


Figure 5. Regression model (Eq. 3.1–3.2) showing the relationship between expected forage fish density ($\mu / 112.5\ m^2$) and average daily flow the day seining occurred (posterior median = solid black line; 95% CIs = dashed black lines).

We expected and found a nonlinear relationship between forage fish abundance and discharge metrics. Our results indicate expected forage fish abundance are highest at low mean daily flows on the day of sampling (hereafter referred to as flows) and declined as flow increases. For the forage fish abundance data, the effect is relatively small in comparison to the variability in the data (Figure 6).

However, at very low flows we would expect seining to result in higher catches of forage fish and this results is corroborated by the observed data (Figure 6).

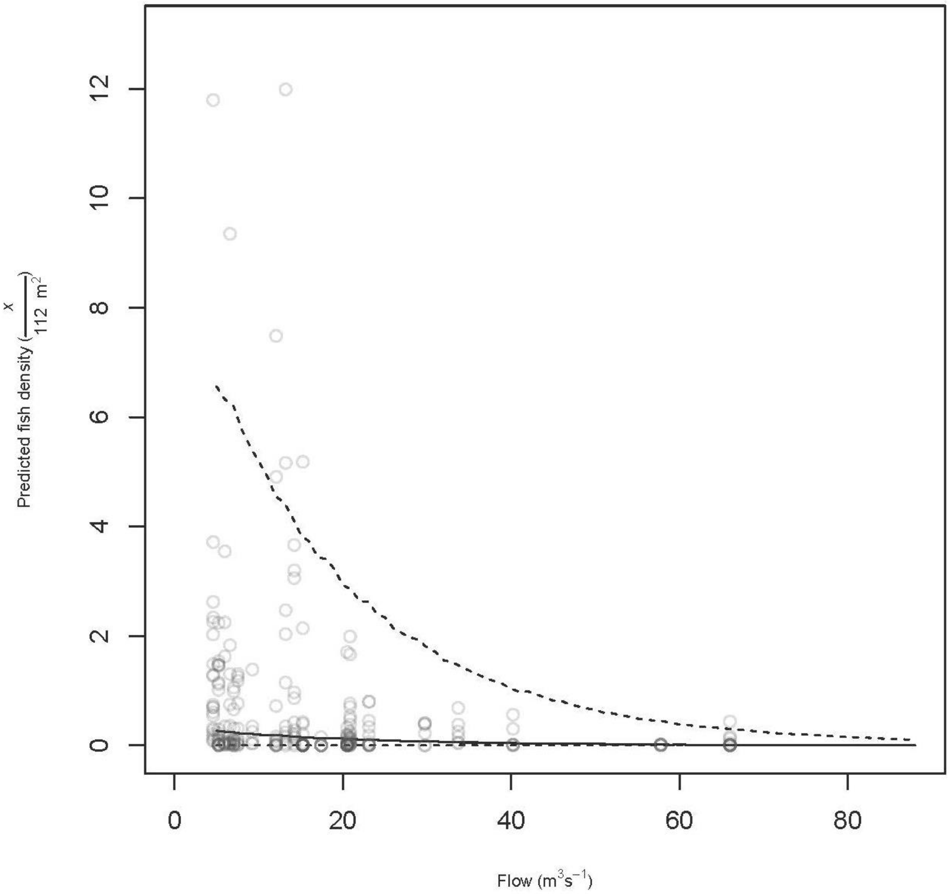


Figure 6. Regression model (Eq. 3.1–3.2) showing the relationship between predicted forage fish density $(x/112.5\ m^2)$ and average daily flow the day seining occurred (posterior median = solid black line; 95% PIs = dashed black lines).The gray circles show the observed data (i.e., number of fish caught in each seine/112.5 m^2; 134.5 yd^2).

These results need to be interpreted with caution due to variable catchability. Variation in catchability occurs when the probability a fish is captured is less than one and variable from sample to sample. For detection of trends, variable catchability is a concern if the probability of catching an individual depends on the explanatory variables (e.g., flow) or other unmeasured variable that correlates with the predictors used in our analysis. For example, assume forage fish abundance is constant across mean flow on day of sampling. Then assume the probability of catching forage fish is near one at low flows, but the probability is near zero at high flows. The number of forage fish caught while seining will be much greater when the flow is low. If this scenario were true, the forage fish abundance would appear to decline as flows increased. Variable catchability, also known as non-detection, has the potential to be the sole driver of the trend in our analysis. However, given the data used in our analysis, we cannot confirm, nor refute, this claim.

Summary

Based on the Districts' forage fish sampling data and USGS flow records, we were able to establish a relationship between forage fish abundance and mean daily flows. This relationship was opposite of what was hypothesized as the abundance of forage fish caught in each sample, though variable, was higher during periods of low flow. Results of this investigation, however, should not be used as the sole source of evidence that forage fish abundance does not limit least tern productivity as the relationship we found was small as compared to variability in sampling data and potential differences in catchability under various flow conditions.

SECTION 3 – Relationships between Flow, Forage Fish Abundance, and Interior Least Tern Foraging Behavior and Success

We used data collected by the Districts and least tern foraging behavior data to provide another line evidence for answering the Big Question and assessing this premise. The objective of this evaluation was to determine impacts of flow and forage fish abundance on least tern foraging behavior and success in open channel habitat. Although indirect to productivity of least terns, we might expect flow and forage availability to influence foraging behavior and success of the birds. We use this indirect evidence to build empirical support to test the forage fish-related hypotheses in the Program's AMP (Program 2006).

Least tern foraging model

We constructed two models. We related the total number of plunges observed during each behavioral session to a set of covariates in model one. In model one, y_j corresponded to total number of plunges (successful, unsuccessful and unknown outcome) that occurred during the j^{th} behavioral observation session for j = 1,2,…72. We assumed y_j followed a negative binomial distribution with expected value λ_j and dispersion θ:

$$y_j \sim Negative\ Binomial(\lambda_j, \theta). \qquad (4.1)$$

The log of the expected plunge rate (λ_j) depended on three covariates:

$$\log(\lambda_j) = \beta_3 + \beta_4 \frac{x_j}{112.5\ m^2} + \beta_5 f_j + \beta_6 {f_j}^2 + \beta_7 \log(h_j), \qquad (4.2)$$

which are the predicted fish abundance per m^2 ($x_j/112.5\ m^2$), mean daily flow at the location on the day of the observation (f_j) and the session length in hours (h_j). The numerator in the predicted fish abundance per m^2 in eqn 3.2 (i.e., x_j) was predicted from the model described in eqn 3.1 and 3.2 in Section 3. We used the forage fish model to predict fish abundance for flow (f_j).

We related the number of fish captured during each behavioral session to a set of covariates in model two. The observed number of fish captured (z_j) in the j^{th} session followed a binomial distribution with total number of plunges (N_j) and probability of success (π_j):

$$z_j \sim Binomial(N_j, \pi_j), \quad (4.3)$$

where N_j is the observed sum of the number of successful and unsuccessful plunges. The logit of π_j depends on fish abundance per m^2 and mean daily flow at the location on the day of the observation:

$$\text{logit}(\pi_j) = \beta_8 + \beta_9 \frac{X_j}{112.5\ m^2} + \beta_{10} f_j + \beta_{11} {f_j}^2. \quad (4.4)$$

We were also interested in the expected catch rate (γ_j), which we define as the expected plunge rate multiplied by the probability a plunge results in a fish capture:

$$\gamma_j = \lambda_j \pi_j\ . \quad (4.5)$$

Biologically, we expected the plunge rate and probability of fish captured to depend on both flow and forage fish abundance. We expected plunge rates and capture success were higher at locations with greater fish densities. Likewise, because it seems there would be a minimum depth of water a least tern can plunge into without injury, we expected flow to influence the plunge rate (i.e., least terns would not plunge because the water is too shallow) or capture success (i.e., least terns dive but do not plunge into the water). We also expected plunge rate and probability of fish capture to decrease as flow increased because at higher flows the water in the channel is deeper, moves with greater velocity, and is more turbid. Under these conditions, forage fish may not be visible or catchable (i.e., forage fish may be located at depths greater than the maximum viewing or diving capabilities of least terns). Allowing for a quadratic effect of flow in eqn 3.2 and 3.4 captured this dynamic.

Use of forage fish model

The least tern foraging model required, as a covariate, the density of forage fish present at each plunge location. We did not have data pertaining to the density of forage fish present at each location during the time a plunge was observed. Furthermore, it is not clear how forage fish abundance could be measured instantaneously at each plunge location (although see Safina & Burger 1985). We have the required data at several locations and points in time, but not at the locations or time we need. This is a common problem in spatial statistics and is known as spatial misalignment (Carol & Young 2002). A solution to this problem is to make a prediction of the covariate at the location and time when and where it is needed. For example, it is common to use environmental data (e.g., average temperatures) collected at various locations (e.g., weather stations) to provide predictions across a spatial domain (e.g., the United States). The predicted covariates are then extracted, usually from geographic information systems, and treated as if they were actually measured at the location and time the biological data was collected. This process, however, can produce inference biases if uncertainty in predictions is not accounted for (Foster *et al.* 2012; Stoklosa *et al.* 2014).

We used the predicted abundance as a surrogate for measured fish abundance at each observation location in our analysis. We incorporated prediction error into our Bayesian hierarchal models (Cressie *et al.* 2009; Cressie & Wikle 2011). For the purposes of this study, we implemented the negative binomial regression model to: 1) make inference with regard to the relationship between forage fish abundance and flow, and 2) predict forage fish abundances for use as a covariate.

Model selection and inference

Model selection for our model could occur at many levels. For example, we could test if the negative binomial distribution fit the data better than a Poisson distribution. We could try to determine if the functional form, for example in eqn. 3.2, best fit the data. We could also try to determine which β's should be included in the model. The first two examples involved checking model assumptions, which can also be accomplished by posterior predictive checks (Gelman *et al.* 1996, 2013). We preformed posterior predictive checks on our model to assess model assumptions and show the results for the two best models. We then proceeded with model selection, where our goal was to determine which, if any, covariates—forage fish, abundance, or flow—effectively predicted tern forage rate and forage success.

We agree with Hooten & Hobbs (2014) that out-of-sample validation would be the gold standard for predictive model selection, however, we feel our datasets were too small to split into training and test sets. As such, we used K-fold cross validation which required K runs of the Markov Chain Monte Carlo (MCMC) algorithm as recommended by Hooten and Hobbs (2014). For our model, we defined the score function as:

$$-2\sum_{k=1}^{K}\log\left(\frac{\sum_{t=1}^{T} Negative\ Binomial(\boldsymbol{y}|\boldsymbol{\mu}(t),\phi(t)\cdot Binomial(\boldsymbol{z}|\boldsymbol{N},\pi(t))}{T}\right), \tag{3.6}$$

where K is the number of folds and T is the MCMC iteration in the Kth fold. We calculated the score for four different models where the plunge rate and fish capture rate depended on: 1) fish abundance and flow (M1); 2) flow only (M2); 3) fish abundance only (M3); and neither flow or fish abundance (M4). We assumed plunge rate depended on effort in all four models. We identified the best predictive model by finding the model with the smallest value of the score function using 10-fold cross validation (i.e., K=10 in Eq. 8).

Finally, we reported the median and 95% equal-tailed credible intervals (CIs) for the posterior distributions of the expected plunge rate, the probability of fish capture, and the expected capture rate for the model or models with the lowest score after model selection. We calculated the median and 95% CIs for all variables that depended on the covariate for a grid of values between the minimum and maximum observed from the data so that, when plotted against the covariate, the lines appeared continuous. We standardized all quantities that depended on survey effort (eqn 3.2 and 3.4) to an hourly rate (i.e., $h = 1$).

Results

Results of cross-validation indicate M4 (score = –9.5) had the highest predictive ability which suggests neither fish density nor flow influenced plunge and fish capture rates. The model that only allowed for an influence of flow (M2), however, had only slightly less predictive ability (score = –8.8). Both M1 (score = 20.0) and M3 (score = 11.5), which allowed for an influence of fish density on plunge and fish capture rates, had much lower scores indicating the predictive ability of those model was degraded. We present results for M4 and M2 since these models had the lowest, but nearly equal scores. We present results of M2 (second ranked model) in more detailed given M4 (top model) suggests neither flow nor fish density influenced plunge and fish capture rates, and thus a detailed presentation is not necessary (Figure 7–10).

Presented as an hourly rate (i.e., h = 1), M2 indicates the expected plunge rate increased from around 4 plunges per hour at the lowest observed flows (5 m^3s^{-1}; 177 ft^3s^{-1}) to a peak of 9 plunges per hour at flows of 45 m^3s^{-1} (1,589 ft^3s^{-1}). After the peak of 9 plunges per hour, the plunge rate decreased to around 3 plunges per hour at the highest observed flow (87 m^3s^{-1}; 3,072 ft^3s^{-1}). The probability of fish capture increased from approximately 0.10 at 5 m^3s^{-1} (177 ft^3s^{-1}) to around 0.30 at 87 m^3s^{-1} (3,072 ft^3s^{-1}). When the plunge rate and probability of fish capture were combined, the catch rate increased from 0.25 fish per hour at 5 m^3s^{-1} (177 ft^3s^{-1}) to about 2.00 fish per hour around 60 m^3s^{-1} (2,119 ft^3s^{-1}), but decreased at higher flows. Based on incidental field observations, we assume the variability in catch rates are more an artifact of changes in foraging strategy (skimming verses plunging to capture forage) than forage fish abundance. It is also important to note that 95% CIs for all relationships are wide, particularly at higher flows, which indicates there is a lot of uncertainty in the relationships at high flows.

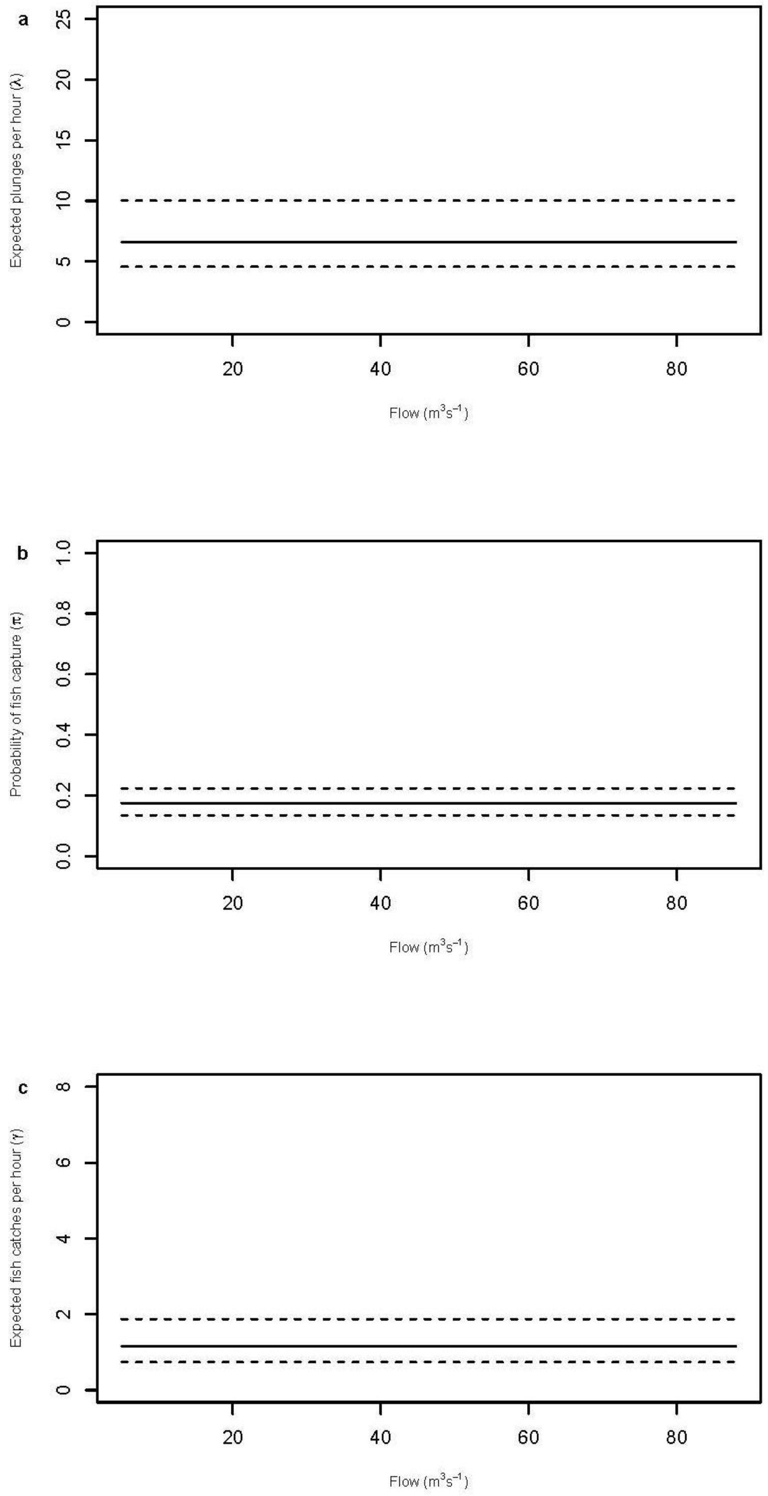


Figure 7. Hierarchal regression model (Eq. 4.1–4.5) showing the relationship between average daily flow on the day of the observation and expected plunge rate (λ; a), probability of fish capture (π; b) and expected fish capture rate (γ; c). Results shown are for model M4, which was the best predictive model. In each figure the posterior median (solid lines) and 95% CIs are shown (dashed lines).

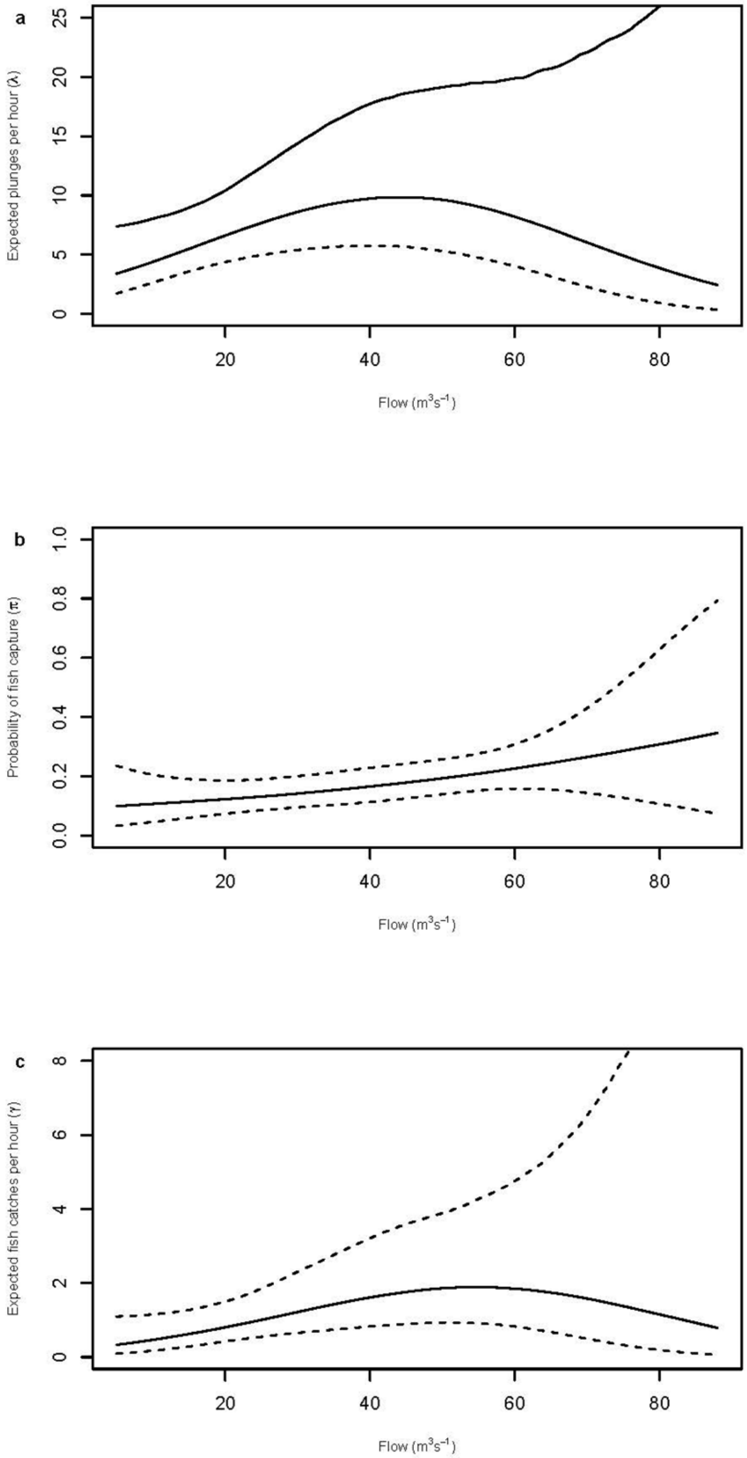


Figure 8. Hierarchal regression model (Eq. 4.1–4.5) showing the relationship between average daily flow on the day of the observation and expected plunge rate (λ; a), probability of fish capture (π; b) and expected fish capture rate (γ; c). Results shown are for model M2, which was the second best predictive model (see Fig. 3 for best model). In each figure the posterior median (solid lines) and 95% CIs are shown (dashed lines).

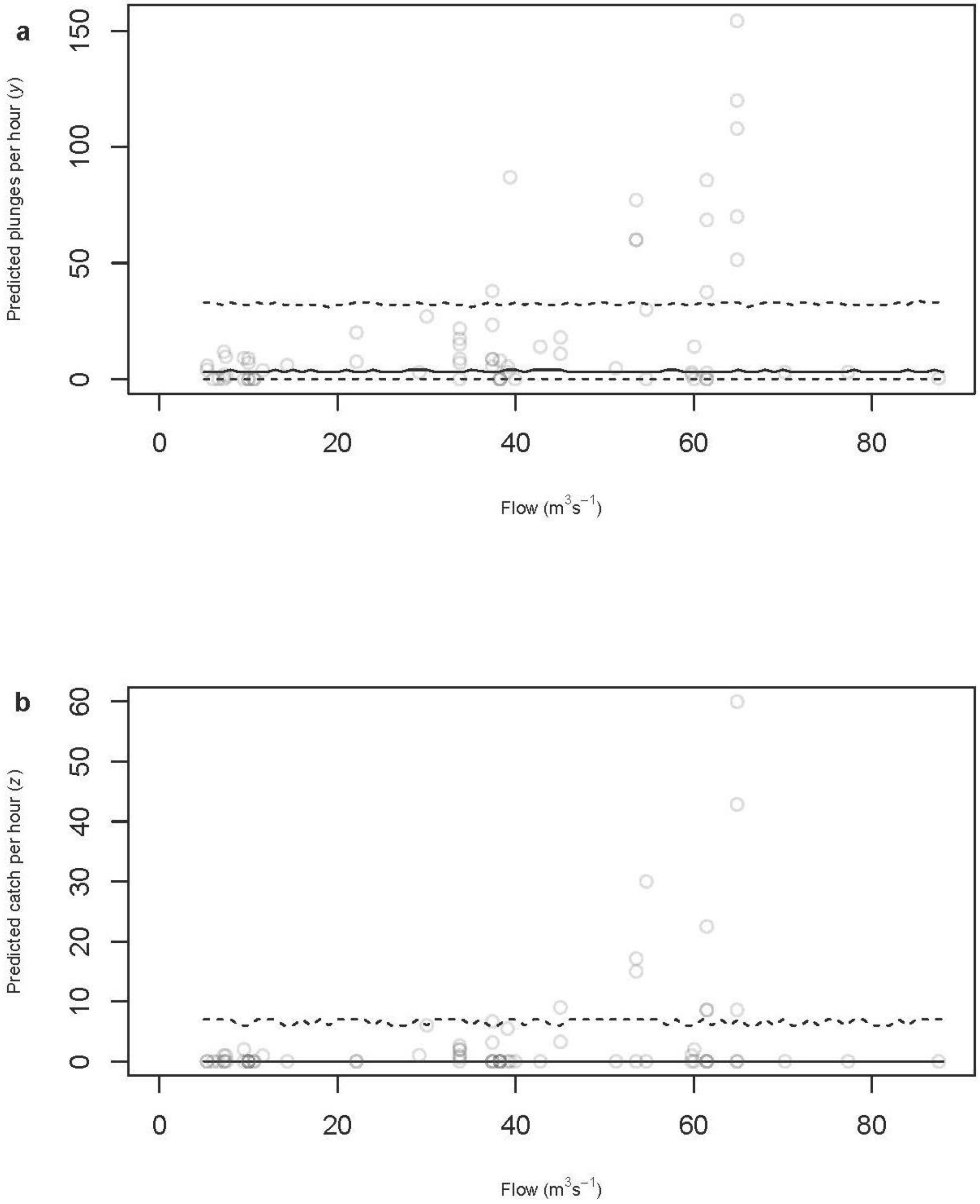


Figure 9. Posterior predictive plots from a hierarchal regression model (Eq. 4.1–4.5) showing how the observed plunge rate (*y*; **a**) and catch rate (*z*; **b**) is related to average daily flow on the day of observation (median and 95% CIs). Results are for model M4, which was the best predictive model. See Fig. S1 for alternative results which suggest flow may have a slight influence on *y* or *z*. Gray circles designate the raw data. Note both the observed *y* and *z* have been scaled to an hourly rate. Also note the high values for the observed plunge and catch rate are mostly due to opportunistic samples that were short in duration.

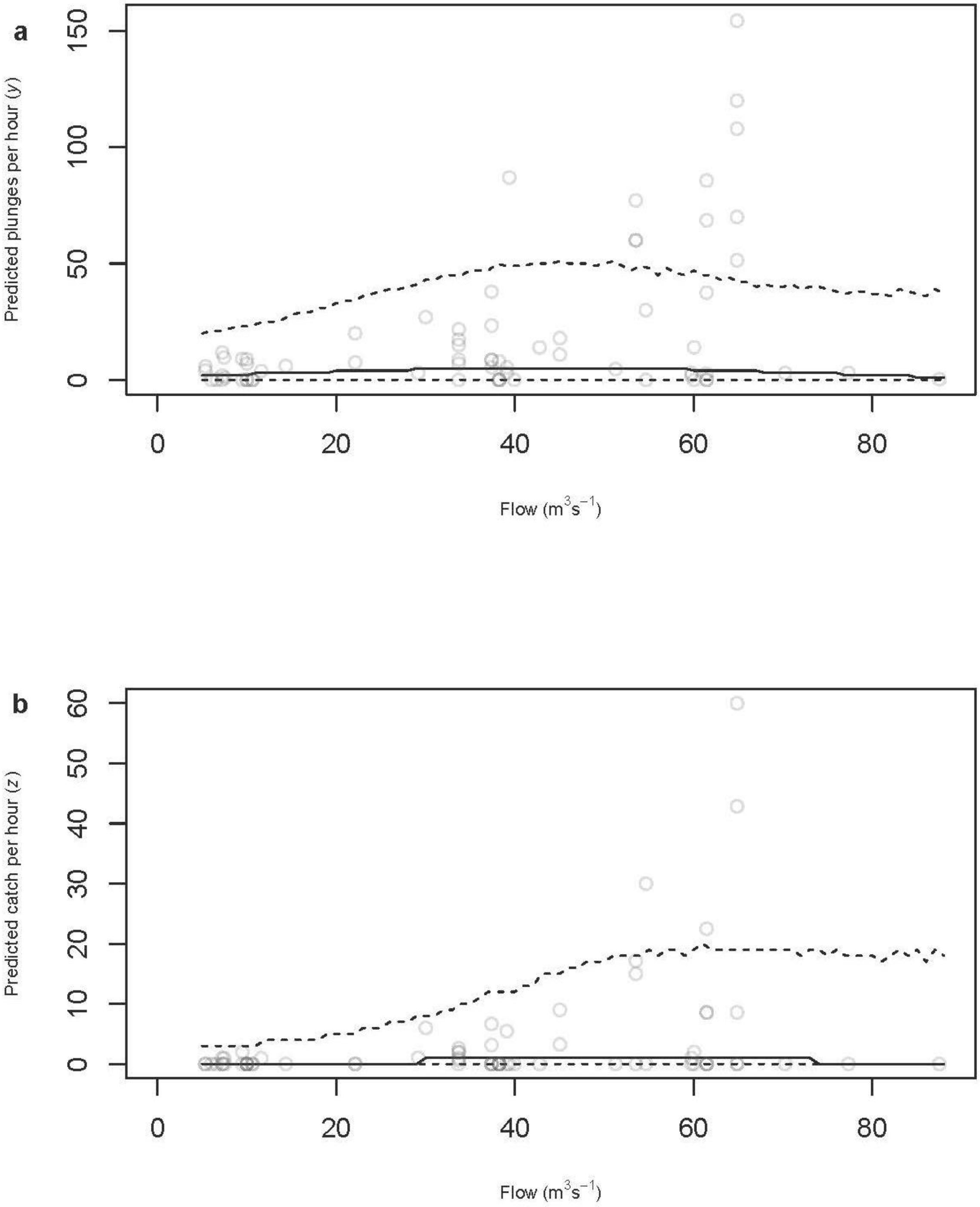


Figure 10. Posterior predictive plots from a hierarchal regression model (Eq. 4.1–4.5) showing how the observed plunge rate (*y*; **a**) and catch rate (*z*; **b**) is related to average daily flow on the day of observation (median and 95% CIs). Results are for model M2, which was not the best predictive model. See Fig. S1 for alternative results which suggest flow may have a slight influence on *y* or *z*. Gray circles designate the raw data. Note both the observed *y* and *z* have been scaled to an hourly rate. Also note the high values for the observed plunge and catch rate are mostly due to opportunistic samples that were short in duration.

Discussion

Numerical relationships between predators (least tern) and prey (fish) are often unknown, but can be approximated empirically (e.g., Cury et al. 2011) or indirectly (e.g., by observing foraging behavior). We assumed if forage fish abundance was limiting, least terns would develop compensatory strategies and mitigate relationships between prey availability and reproductive success by increasing foraging effort (Piatt et al. 2007). That is, even if there was no observable effect of forage fish densities on productivity, we might expect to observe a measurable effect on least tern foraging behavior.

Prey availability, as measured through forage fish density, did not appear to affect the plunge rate, the probability of fish capture, or the fish capture rate. This is substantiated by the scores for M1 and M3, which indicate predicted fish densities decreased the predictive ability of the models substantially. We suspect the reduced predictive performance of M1 and M3 could be caused by one or a combination of the two factors: 1) the predicted fish densities are too “noisy”, and/or 2) tern foraging behavior is independent of fish densities over the ranges observed in this study. Predictions, and hence predicted fish densities, have error that reduces the predictive ability of the model when compared to analyses that have perfectly measured values of the covariates. We cannot confirm, nor refute, if this is the case in our analysis. In our study, it would be difficult or impossible to accurately measure fish densities at each plunge location during each observational session, therefore, predicted fish densities were required. Numerous studies have used predicted or estimated fish densities to explain variations in seabird productivity (Cury *et al.* 2011; Santora *et al.* 2014). These studies, however, did not propagate the error associated with the covariate through their analyses to the final result. Recently, multiple authors have recognized the importance of accounting for the uncertainty associated with covariates that are predicted in ecological models (Foster *et al.* 2012; Stoklosa *et al.* 2014). However, the loss of ability to detect significant effects when covariates are predicted is a needed area of research. Secondly, it could be the plunge rate, probability of fish capture, and fish capture rate were independent over the range of flows observed during the foraging habits study (5–87 m^{3}s^{-1}; 177–3,072 ft^{3}s^{-1}).

Models M2 and M4 had the highest, but nearly equal predictive ability. The most parsimonious model and the one with the best predictive score, model M4, suggests neither fish density nor flow is related to the plunge rate or probability of fish capture (Figures 7 and 9). The result and interpretation of this model is fish capture rate is constant across all flows observed during our study. The model that only included an effect of flow (M2) suggests as flow increased, plunge rate, probability of fish capture, and fish catch rate increased. Although at higher flows (≥45 m^{3}s^{-1}; 1,589 ft^{3}s^{-1}) these rates decreased (Figure 8). Given the predictive performance of M2, there is a little evidence supporting this conclusion. Furthermore, the fact M4, which contained no effect of flow or fish density, outperformed M2 in terms of predicative accuracy would suggest the true effect of flow may be zero or relatively small compared to that estimated by M2 (Figures 7–10).

Spatial variability in landscape features can affect predator-prey interactions and responses (Hunsicker *et al.* 2011). For example, in marine environments water temperature can affect predatory swimming speed and encounter rates with prey (Sanford 1999). Turbulence has also been shown to affect encounter rates and prey pursuit probabilities (MacKenzie *et al.* 1994). Therefore, it seems reasonable that flow could influence least tern foraging behavior. For example, there has to be a minimum flow and channel topography that results in water depths too shallow for plunging. However, even at the lowest flows observed (5 m^{3}s^{-1}; 177 ft^{3}s^{-1}), plunge rates of 4 plunges per hour would be expected in open channel habitat (Figure 8). Empirically, in two session Sherfy et al. (2012) observed 12 plunges and 2 fish captures at a flow of 7.2 m^{3}s^{-1} (254 ft^{3}s^{-1}) and 7.4 m^{3}s^{-1} (261 ft^{3}s^{-1}), respectively. This suggests least terns are capable of plunging and capturing fish at flows much lower than 22.7 m^{3}s^{-1} (802 ft^{3}s^{-1}). However, we suspect the actual minimum amount of flow necessary for successful foraging would depend on channel morphology. Furthermore, M2 suggests higher flows (e.g., 80 m^{3}s^{-1}; 2,825 ft^{3}s^{-1}) may have similar effects on foraging success for least terns as extremely low flows (Figure 8c). We believe there may be a small influence of flow on least tern foraging behavior in open channel habitat given the score of M2 and M4 were nearly equal. If the effect exists, we suspect the effect size is not very large and that higher flows have similar negative effects as low flows as measured by reduce plunging rate, probability of fish capture, and fish capture rate.

Summary

We were unable to establish a strong relationship between fish density and flow and plunge and fish capture rates. However, our second ranked model suggests expected plunge rates more than double from the lowest flows observed (5 m^3s^{-1}; 177 ft^3s^{-1}) until flows reach 45 m^3s^{-1} (1,589 ft^3s^{-1}) and then plunge rates decrease as flows continue to increase. Probabilities of fish captures increased linearly from the lowest to highest flows observed during our study. We believe there may be a slight influence of flow on least tern foraging behavior in open channel habitat. We suspect the effect size is not very large and that higher flows have similar negative effects as low flows. Based on confidence intervals, it appears there is a lot of uncertainty in the relationships at high flows. Furthermore, the fact best model contained no effect of flow or fish density would suggest the true effect of flow may be zero or relatively small compared to that estimated by the second best model.

SECTION 4 – Least Tern Productivity in the Central Platte River Valley

We used least tern productivity data collected via the Program's monitoring protocol (Program 2011) and USGS gaging station data collected on the Platte River to provide a line evidence for answering the Big Question and assessing this premise. The objective of this study was to determine impacts of flow on least tern productivity within the AHR. Although indirect, we might expect flow, and thus forage availability, to influence productivity of least terns within the AHR. We use this indirect evidence to build empirical support to test the forage fish-related hypotheses in the Program's AMP (Program 2006).

Sherfy et al. (2012) found least terns made longer distance movements during the nonbreeding and post fledging periods and shorter movement distances occurred during the incubation and brood rearing periods. This finding would suggest least terns are possibly constrained to foraging relatively close to nesting and brood rearing locations. Given foraging demands are presumably greatest and yet most constrained during the brood rearing period, we expected productivity to be most sensitive to flow, and thus prey availability, during the brood rearing period. Our analysis, therefore, is focused exclusively on the number of fledglings produced per hatched nest and river discharge data.

Flow measurements

Our analysis of the fledgling success data included average daily flow records for the date on which a brood's fate was determined as well as the previous 7 days. Initially we considered testing several different measures of flow as covariates. For example, we considered mean daily flow on all seven days before fate determination, the minimum mean daily flow seven days prior to the date the fate was determined, etc. We found, however, the flow covariates were highly correlated which would make comparisons of the covariates very difficult in our regression analysis (Dormann *et al.* 2013). Therefore, we used the minimum daily flow that occurred during the seven day period prior to date the fate of each brood was determined and recognized our results and interpretations could apply to several different measures of flow.

Least tern productivity model

We used logistic regression models to relate flow measurements to least tern productivity. An assumption of our logistic regression model is the numbers of fledglings from each brood (b_k) follow a binomial distribution:

$$b_k \sim Binomial\ (C_k, \eta_k), \tag{5.1}$$

where C_k is the number of chicks hatched from each nest and η_k is the probability a chick fledged from the k^{th} brood (k=1,2,…,486). We expected the probability of fledging to be related to the flow, and thus abundance of forage fish, near the location of the brood. Initially, it would seem we could use the relationship between flows and forage fish abundance developed in Chapter 2 to predict forage fish abundance near the location of the brood. Doing so presents at least two problems: 1) the probability of fledging likely depends on the cumulative effects of forage fish abundance some unknown time before the fate was determined, and 2) for a given flow, total forage fish catch most likely depends on the expected forage fish density ($\mu/112.5\ m^2$) and not predicted forage fish density ($x/112.5\ m^2$). For example, low forage fish abundance several days prior to chick mortality may be the cause of mortality. It was not exactly clear how to use the forage fish abundance model to incorporate this temporal dynamic. Secondly, although the plunge rate and probability of fish capture are likely to respond to small scale variability in forage fish abundance captured by the seining data, a larger area is available to each least tern for foraging. For example, Sherfy et al. (2012) reported least terns routinely traveled distances of 3 km (1.9 mi) while rearing broods. As a result, the probability of a chick fledging is likely not dependent on the small scale variability captured by the seining data, and hence predicted by the forage fish model, but rather the expected forage fish abundance. Because of the high correlation between flow and expected fish abundance, flow can be used as a surrogate covariate (Section 3). Given the two issues discussed above, we choose to model the probability of fledging using various measurements of flow. Although such an analysis is less mechanistic as compared to the foraging model in Section 4, given the data limitations we believe this was the most appropriate approach to link flow to productivity.

We assumed the logit of η_k depended on f_k, the minimum flow within 7 days prior to the date of fate determination:

$$\text{logit}(\eta_k) = \alpha_1 + \alpha_2 f_k. \tag{5.2}$$

We also tested to see if minimum flows <22.7 m^3s^{-1} (802 ft^3s^{-1}) during the 7 days prior to the date of fate determination influenced η_k with the linear predictor:

$$\text{logit}(\eta_k) = \alpha_3 + \alpha_4 I(f_k < 22.7), \tag{5.3}$$

where $I(\min(f_k) < 22.7)$ takes on a value of zero when minimum flows were ≥22.7 m^3s^{-1} (802 ft^3s^{-1}) and one if the flow were <22.7 m^3s^{-1} (802 ft^3s^{-1}).

Sherfy et al. (2012) discovered high rates of foraging at the Kearney Canal Diversion structure (Figure 4) and that least terns occasionally made long distance movements. Based on observations by the authors, the diversion structure supported large abundances of fish and pools deep enough for plunging at low flows. Therefore, we suspected when flows were low, least terns may travel at an increased frequency to the diversion structure to forage. If this is true, we would expect the distance from the location of the brood to the diversion dam may influence least tern productivity. To test this relationship we included distance to the diversion structure as a covariate:

$$\text{logit}(\eta_k) = \alpha_5 + \alpha_6 d_k, \tag{5.4}$$

where d_k is the distance between the k^{th} brood and the Kearney Canal Diversion in km (Figure 4). We also included a two-way interaction with the covariates minimum flow and $I(\min(f_k) < 22.7)$, as we expected the effect of d_k to depend on flow, that is, traveling to the diversion structure only when there is a flow that results in reduced fish capture success or a shortage of fish. We therefore used the linear predictors:

$$\operatorname{logit}(\eta_k) = \alpha_7 + \alpha_6 d_k + \alpha_7 \min(f_k) + \alpha_8\, d_k \min(f_k) \tag{5.5}$$

and

$$\operatorname{logit}(\eta_k) = \alpha_9 + \alpha_{10} d_k + \alpha_{11} I(\min(f_k) < 22.7) + \alpha_{12}\, d_k\; I(\min(f_k) < 22.7). \tag{5.6}$$

Lastly, we included a model that did not include an influence of flow, which was:

$$\operatorname{logit}(\eta_k) = \alpha_{13} \tag{4.7}$$

We randomly split the data into a training set with 241 observations and test set with 241 observations. We used a generalized linear model and maximum likelihood to obtain parameter estimates using the training data set (Stroup 2012). We calculated the predictive deviance (i.e., –2 times the predictive log likelihood) using the test data. Predictive deviance is a measure of the models predictive ability and has a similar interpretation as Akaike information criterion (AIC; Burnham & Anderson 2002; Hooten & Hobbs 2015). We also calculated and reported AIC scores for comparison.

Results

Of 551 broods monitored, 416 broods fledged at least one chick, 65 resulted in an unknown status and 70 failed. Of the 70 broods that failed, 43 had an unknown cause of failure, 8 failed due to weather, and 19 failed due to predation. Of the 486 broods that had a known fate (i.e., “fledged” or “failed”), 478 included records of the number of chicks that hatched and fledged. These 478 broods produced 1,092 chicks, of which 830 chicks fledged. Of these 478 broods, 378 had fates determined when the flow was <22.7 m^3s^{-1} (802 ft^3s^{-1}) and resulted in 648 fledged chicks (see raw data in Figure 11c). Though observed fledging rates have been extremely high, it is unknown whether fledged individuals were physically fit to complete migration and eventually recruit to the population.

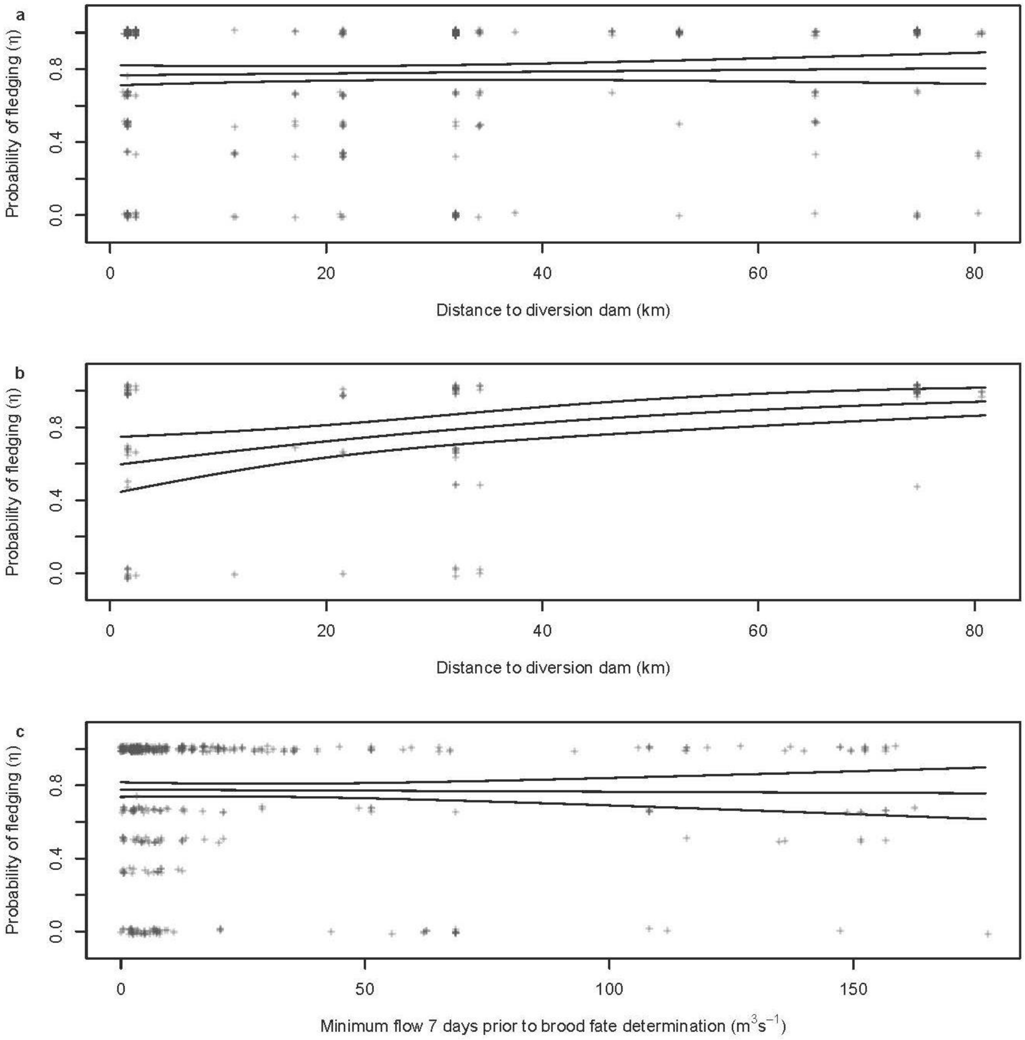


Figure 11. Logistic regression model (Eq. 5.5) showing the relationship between probability of a chick fledging (η) and the distance to the Kearney Canal Diversion when the minimum average daily flows were less than (a) and greater than (b) 22.7 m^3s^{-1} (802 ft^3s^{-1}) seven days before fate determination of the brood (estimate and 95% CIs). Logistic regression model (Eq. 5.2), showing how the probability of a chick fledging (η) is unrelated to minimum average daily flows on the seven days before fate determination (c; estimate and 95% CIs). Note model in Eq. 5.5 had the best predictive deviance and AIC score. The gray plus signs (+) show the empirical probabilities of fledging for each brood ($\frac{number\ of\ chicks\ fledged}{number\ of\ chicks\ hatched}$).

Analysis of brood data showed the best model (Eq. 4.6) had a predictive deviance of 476, an AIC score of 496, and included distance to the Kearney Canal Diversion and minimum flow <22.7 m^3s^{-1} (802 ft^3s^{-1}; Figure 11). For comparison, the model that included no covariates (Eq. 4.7) had a predictive deviance of 488 and an AIC of 500 and suggested the probability a chick fledged was 0.77 (0.73–0.81; 95% confidence interval). The predictive performance of all other models was similar to the model with no covariates, with the exception of the models presented in Eq. 5.4 and 5.5, which slightly outperformed the model with no covariates (predictive deviance of 483 and 479 and AIC of 499 and 498, respectively).

Within the AHR, least terns forage at a variety of locations including open channels, sandpits and the Kearney Canal Diversion. Our data, and hence conclusions, are limited to open channel habitat. Although the Program's priority hypothesis is not limited to open channel habitat, species of fish captured by least tern are typically found in open channel habitat (Wilson *et al.* 1993; Stucker *et al.* 2012). Consequently, open channels were thought to be the most important foraging habitat for least terns and thus were the focus of our study. Sherfy et al. (2012) found least terns rarely foraged at sandpits and were quite unsuccessful when they did so within the AHR. Sherfy et al. (2012) observed plunge rates of 1.2 plunges per hour at sandpit sites, which was more than 7 times lower than what was observed at riverine sites (8.5 plunges per hour). Furthermore, during 230 behavioral observation sessions totaling 234 hours of observation at sandpit sites, only 7 successful plunges were observed. Given this information, it seems unlikely sandpits contributed greatly to least tern foraging within the AHR. Sherfy et al. (2012), however, did discover a high rate of foraging at the Kearney Canal Diversion. During 76 sessions, which totaled 77 hours of observation, 503 successful plunges were observed. For comparison, during 72 sessions totaling 48 hours of observation, 49 successful plunges were observed in open channel habitat (Sherfy et al. 2012).

Based on results of Sherfy et al. (2012), we suspected the Kearney Canal Diversion may be particularly important for providing least terns foraging opportunities during low flow events as we were unaware of any area where such high frequency of successful foraging regularly occurred. At flows <22.7 m^3s^{-1} (802 ft^3s^{-1}), it does not appear distance to the Kearney Canal Diversion had any influence on the probability of fledging (Figure 11a). Rather, our results indicate the distance to the Kearney Canal Diversion influenced the probability of fledging only when flows were >22.7 m^3s^{-1} (802 ft^3s^{-1}) and that the probability of fledging increased the further broods were from the Kearney Canal Diversion. Though this result is counter to what we expected, further examination of the data resulted in a fairly logical explanation (Figure 11b). In 2010 and 2011 a site located approximately 75 km (46.6 mi) downstream from the Kearney Canal Diversion had exceptionally high productivity; 45 out of 46 chicks fledged. Flows were high during 2010 and 2011 and we have no reason to believe the high survival rate was the result of increased foraging success. Rather, we attribute the high success rate to good fortune in that adverse weather events and predation did not impact the site during either year. Furthermore, this site experienced exceptionally low flows during 2012 and 2013 when 77% (37 of 48) of the chicks observed fledged; the average flow for each brood 7 days prior to the date their fate was determined was 0.8 m^3s^{-1} (28 ft^3s^{-1}). Of the 11 chick mortalities recorded, 10 chicks were associated with four broods of which no chick fledged. In all cases, cause of mortality was undetermined. However, given the four broods were located on a site <0.5 ha (1.24 ac) in size and 38 eggs from 15 additional nests hatched and resulted in 37 fledged chicks, it seems highly unlikely the 4 broods failed due to a lack of forage.

It could be argued an analysis such as this requires specific information about each chick within a brood (e.g., cause of death, time of death, etc. for each chick). Our data was collected at the brood level. For example, if three chicks hatched, but only a single chick fledged (i.e., the other two chicks died), the status of the brood would have been recorded as “successful” and the date of when the two chicks died would be unknown or not recorded. As a result, covariates such as flow correspond to the date when the single chick fledged and not the date when the two chicks died. In other words the value of the covariate may not correspond to the values actually experienced by chicks that died. Such measurement error in covariates has the potential to result in incorrect conclusions when making inference from regressions model (Carroll *et al.* 2006). However we proceeded under the assumption measurement error in covariates did not influence inference.

Summary

From 2001–2014, we observed 478 broods with records of numbers of chicks that hatched and fledged within the AHR. These broods resulted in 1,092 chicks, of which 830 fledged. Of these broods, 79% had fates determined when the flow was <22.7 m^3s^{-1} (802 ft^3s^{-1}) and resulted in 78% of the fledged chicks observed. We only observed 43 broods that hatched and failed due to unknown causes. Thus, these are the only broods where starvation could have resulted in the loss of the entire brood. However, our analysis was conducted at the scale of the brood rather than individual chicks and we have no evidence of the cause of loss for partially fledged broods (i.e., broods where only 1 chick out of 3 fledged). Given a lack of information as to the cause of partial brood losses (>100 chicks lost when a sibling fledged), it is conceivable that a shortage of forage and thus sibling rivalry could have contributed to some of these losses. We found no evidenced least tern productivity was negatively influenced by low flow events. The best model indicated flows below 22.7 m^3s^{-1} (802 ft^3s^{-1}) had higher predicted probability of fledging than higher flows. We also found least tern productivity was positively influenced by distance to the Kearney Canal Diversion; a common foraging site for least terns (Sherfy et al. 2012). However, this relationship was likely driven by one site that had exceptionally high reproductive success. In summary, we found nests that hatched had in unusually high success rate (fledged ≥1 chick) even though nearly half of our study period occurred during times of extreme drought.

SECTION 5 – A Bioenergetics Approach to Estimating Forage Fish Demand of Least Terns in the Central Platte River Valley

Our goal thus far has been to approach priority hypothesis T2 using multiple lines of evidence that are not direct links between flows, forage fish abundance, and least tern productivity. In the previous Sections, we relied on a “top down” approached to detect direct and indirect influences of forage fish availability on least tern productivity (see Sections 3, 4 and 5). An alternative “bottom up” approach, where one attempts to estimate the population size a prey base can support (hereafter referred to as a “bioenergetics approach”), is applied in this Section. We use this indirect evidence to build empirical support to test the forage fish-related hypotheses in the Program’s AMP (Program 2006). The objective of this study was to utilize the Districts’ existing central Platte River forage fish monitoring data and available references to determine the number of least terns the forage fish population in the AHR can support.

Channel area calculations

We used a HEC-RAS 1D hydraulic model to estimated average wetted channel width at 453 locations within the main channel of the AHR for flows ranging from 3–85 m^3s^{-1} (106–3,002 ft^3s^{-1}). The spacing between, and hence the location of, each wetted width measurement was generally determined so that the distance between successive measurements was approximately equal to the channel width measurement at the location. As a result, the average distance between wetted width measurements was 355.2 m (SD = 187.0 m; 388.5 yd; SE = 204.5 yd). Wetted widths were calculated for flows listed in Table 2. Next we calculated the area of open channel habitat as the wetted width measurement at the location multiplied by the sum of half the distances to the nearest wetted width measurements expressed as:

$$A_i = w_i\left(\frac{d_{i-1}+d_{i+1}}{2}\right) \tag{6.1}$$

where A_i is the channel area representative of the i^{th} wetted width measurement (i = 2,…452) and d_{i-1} is the distance between the location i and location $i-1$. Similarly, d_{i+1} is the distance between the location i and location $i+1$. Then the total channel area is the sum (Table 2):

$$open\ channel\ area = \sum_{i=2}^{452} A_i. \tag{6.2}$$

Table 2. Calculations used to determine the number of family units (defined as 2 adults + 3 chicks) the prey fish population in the AHR could potentially support.

Flow m^3s^{-1} (ft^3s^{-1})	Open channel area (km^2)	Expected fish catch per seine haul	Fish/m^2	Millions of fish in main channel habitat	Available forage (kg) wet weight	Available forage (kg) dry weight	Available energy (mj)	Total number of family units supported
2.83 (100)	8.02	131.62	1.17	9.38	3,003	901	61,853	825
5.66 (200)	10.20	113.28	1.01	10.27	3,287	986	67,703	903
8.50 (300)	11.63	97.49	0.87	10.08	3,225	968	66,437	886
11.33 (400)	12.87	83.90	0.75	9.60	3,072	921	63,275	844
14.16 (500)	14.19	72.21	0.64	9.11	2,915	874	60,042	801
21.24 (750)	16.65	49.62	0.44	7.34	2,350	705	48,411	646
28.32 (1000)	18.81	34.10	0.30	5.70	1,824	547	37,581	501
35.40 (1250)	20.78	23.43	0.21	4.33	1,385	415	28,528	380
42.48 (1500)	22.60	16.10	0.14	3.23	1,035	310	21,320	284
49.55 (1750)	24.38	11.06	0.10	2.40	767	230	15,804	211
56.63 (2000)	26.20	7.60	0.07	1.77	567	170	11,671	156
70.79 (2500)	29.62	3.59	0.03	0.95	302	91	6,230	83
84.95 (3000)	33.16	1.69	0.02	0.50	160	48	3,293	4

Forage fish abundance

The relationship between flow and forage fish abundance was estimated using the negative binomial regression model in Chapter 2. We showed that the expected number of forage fish caught in each seine haul was:

$$E(x) = e^{\beta_1 + \beta_2 f}. \tag{6.3}$$

We used the posterior median of β_1 and β_2 as point estimates for the following calculations, which resulted in $\hat{\beta}_1 = 5.03$ and $\hat{\beta}_2 = -0.053$. We used this relationship to calculate the expected fish catch per seine haul for flows ranging from 3–85 m^2s^{-1} (106–3,002 ft^3s^{-1}; Table 1). We also calculated the number of fish per m^2 (i.e., $E(x)/112.5\ m^2$) and multiplied this by the area of open channel habitat to estimate the how many millions of fish were predicted to be in main channel habitat (Table 2).

Energetic calculations

We assumed a breeding pair consists of two adult least terns and a successful brood consists of three chicks (hereafter, a breeding pair with three chicks is referred to as a “family unit”) for the following calculations. We assumed each breeding pair produced one successful brood with three chicks (i.e., no chick mortality occurred and no double brooding). We also made the assumption that all forage fish available and consumed by least terns are age-class 0 (young-of-year) red shiners (*Cyprinella lutrensis*). We made these assumptions because we were able to find the required information for our calculations for red shiners (e.g., energy content and body mass) and so that our estimates will be conservative as young-of-year fish were likely the smallest bodied forage collected in our forage fish sampling protocol (see Section 3). Yildirim & Peters (2006) reported average total weight for male and female red shiners of age class 0 had a total wet weight of 0.32 gram (SE = 0.03; 0.01 oz; SE = 0.001). We multiplied their estimated by the number of forage fish estimated to be in open channel habitat by the lowest weight (0.32 grams; 0.01 oz) to obtain the weight of available forage fish in main channel habitat (Table 2; "Available forage (kg) wet weight"). Franssen et al. (2006) reported red shiners averaged 4923.2 (SE = 522.1) calories per gram of dry mass (20.60 kj per gram). Since the caloric value of red shiners is reported in dry weight, we converted the wet weight of red shiners to dry weight assuming the dry weight was 30% of the wet weight (i.e., $0.32g \times 30\% = 0.096g$; Table 2; "Available forage (kg) dry weight"). We then multiplied the dry weight by the energy content (20.60 kj per gram) to obtain the minimum amount of energy that may be available from forage fish (Table 2; "Available energy").

Roby *et al.* (2003) reported that the daily energy expenditure of free-ranging breeding Caspian terns was 1040 kj/day. Adult Caspian terns weigh 600–700 grams (21.16–24.69 oz; male) and 500–640 grams (17.64–21.16 oz; female), whereas adult least terns are reported to weight 30–45 grams (1.06–1.59 oz; Olsen & Larsson 1995; Roby *et al.* 2003). The empirical relationship estimated by Nagy (2005) was:

$$FMR = 2.25{M_b}^{0.808} \tag{6.4}$$

where FMR is the field metabolic rate (in kj metabolized per day), and M_b is the body mass (in grams). We used equation 6.4 to estimate daily energy expenditure for adult least terns using what has been reported for Caspian terns. Assuming Caspian terns weigh 600 grams (21.16 oz) and least terns weigh 45 grams (1.59 oz), it could be estimated that a least tern will have a FMR that is 0.123 times less than a Caspian tern ($\frac{2.25(45)^{0.808}}{2.25(600)^{0.808}} = 0.123$). Using the reported energy expenditure of free-ranging breeding Caspian terns of 1040 kj/day, we estimate that an adult least tern requires 128.25 kj/day.

We estimate adult least terns are present and require 128 kj/day of forage for 60 days each nesting season. Therefore, the total energy requirement for an adult least tern during the nesting season is 7,695 kj ($\text{i.e.}, 60 \text{ days} \times 128.25\text{kj/day} = 7{,}695 \text{ kj}$). Roby et al. (2003) also reported that total metabolic energy requirements for Caspian tern chicks (from hatch to fledgling) were 19,200 kj. If we assume the same allometric relationship as we did for adults, the seasonal energy requirement for a fledgling would be

2,368 kj (i.e.$19{,}200\text{ kj } \times 0.123 = 2{,}368\text{ kj}$). Therefore a breeding pair family unit that fledges 3 chicks would require 22,494 kj $(2 \times 7{,}695\,kj + 3 \times 2{,}368\,kj = 22{,}494\,kj)$ per season. The energy requirement of $22{,}494\,kj$ can be divided by the amount of energy available from forage fish ("Available energy (mj) "; Table 2) to estimate the number of family units the forage fish population in AHR could potentially support.

Results

The number of family units the forage fish population in AHR could potentially support is maximized at 5.66 m^3s^{-1} (200 ft^3s^{-1}) with an estimated 903 family units supported. At flows <5.66 m^3s^{-1} (200 ft^3s^{-1}) the number of family units decreases due to a decrease in channel area, whereas at higher flows the decrease is a result of decrease in forage fish densities (Figure 12; Table 2).

Discussion

Our calculations indicate forage fish in main channel of the central Platte River within the AHR should be able to support >100 family units at flows between 2.83–56.63 m^3s^{-1} (100–2,000 ft^3s^{-1}; Table 2). In the nesting season of 2014 there was an estimated 98 breeding pairs. Our results suggest the abundance of forage fish within the AHR may be able support substantially more family units. Given relatively low flows (5.66 m^3s^{-1}; 200 ft^3s^{-1}), the maximum number of family units the AHR was estimated to be capable of supporting was 903 family units, which is >9 times the maximum number of pairs observed, 2001-2014. Although most of our calculations could be viewed as conservative (e.g., restricting our calculations of channel area to the main channel, using the smallest age and sex class of fish, etc.), there are at least four factors that should be considered: 1) study design; 2) forage fish availability; 3) forage fish population dynamics; and 4) estimation uncertainty. The forage fish sampling sites were established based on their close proximity to areas managed as least tern nesting habitat. As a result, inference from the forage fish data is limited to sites in “close proximity to areas managed as least tern nesting habitat.” The forage fish sampling design did not result in data for which results can or should be generalized to the AHR. Secondly, our calculations assume forage fish are equally available to each individual tern. This is an unrealistic assumption for several reasons. Most notably, the maximum distance traveled by adult least terns in the AHR is known to be substantially less than the length of the AHR (e.g., 10 km; 6.2 mi; Sherfy *et al.* 2012). Thirdly, our calculations assume the estimated forage fish prey base can be completely consumed by least terns and experience population recovery during subsequent years. If the estimated prey base is accurate, then it is unlikely all or even a large percentage of the fish can be

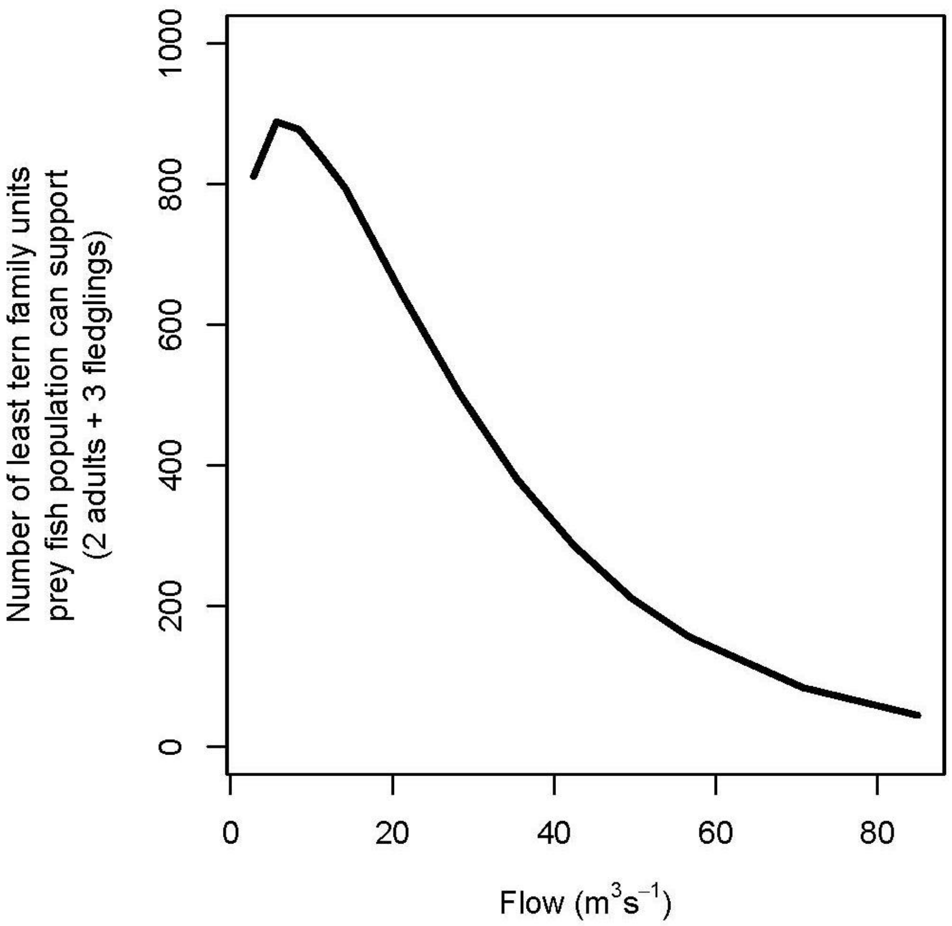


Figure 12. Numbers of least tern family units (defined as 2 adults + 3 chicks) the prey fish population in the Program Associated Habitat Area could potentially support. See Table 1 and text for details of calculations.

consumed sustainably. Given the limited data it would be difficult to estimate what proportion of the forage fish can be sustainably consumed annually by least terns. However, if half of the forage fish could be consumed and recover annually, we estimate the AHR could support approximately 450 family units at low flows (5.66 m^3s^{-1}; 200 ft^3s^{-1}). Finally, we calculated a single estimate of the number of family units the forage fish population could potentially support at a given flow. We did not attempt to propagate the uncertainty associated with each component of our calculations. At each step (e.g., channel area calculations, estimated forage fish density, energetic calculations, etc.) there is likely a large amount of uncertainty surrounding the estimate. It would be challenging if not impossible to obtain accurate estimates of uncertainty and propagate it throughout at each step. Error propagation and estimation, however, may be feasible under a Bayesian paradigm using the so-called "prior predictive distribution" if suitable priors can be determined (Gelman *et al.* 2013). Given we found it difficult to obtain suitable point estimates for some quantities (e.g., forage fish energy content) it seems unlikely meaningful priors are determinable.

Summary

The maximum numbers of least tern pairs observed within the AHR between 2001 and 2014 was 98 (Cahis and Baasch 2014). We estimate the forage base in the AHR could support more than twice that many least tern family units at flows <50 m^3s^{-1} (1,766 ft^3s^{-1}) and a maximum of 903 least tern family units at 5.66 m^3s^{-1} (200 ft^3s^{-1}). However, there is a high degree of uncertainty in our estimates. In order to fully evaluate the adequacy of the forage base within the AHR as compared to other river systems believed to have an ample forage base (e.g., Mississippi River), one would likely need to compare growth rates of least tern chicks within each system to see if they are similar. Program participants, however, have agreed the risks outweigh the benefits of implementing a research protocol that involves weighing chicks multiple times throughout the breeding season to allow for a comparison between river systems that support subpopulations of least terns.

SECTION 6 – Evaluation of a Program Priority Hypothesis, Sub-hypothesis, and Big Question that Relate Flow, and thus Forage Fish Abundance and Diversity, to Least Tern Productivity

The Program's Biological Opinion includes flow targets to increase forage fish abundance and diversity to increase productivity of least terns within the AHR. One of several purposes for the flow targets is to maintain flows in the central Platte River to increase forage fish abundance and diversity to increase productivity of least terns within the AHR (USFWS 2006). The assertion that flow, and thus forage availability, limits least tern productivity is articulated in Priority Hypothesis T2 in the Program's AMP and states: "Tern productivity is related to the number of prey fish (<3 inches) and fish numbers limit tern production below 800 cfs from May–Sept[ember]." (Program 2006). The Big Question associated with these hypotheses states: "Does forage availability limit tern […] productivity on the central Platte River." Even though this premise is articulated in a priority hypothesis and Big Question for the Program, the Environmental Impact Assessment (EIS) for the Program states:

> "No indication was found in the literature that food currently limits least terns from nesting on channel sandbars in the Central Platte River between Lexington and Chapman. However, no definitive studies have been conducted that evaluated the link between prey abundance and nesting success. Obviously, no flow (i.e., a dry channel) or very low flow conditions would affect forage fish and, thus, least terns if such a flow event occurred during the nesting season." (Department of Interior 2006).

The Biological Opinion (BO) for the Program states:

> "…no studies have been conducted to demonstrate whether, when flows are present in the river, the availability of forage fish and invertebrates in the central Platte River is insufficient to support tern and plover nesting in the river. The Program's IMRP will investigate whether the distribution, abundance, and species composition of the aquatic

> fish community and the invertebrate food base are adequate for the least tern and piping plover, respectively, and if inadequate, what factors are limiting." (USFWS 2006).

In short, at the time of the writing of the EIS and BO there was no evidence supporting the assertion that flow, and thus forage fish abundance, limited least tern productivity but there was a concern that this issue had not been sufficiently addressed. Thus, the Program's Biological Opinion includes an expectation to continue to evaluate any potential relationships between flow, forage fish abundance and diversity, and least tern productivity within the Associated Habitat Reach (AHR) of the central Platte River.

In order to fully evaluate the adequacy of the forage base within the AHR as compared to other river systems believed to have an ample forage base (e.g., Mississippi River), one would likely need to compare growth rates of least tern chicks within each system to see if they are similar. Program participants, however, have agreed the risks outweigh the benefits of implementing a research protocol that involves weighing chicks multiple times throughout the breeding season to allow for a comparison between river systems that support a flourishing sub-population of least terns. As such, we used a weight of evidence approach, several sources of data, and multiple lines of evidence to determine if there is any indication flow, and thus forage fish availability, limits least tern productivity within the AHR. Results of our approach indicate there continues to be no evidence to support the relationships postulated in Hypotheses T2 and T2a. Instead, our results indicate forage fish abundance and least tern productivity increase as flows decrease to 5.7 m^3s^{-1} (200 ft^3s^{-1}). It seems intuitive there is a critical threshold at some level of flow below 5.7 m^3s^{-1} (200 ft^3s^{-1}) where forage fish abundance would diminish and potentially have an influence on productivity. No forage fish data has been collected below this level of flow, but productivity data indicates high productivity within the AHR even during the drought of the 2000s when flow regularly approached 0 ft^3s^{-1}. As such, our results indicate one should reject priority hypothesis T2 and sub-hypothesis T2a as well as the notion least tern productivity is negatively influenced by flows below 800 ft^3s^{-1} articulated in the Program's associated Big Question.

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