North American Journal of Fisheries Management

A Bioenergetics Approach to Assessing Potential Impacts of Avian Predation on Juvenile Steelhead during Freshwater Rearing

Danielle Frechette [a] [b], Alison L. Collins [a] [c], James T. Harvey [b], Sean A. Hayes [a], David D. Huff [a], Andrew W. Jones [a] [h], Nicolas A. Retford [a], Alina E. Langford [d], Jonathan W. Moore [e], Ann-Marie K. Osterback [a] [d], William H. Satterthwaite [a] [f] & Scott A. Shaffer [g]

[a] Southwest Fisheries Science Center, Fisheries Ecology Division , 110 Shaffer Road, Santa Cruz , California , 95060 , USA

[b] Moss Landing Marine Labs , 8272 Moss Landing Road, Moss Landing , California , 95003 , USA

[c] Department of Forest Sciences , University of British Columbia , 2424 Main Mall, Vancouver , British Columbia , V6T 1Z4 , Canada

[d] Department of Ecology and Evolutionary Biology , University of California , 100 Shaffer Road, Santa Cruz , California , 95060 , USA

[e] Earth to Ocean Research Group , Simon Fraser University , 8888 University Drive, Burnaby , British Columbia , V5A 1S6 , Canada

[f] Department of Applied Mathematics and Statistics, Baskin School of Engineering , University of California , 1156 High Street, Santa Cruz , California , 95064 , USA

[g] Department of Biological Sciences , San Jose State University , One Washington Square, San Jose , California , 95192 , USA

[h] Department of Ecology and Evolutionary Biology , Yale University , 165 Prospect Street, New Haven , Connecticut , 06511 , USA

PLEASE SCROLL DOWN FOR ARTICLE

ARTICLE

A Bioenergetics Approach to Assessing Potential Impacts of Avian Predation on Juvenile Steelhead during Freshwater Rearing

Danielle Frechette*

Southwest Fisheries Science Center, Fisheries Ecology Division, 110 Shaffer Road, Santa Cruz, California 95060, USA; and Moss Landing Marine Labs, 8272 Moss Landing Road, Moss Landing, California 95003, USA

Alison L. Collins

Southwest Fisheries Science Center, Fisheries Ecology Division, 110 Shaffer Road, Santa Cruz, California 95060, USA; and Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada

James T. Harvey

Moss Landing Marine Labs, 8272 Moss Landing Road, Moss Landing, California 95003, USA

Sean A. Hayes, David D. Huff, Andrew W. Jones,[1] and Nicolas A. Retford

Southwest Fisheries Science Center, Fisheries Ecology Division, 110 Shaffer Road, Santa Cruz, California 95060, USA

Alina E. Langford

Department of Ecology and Evolutionary Biology, University of California, 100 Shaffer Road, Santa Cruz, California 95060, USA

Jonathan W. Moore

Earth to Ocean Research Group, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

Ann-Marie K. Osterback

Southwest Fisheries Science Center, Fisheries Ecology Division, 110 Shaffer Road, Santa Cruz, California 95060, USA; and Department of Ecology and Evolutionary Biology, University of California, 100 Shaffer Road, Santa Cruz, California 95060, USA

William H. Satterthwaite

Southwest Fisheries Science Center, Fisheries Ecology Division, 110 Shaffer Road, Santa Cruz, California 95060, USA; and Department of Applied Mathematics and Statistics, Baskin School of Engineering, University of California, 1156 High Street, Santa Cruz, California 95064, USA

Scott A. Shaffer

Department of Biological Sciences, San Jose State University, One Washington Square, San Jose, California 95192, USA

---

*Corresponding author: danielle.frechette@gmail.com

Abstract

  Avian predation on juvenile salmonids is an important source of mortality in freshwater and estuarine habitats when birds and salmonids overlap spatially and temporally. We assessed the potential impact of avian predation upon juvenile steelhead *Oncorhynchus mykiss* in a coastal watershed in central California. We conducted stream surveys between 2008 and 2010 to determine the composition, distribution, and density of piscivorous birds in areas that provide rearing habitat for juvenile steelhead. The most commonly sighted bird species were common mergansers *Mergus merganser* and belted kingfishers *Megacyrle alcyon*. The density of avian predators varied spatially and temporally but was greatest in the estuary regardless of season and decreased with increasing distance from the estuary. In the absence of local predator diet data, we applied a bioenergetics model to estimate the potential predation on juvenile steelhead by mergansers and kingfishers in the Scott Creek estuary. Model parameters included (1) published values of bird energetic requirements and steelhead energy density, (2) the number of birds present in the estuary during the closure period (from stream surveys), and (3) the size frequency and abundance of steelhead present in the estuary during closure. We predicted the extent of predation for different values of steelhead in bird diets, accounting for uncertainty in the estimates using a Monte Carlo simulation approach. With the assumed contribution of steelhead to the diet ranging from 20% to 100%, the population of kingfishers foraging in the Scott Creek estuary had the potential to remove 3–17% of annual production, whereas mergansers had the potential to remove 5–54% of annual steelhead production. Our results suggest that predation by avian species, particularly mergansers, is an important source of mortality for threatened steelhead populations in central California and should be addressed in future salmonid research and recovery planning.

Avian predation upon juvenile fish in freshwater and estuarine habitats has been the focus of considerable research in European and North American watersheds (reviewed in Hoeinghaus and Pelicice 2010). Because of the commercial and recreational value of salmonid species of the genera *Oncorhynchus* and *Salmo*, a number of studies have focused on estimating the consumption of juvenile salmonids by piscivorous birds (Elson 1962; Feltham 1995; Wiese et al. 2008). These studies typically used estimates of the daily consumption of salmonids by specific avian predators and extrapolated to the proportion of the population or cohort that was consumed. For example, Wood (1987a) estimated that in a British Columbia watershed the mortality attributed to mergansers removed 6.9–8.4% of hatchery-raised Chum Salmon *Oncorhynchus keta* smolts and 3.3–6.0% of wild Chum and Coho Salmon *O. kisutch* fry, whereas Feltham (1995) estimated that mergansers ate 3–16% of the Atlantic Salmon *Salmo salar* smolts out-migrating from the North Esk River in Scotland.

Many studies have applied bioenergetics models to estimate the consumption of salmonids by avian predators (Forsell 1983; Feltham 1995; Roby et al. 2003; Wiese et al. 2008). Such models, however, require accurate measurement or estimation of predator diet (species composition and prey size), energetic requirements, and population size (Wood 1987b; Feltham 1995; Roby et al. 2003; Wiese et al. 2008). A variety of methods have been employed to estimate these variables for different avian predators. Bird diets have been estimated by examination of the stomach contents of lethally captured birds, forced regurgitations, and regurgitated pellets (reviewed in Cairns 1998 and Gagliardi et al. 2007) or via observation of birds foraging (e.g., Forsell 1983). Energy consumption by predators commonly has been calculated from measurements of "daily energy expenditure" (DEE, also referred to as the field metabolic rate), which may be estimated using allometric relationships between metabolism and body mass (Wiese et al. 2008) or directly using doubly labeled water (Feltham 1995; Roby et al. 2003). In other studies (e.g., Wood and Hand 1985), energy consumption has been estimated via observations of prey handling time.

Consumption estimates are sensitive to the values used for calculation; ideally, data specific to a given system should be used when estimating predation rates on salmonids (Feltham 1995). However, it may not always be possible to directly measure the diet or energetic requirements of predators in a system of interest. For example, protective measures may prevent the collection of stomach contents. Alternatively, habitat characteristics or bird behavior may preclude capture of foraging birds or observations of foraging. For imperiled prey populations, however, establishing boundaries on the plausible range of predation-caused mortality in the absence of rigorous local diet data may be essential for focusing future research or informing management strategies.

Pacific salmonids (genus *Oncorhynchus*) have undergone population declines across much of their range, and currently many populations are listed as threatened or endangered under the U.S. Endangered Species Act (ESA; Gustafson et al. 2007). The Central California Coast steelhead *Oncorhynchus mykiss* Distinct Population Segment (CCC–steelhead DPS) is listed as threatened under the ESA (Good et al. 2005). Water diversions, habitat degradation, and reduced ocean productivity are cited as the main reasons for continued population decreases (Good et al. 2005), with little consideration of the potential role of predation by piscivorous birds. Although the mortality associated with avian predators has been quantified in larger systems in

California (Evans et al. 2011; Adrean et al. 2012; Collis et al. 2012), relatively little attention has been focused on the effects of avian predation on Pacific salmonids in smaller coastal watersheds. Recent observations, however, suggest that predation is an important source of mortality that may slow the recovery of steelhead in central California (Frechette et al. 2012). For example, passive integrated transponder (PIT) tags originally deployed in juvenile steelhead were found on a seabird breeding colony, indicating that western gulls *Larus occidentalis* eat a minimum of 1–4% of out-migrating salmonids from central California watersheds (Frechette et al. 2012). However, the extent of predation on juvenile steelhead by other species of piscivorous birds, particularly predation occurring during the period of freshwater rearing, remains largely unknown. There is also a lack of the data necessary to estimate the extent of avian predation on steelhead in the small coastal watersheds of central California, including predator identity, numbers, distribution, diet, and energetic requirements. For some watersheds within the range of the CCC–steelhead DPS, however, steelhead populations have been well characterized.

Scott Creek, located 80 km south of San Francisco, is one such watershed. Although predation on steelhead by western gulls at the mouth of Scott Creek was the focus of previous research (Frechette 2010; Frechette et al. 2012), little is known regarding predation on steelhead by other species of avian predators. Our study had two main objectives. The first was to identify the common avian predators in Scott Creek and determine where they were concentrated spatially and temporally. The second was to create a simple bioenergetics model for estimating predation on steelhead by piscivorous birds in the absence of local avian diet and energetic requirements given (1) local fish abundance and size frequency and (2) predator identity and abundance. This model allowed assessment of the extent of predation on a threatened steelhead population and will help identify future research needs.

METHODS

Study Site

Scott Creek is a small, coastal watershed in Santa Cruz County (Figure 1) that empties into the Pacific Ocean 80 km south of San Francisco (37°02′28″N, 122°13′50″W). Located near the southern extent of the CCC–steelhead DPS, steelhead life history has been well characterized for Scott Creek, and annual estimates are available for out-migrating steelhead smolts, returning adults, and estuary-reared juveniles (e.g., Smith 1990; Bond et al. 2008; Hayes et al. 2008, 2011; Satterthwaite et al. 2012). Coho Salmon also occur in Scott Creek, although during the course of this study Coho Salmon were considered functionally absent from the system because of a recent population decrease (Spence and Williams 2011).

Scott Creek is typical of the watersheds in central California, terminating in a small estuary that is seasonally closed by a sandbar to form a lagoon. The physical characteristics of the
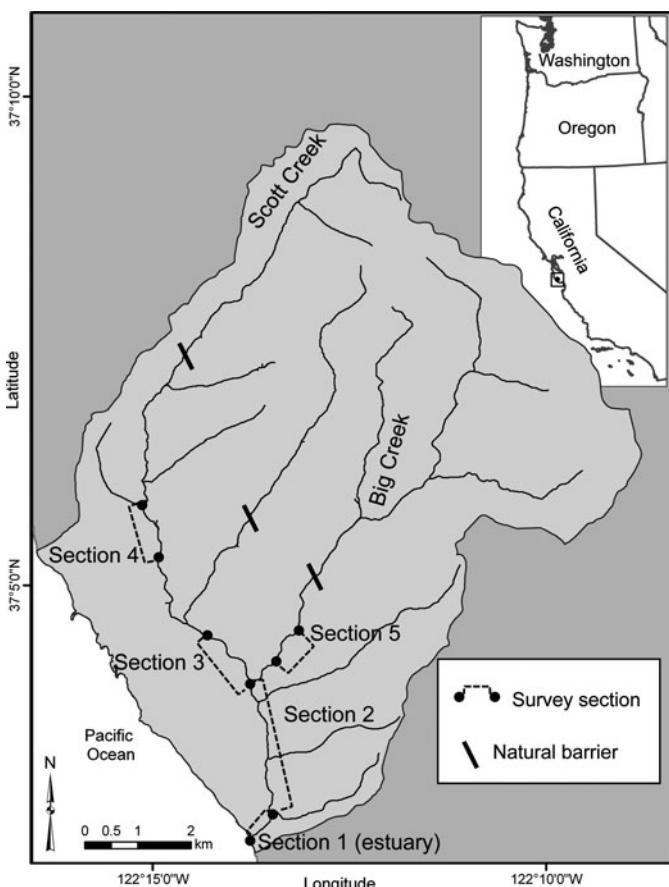
FIGURE 1. Map of the Scott Creek watershed showing the locations of the survey sections and natural barriers to anadromy.

watershed have previously been well described (Bond et al. 2008; Hayes et al. 2008, 2011). Briefly, Scott Creek experiences highly variable flows, with winter flows reaching 28 m^3/s whereas summer flows may be as low as 0.08 m^3/s. Sandbar formation generally occurs during low-flow periods in late summer and autumn (Shapovalov and Taft 1954). Water clarity and depth in the estuary vary throughout the year, ranging from very clear during periods when the estuary is connected to the ocean and water depth is low to very turbid during estuary closure (D. Frechette, personal observation). Shelter from predators may exist in the form of woody debris, freshwater algae, and parts of the surrounding bulrush marsh. Water clarity is generally good in the upper and middle watershed (sections 2–5; Figure 1), except during winter storms; shelter from predators is in the form of woody debris, vegetation, boulders, and overhanging banks (Hayes, unpublished data).

Although juvenile steelhead may rear exclusively in the upper watershed, many juveniles migrate downstream to the estuary (lagoon), where they take advantage of enhanced growth opportunities (Bond et al. 2008; Hayes et al. 2008). After spending time in the estuary, steelhead may either migrate to sea in the same year before sandbar formation or remain in the lagoon after

sandbar closure (Shapovalov and Taft 1954; Bond et al. 2008; Hayes et al. 2008, 2011). Steelhead that remain in the lagoon throughout the summer and autumn migrate back upstream in late autumn as decreasing dissolved oxygen, increasing temperature, and an influx of saltwater cause environmental conditions in the closed lagoon to become unfavorable (Hayes et al. 2011). These lagoon-reared juveniles then perform a second downstream migration the following spring in which they enter the ocean (Shapovalov and Taft 1954; Hayes et al. 2011).

Bird Surveys

We assessed the species composition and distribution of piscivorous water birds by walking transects that were randomly selected using a general randomized tessellation stratified (GRTS) sampling program (Larsen et al. 2008), giving all habitat units within the watershed an equal, nonzero probability of being selected. For logistical reasons, the transects were then grouped into five survey units, hereafter referred to as stream sections. Stream section length ranged from 0.59 km to 2.2 km (mean length = 1.2 km). The stream sections were representative of all habitat types within Scott Creek and encompassed 40% of the 23 km of habitat available to steelhead.

We conducted surveys between December 2008 and December 2010, with a mean intersurvey interval of 13 d. During winter and spring (December through early June), the surveys were conducted in conjunction with surveys for spawning steelhead. During the remainder of the year the surveys were solely for the purposes of counting birds. The survey methods were consistent throughout the study, namely, a modification of the double-observer approach described by Nichols et al. (2000). Two observers walked stream sections from downstream to upstream and recorded visual sightings of birds. For each sighting, the observers recorded the species, number present, location, behavior, time of observation, and GPS location when possible. The second observer followed the primary observer, so as to not influence the sightings made by the primary observer (Nichols et al. 2000). Unlike the methods described by Nichols et al. (2000), the second observer alerted the primary observer of missed birds, which were subsequently recorded after the sighting occurred. We used this approach to enable the second observer to carry the equipment necessary to record steelhead spawning data during the winter and spring surveys. All stream sections were surveyed in 1 d. The order in which sections were surveyed was randomly selected, and all surveys began within 2 h of sunrise to minimize the effects that daily patterns of bird activity may have had on observations.

To identify the most common avian predators in Scott Creek, we calculated the percent of total sightings represented by each species observed during each year. We used a generalized linear model to test the hypothesis that the density of birds in the Scott Creek watershed varied spatially and temporally, using a quasi-Poisson error distribution with log link to account for overdispersion in the bird density data; the residual deviance greatly exceeded the residual degrees of freedom for the corresponding Poisson errors model. The terms included in the model were the month, distance from the creek mouth, and the interaction between month and distance. The response variable was bird density. The midpoint of each stream section was used to define the distance from the creek mouth.

Bioenergetics Modeling

We estimated the consumption of salmonids by avian species in the Scott Creek estuary by means of a bioenergetics model that incorporated bird abundance data from the stream surveys and steelhead abundance and size frequency data from long-term monitoring programs in Scott Creek (Figure 2). We lacked sufficient predator diet composition and energy requirement data for this system, so we used published values for the daily energy requirements of predators and conditioned the model using a range of values for the percentage of steelhead in bird diets (hereafter referred to as the "target contribution" of steelhead to the diet). Specifically, we used five different values for the target contribution: 20, 40, 50, 70, and 100% steelhead, which approximately encompassed the range of values presented in the literature for kingfishers and mergansers (Forsell 1983; Shearer et al. 1987; Kålås et al. 1993; Feltham 1995; Cairns 1998; Wiese et al. 2008). We applied the bioenergetics model to the estuary during the period of bar closure because we lacked the data on total fish abundance and year-round size distributions necessary to apply the model to the upper watershed. We conducted bioenergetic modeling using custom-written R code (R Development Core Team 2011; available in the online supplement).

To estimate the consumption of fish by avian predators, we first estimated the energy content per fish based on the size distribution of the fish captured via seine net in the Scott Creek lagoon during 2009 and 2010. We pooled all fish captured in the lagoon each year between July and November, for which mass were recorded, and calculated the energy content of each fish by multiplying its mass by 4.6 kJ/g (Roby et al. 2003; Adrean et al. 2012). We then followed one of two pathways to estimate the number of fish eaten during the period of lagoon closure; we used the first pathway (Monte Carlo simulation 1; Figure 2) when the target contributions resulted in a bird's eating more than one fish per bird-day on average. We used the second pathway (Monte Carlo simulation 1a) when the target contributions resulted in a bird's eating less than one fish per bird-day. Although the second pathway is the only one that can be applied in situations when birds have low energetic requirements compared with average fish energy content, Monte Carlo simulation 1 was preferred when possible due to its ability to incorporate the variability introduced into the estimates by explicitly considering individuals.

Monte Carlo simulations 1 and 2.—To estimate the number of fish eaten by an individual bird on a single day (hereafter referred to as a bird-day), we simulated an individual bird's consumption by randomly sampling individual fish with replacement from the distribution of fish sizes until the estimated amount of energy "consumed" was equal to the target contribution, within the
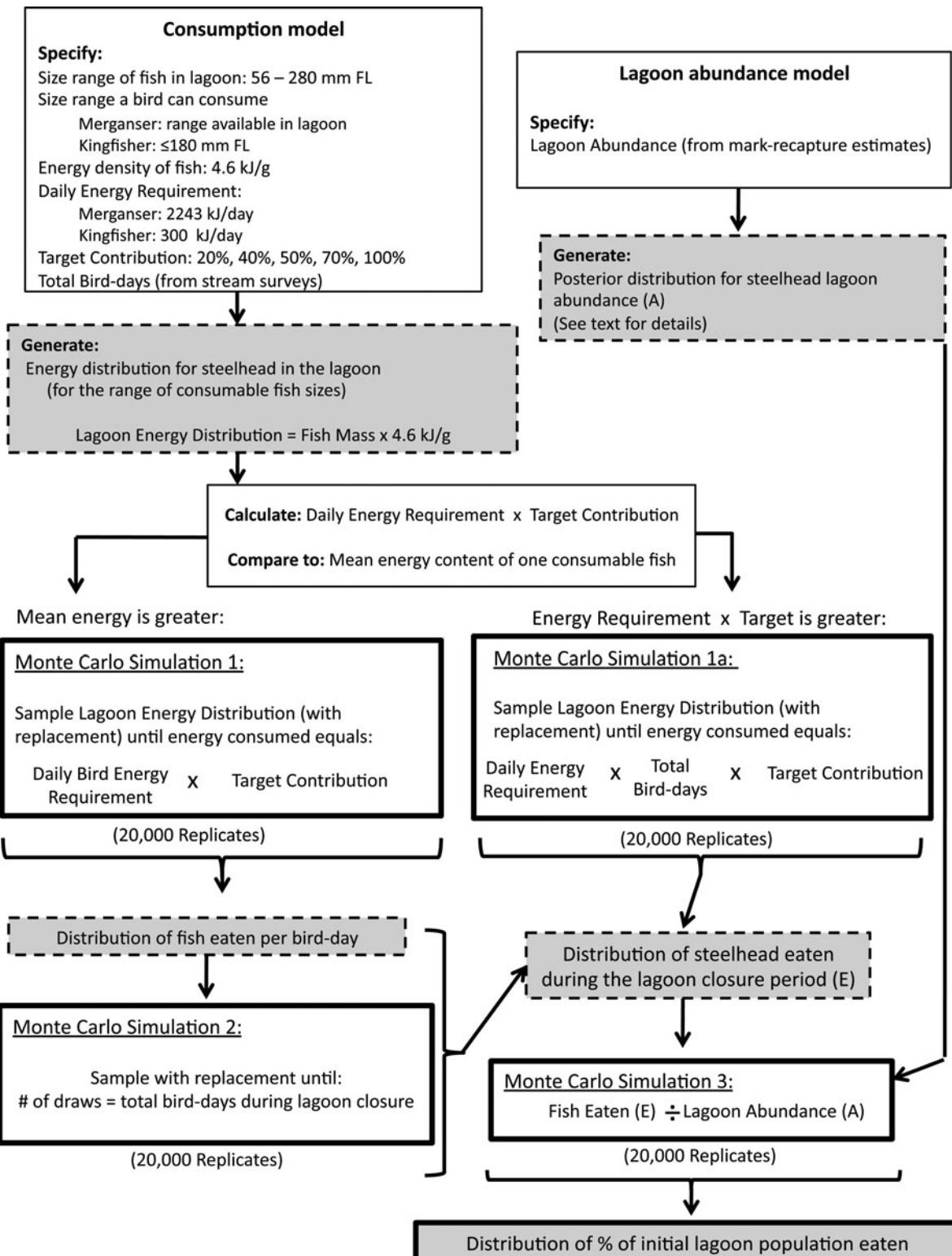
FIGURE 2. Flow chart for the bioenergetics model used to estimate steelhead consumption by avian predators in Scott Creek.

average energy content of a single fish. We generated a distribution of the expected number of fish eaten per bird-day and 95% CIs for the number of fish eaten by a single bird during 1 d using a Monte Carlo simulation (20,000 replicates; Figure 2; Monte Carlo simulation 1).

To estimate the number of fish eaten during the lagoon closure period, we determined the total number of bird-days during the lagoon closure period from counts made during stream surveys. To estimate the number of birds present in the estuary for each day between counts (inferred counts), we used linear interpolation. We then summed the total observed or inferred daily counts between July and November of each year to calculate the total number of bird-days during the lagoon period for each species (Figure A.1 in the appendix). To estimate total steelhead consumption during this period, we made a number of draws equal to the estimated number of bird-days from the distribution of total fish eaten per bird-day. We extracted the median and 95% CIs by repeating this process in a Monte Carlo simulation (20,000 replicates; Figure 2; Monte Carlo simulation 2).

Monte Carlo simulation 1a.—When target contributions resulted in a bird's eating less than one fish per bird-day on average, we dropped the focus on individual consumption. Instead, we multiplied the daily energy requirement of an individual bird by the total number of bird-days during the lagoon period to obtain the total energy requirement for a given species for the duration of the lagoon closure period. We then simulated the consumption of steelhead by that species by randomly sampling individual fish (with replacement) from the distribution of fish sizes until the estimated amount of energy "consumed" was equal to the target contribution, within the average energy content of a single fish. We generated a distribution of the expected number of fish eaten by a single species during the lagoon period (with 95% CIs) using a Monte Carlo simulation (20,000 replicates; Figure 2; Monte Carlo simulation 1a).

Monte Carlo simulation 3.—We applied an additional Monte Carlo simulation to estimate the percentage of the initial lagoon production in Scott Creek eaten by birds each year (Figure 2; Monte Carlo simulation 3). We defined the initial lagoon population as the abundance estimated during the first month after sandbar closure in each year (July in 2009 and August in 2010), which approximates lagoon recruitment prior to predation during the lagoon closure period in a given year. We estimated the monthly lagoon population using the 2-d mark–recapture sampling design described in Satterthwaite et al. (2012). Briefly, we conducted beach seining in the lagoon using a 30-m × 20-m nylon seine net and the methods described by Bond et al. (2008). We estimated lagoon abundance using the Ricker modification of the Peterson method (Ricker 1975), quantifying the uncertainty in the lagoon abundance using a Bayesian posterior distribution corresponding to a uniform prior. We estimated the proportion of the initial lagoon production consumed by birds by iteratively drawing from the posterior distribution of the lagoon abundance estimate and comparing this with the previously described distribution of bird predation.

Merganser Diet Analysis

We opportunistically collected mergansers that were found dead during field efforts for diet analysis ($n = 5$ adults). Although we recognize that these birds may not be representative of the population of mergansers foraging in Scott Creek, we thought it useful to analyze their stomach contents to determine whether the mergansers in Scott Creek consumed steelhead in the size range available in the estuary. We identified fish otoliths, scales, and bones; invertebrate parts, intact fish and invertebrates; and PIT tags from previously tagged salmonids. We used scales, otoliths, and PIT tags to determine the presence of salmonids in diet samples. We determined the minimum number of individual fish in each diet sample using intact otoliths (all species) and PIT tags (salmonids only).

We determined the minimum number of individuals eaten by each bird using otoliths by first counting the number of right and left otolith pairs and then adding the number of unpaired otoliths (left or right) depending on which were most numerous (e.g., Lance et al. 2001). We also calculated the percent frequency of occurrence for each prey taxon, defined as the percent of stomachs examined that contained a given prey taxon (described by Cairns 1998). We then determined the FLs of putative steelhead eaten by mergansers based on back-calculation of fish length using a fish length–otolith width relationship (see below). Otoliths recovered from the diet samples were photographed with a microscope-mounted Nikon digital camera (DXM1200; 3,840 × 3,072 pixels) and identified to genus. We measured otolith width along the transverse axis from the dorsal to the ventral margin at the widest point of the otolith using OPTIMAS software (Media Cybernetics, Silver Spring, Maryland).

To calculate a relationship between FL and otolith size, we extracted otoliths from 24 steelhead from Scott Creek of known length. The fish included in this analysis represented the size range of steelhead captured in juvenile traps in Scott Creek and individuals captured in both the upper watershed and estuary habitat (Figure A.2). The relationship between FL and otolith width was approximately linear and is described by the equation

$$\text{FL (mm)} = 115.11 \cdot \text{otolith width (mm)} - 56.656 \quad (1)$$

($R^2 = 0.847$, $P < 0.0001$). This regression was then applied to either the right or left otoliths recovered from merganser diet samples to determine the size of the salmonids eaten by each bird. We used only otoliths that were at most moderately eroded for back-calculation of fish length (Tollit et al. 1997).

Functioning PIT tags were scanned using a portable PIT tag reader (Allflex USA, Dallas-Fort Worth Airport, Texas). Tag identity was matched to individual statistics for each fish from a database held by the NOAA Fisheries Southwest Fisheries Science Center in Santa Cruz, California. We determined whether tagged steelhead were of hatchery or wild origin and the length and mass from the most recent date on which each fish was

captured. Further (anecdotal) information on the size of steelhead preyed upon came from common mergansers ($n = 3$) and belted kingfishers ($n = 1$) that were scanned for PIT tags when they were captured alive in the watershed. These birds were captured as part of an associated study (Frechette, unpublished data) using mist nets, a method that has been commonly employed for bird capture (e.g., Remsen and Good 1996). We also obtained anecdotal information on the sizes of salmonids preyed upon by mergansers from dead steelhead that were visually observed being regurgitated by foraging mergansers. Visual observation of regurgitation occurred when observers disturbed a flock of six foraging mergansers during a bird survey.

RESULTS

Bird Surveys

We conducted 25 surveys in Scott Creek during the first year (December 2008–November 2009) and 30 surveys during the second year (December 2009–November 2010). At least one predatory bird was seen during each survey (Table 1). The most commonly observed birds were belted kingfishers and common mergansers, which were the only species observed in sections 4 and 5 of the upper watershed. Kingfishers were observed during 18 of the 25 surveys during 2008–2009 and 24 of the 30 surveys during 2009–2010 and were more commonly observed in the upper watershed than in the estuary. We observed mergansers during 15 of the 25 surveys in 2008–2009 and 18 of the 30 surveys in 2009–2010. Mergansers and kingfishers accounted for 61% (2009) and 77% (2010) of all sightings of piscivorous birds in Scott Creek.

The generalized linear model demonstrated that stream section, month, and the interaction of stream section and month were important explanatory covariates of total bird density. Specifically, these terms led to significant reductions in model deviance (Table 2). The mean density of birds (birds/river kilometer) was greatest in the estuary and decreased with increasing distance from the estuary. Mean bird density varied considerably with time (Figure 3).

Bioenergetics Modeling

We applied the bioenergetics model to common mergansers and belted kingfishers because sightings of these two species were far greater than sightings of all other species combined (Table 1). We used the daily food intake for female common mergansers estimated by Feltham (2,243 kJ/d, which accounts for 80% of the assimilation efficiency of fish) in our model because we could not distinguish between female and immature male mergansers (Gregory et al. 1997) and most sightings during surveys were of female or immature mergansers. Feltham (1995) estimated daily food intake from predictions of the field metabolic rate (FMR) from the body mass of 16 mergansers using the relationship between body mass and FMR of 9 mergansers (from the same system) obtained with the doubly labeled water technique. We used 300 kJ for the daily energetic requirement of belted kingfishers, which is intermediate between the daily food intake estimated from visual observations of kingfisher foraging (294 kJ) and estimates made using a bioenergetics model (303 kJ) for kingfishers on the Mad River, California (Forsell 1983). All estimates of kingfisher daily energy intake accounted for an assimilation efficiency of 82.1% (after Vessel

TABLE 1.   Number and percentage of surveys during which piscivorous birds were observed in Scott Creek during the 2 years of this study, by species, and sightings of each species expressed as percentages of the total sightings per year (2008–2009: 25 surveys; 2009–2010: 30 surveys).

Species	2008–2009			2009–2010		
	No. of surveys	% of surveys	% of sightings	No. of surveys	% of surveys	% of sightings
Black-crowned night heron *Nycticorax nycticorax*	6	24	7.7	11	37	8.1
Belted kingfisher *Megacyrle alcyon*	18	72	30.8	24	80	37.2
Common merganser *Mergus merganser*	15	60	30.8	18	60	39.9
Double-crested cormorant *Phalacrocorax auritus*	2	8	2.8	1	3	0.7
Great blue heron *Ardea herodias*	14	56	13.4	5	17	3.4
Great egret *Ardea alba*	3	12	2.9	2	7	1.4
Green heron *Butorides virescens*	8	32	7.7	5	17	3.4
Hooded merganser *Lophodytes cucullatus*	2	8	2.9	4	13	4.1
Pied-billed grebe *Podilymbus podiceps*	0	0	0.0	1	3	0.7
Snowy egret *Egretta thula*	1	4	1.0	2	7	1.4

TABLE 2. Analysis of deviance for the generalized linear model of avian predator density in Scott Creek. Model terms were added sequentially from first to last.

Model	Deviance reduction	Residual df	Residual deviance	F	P
Null		274	502.29		
Month	47.85	251	454.44	1.69	0.03
Distance from estuary	180.62	250	273.82	147.52	<0.001
Month × distance	67.44	227	206.38	2.39	<0.001

1977). The bioenergetics model that Forsell (1983) used incorporated mean air temperature, time and energy budgets, and bird body mass (Koplin 1972; Koplin et al. 1980).

We could not directly infer the size selection of steelhead by predators in the Scott Creek estuary, so we assumed equal probabilities of predation on all size-classes of steelhead captured during lagoon seining (56–280 mm FL). We assumed that the steelhead eaten by common mergansers included all

lengths because Kålås et al. (1993) observed that mergansers ate Atlantic Salmon as great as 364 mm TL, with no observed difference in length between hatchery Atlantic Salmon taken by mergansers and those available. We restricted the length of fish eaten by belted kingfishers to 180 mm based on the observations of Forsell (1983).

We estimated that common mergansers would eat a median of two steelhead per day when the target contribution
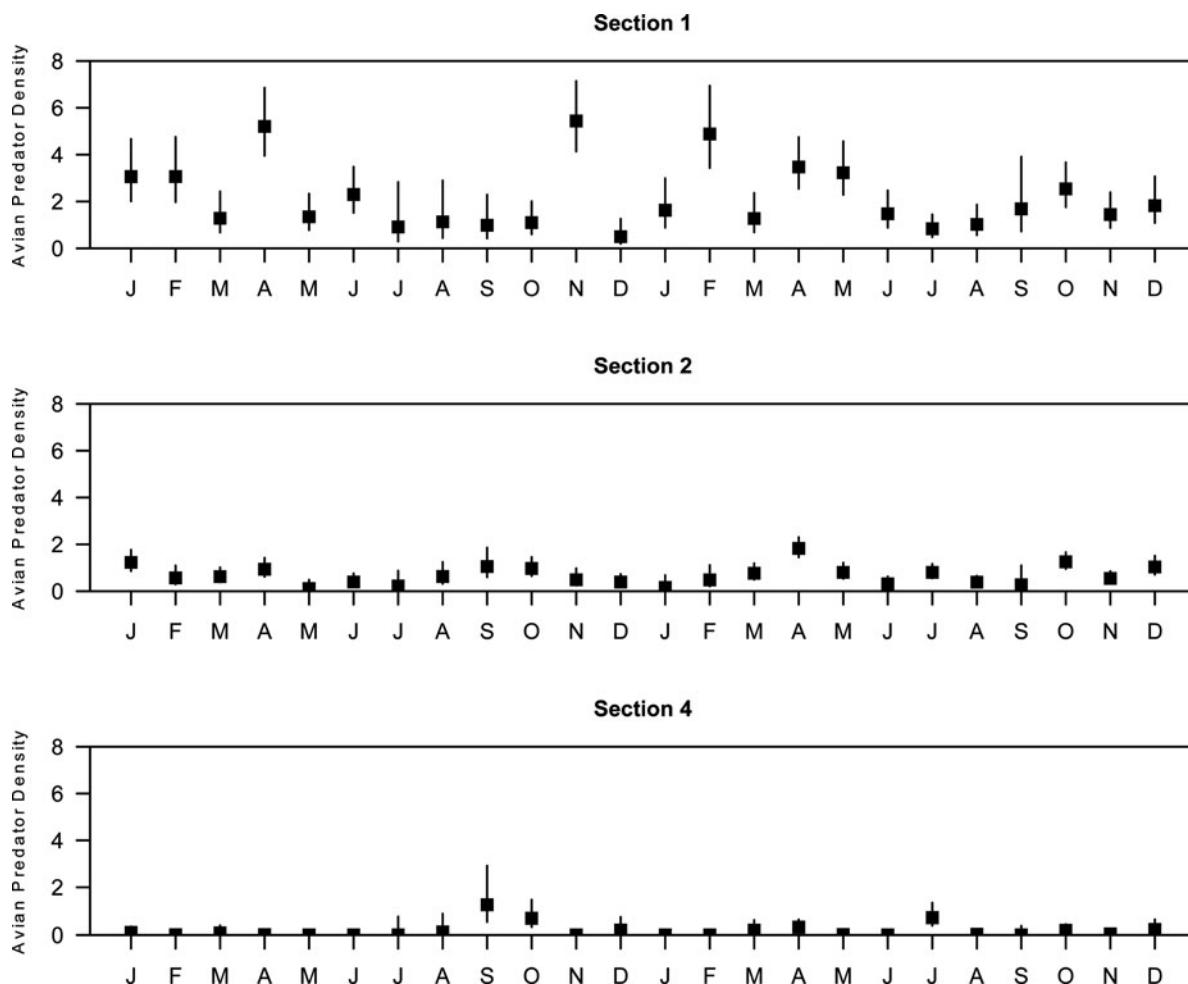
FIGURE 3. Generalized linear model–predicted monthly densities of avian predators in the Scott Creek estuary (section 1), the upstream section contiguous with the estuary (section 2), and the uppermost portion of the watershed that was surveyed (section 4) from January 2009 to December 2010. The squares represent means and the whiskers represent standard errors.

TABLE 3.   Results of bioenergetics modeling. Estimates for each target contribution of steelhead to the diet (20, 40, 50, 70, and 100% steelhead) of common mergansers and belted kingfishers are presented with 95% CIs for each metric. It was not possible to calculate the consumption of steelhead by an individual kingfisher for a target contribution less than 70%, so the energy consumed over total kingfisher-days was used to estimate the steelhead eaten by kingfishers for each target contribution during the lagoon period.

Year and predation category	Target contribution (%)	Estimate	95% confidence limits	
			Lower	Upper
Common mergansers				
2009				
Steelhead eaten per bird-day	20	2	1	3
	40	4	1	6
	50	5	2	8
	70	7	3	10
	100	9	5	14
Steelhead eaten in lagoon (61 bird-days)	20	102	92	114
	40	223	203	242
	50	280	258	303
	70	400	372	428
	100	578	544	612
2010				
Steelhead eaten per bird-day	20	2	1	4
	40	5	3	7
	50	6	4	9
	70	9	6	12
	100	13	9	17
Steelhead eaten in lagoon (108 bird-days)	20	250	234	266
	40	537	513	561
	50	682	654	709
	70	968	934	1001
	100	1,398	1,357	1,439
Belted kingfishers				
2009				
Steelhead eaten per bird-day	70	1	1	2
	100	1	1	3
Steelhead eaten in lagoon (107 bird-days)	20	39	33	47
	40	79	71	89
	50	99	89	110
	70	139	127	152
	100	199	185	214
2010				
Steelhead eaten per bird-day	70	1	1	2
	100	2	1	3
Steelhead eaten in lagoon (147 bird-days)	20	59	52	66
	40	118	108	128
	50	147	136	159
	70	206	193	220
	100	295	279	311

was set at 20% (95% CI: 2009 = 1–3 steelhead [FL, 56–280 mm]; 2010 = 1–4 steelhead [FL, 59–270 mm]). When the target contribution was set at 100%, we estimated that mergansers would eat 9 steelhead per day (95% CI = 5–14) during 2009 and 13 steelhead per day (95% CI = 9–17) during 2010 (Table 3). We estimated that there were 61 merganser-days during 2009 and 108 merganser-days during 2010 in the Scott Creek lagoon; the greater number of merganser days during

2010 translated into greater consumption of steelhead in 2010. We obtained Monte Carlo estimates of the median total consumption of 102 (95% CI = 92–114) steelhead eaten during 2009 and 250 (95% CI = 234–266) during 2010 with a target contribution of 20%. A target contribution of 100% resulted in estimates of 578 (95% CI = 544–612) steelhead eaten during 2009 and 1,398 (95% CI = 1,357–1,439) eaten during 2010.

The steelhead in the lagoon that we assumed were of sizes accessible to belted kingfishers (≤180 mm FL) had a mean energy content that was approximately half of the 300 kJ per day required by kingfishers (161 kJ/fish in 2009 and 149 kJ/fish in 2010). Therefore, it was unlikely that a kingfisher would eat more than one steelhead per day at a target contribution of 70%, and it was not possible to estimate the daily consumption of individual kingfishers for target contributions less than 70%. When the target contribution was set at 100%, the median requirement was 1 steelhead per day (95% CI = 1–3 [56–180 mm FL]) during 2009 and 2 steelhead per day (95% CI = 1–3 [59–180 mm FL]) during 2010. We used the total energy required over 107 kingfisher-days (2009) and 147 kingfisher-days (2010) to obtain Monte Carlo estimates of the median total consumption of steelhead during the lagoon closure period in each year. A target contribution of 20% resulted in an estimate of 39 (95% CI = 33–47) steelhead being eaten during 2009 and 59 (95% CI = 52–66) being eaten during 2010, whereas a target contribution of 100% resulted in estimates of 199 (95% CI = 185–215) during 2009 and 295 (95% CI = 279–311) during 2010.

The estimated initial lagoon population was 1,474 steelhead (95% CI = 1,184–1,967) in July 2009 and 2,727 steelhead (95% CI = 2,242–3,480) during August 2010. We estimated that at a target contribution of 20%, the consumption of steelhead in the Scott Creek lagoon by common mergansers would be 5–6% of the initial lagoon population during 2009 and between 10% and 11% during 2010. If mergansers ate only steelhead (target contribution = 100%), we estimated that they would consume 32–37% of the initial lagoon population during 2009 and between 15% and 52% during 2010. We estimated that at a target contribution of 20% the consumption of steelhead by belted kingfishers would be between 3% and 4% of the initial lagoon population during 2009 and 2010. At a target contribution of 100%, kingfishers would consume 15–17% of the initial lagoon population during 2009 and between 13% and 15% during 2010.

Common Merganser Diet Analysis

We examined the stomach contents of five adult mergansers that were collected dead in Scott Creek between March 12, 2008, and March 8, 2010. Because these birds were collected upstream of the estuary and were dead at the time of collection, we do not expect their stomach contents to be representative of the typical merganser diet in Scott Creek. We identified salmonids, sculpins *Cottus* spp., Three-Spined Sticklebacks *Gasterosteus aculeatus*, and several taxa of invertebrates, including Trichoptera (caddis-

flies), Coleoptera (beetles), Orthoptera (crickets), and Decapoda (crayfish). Sculpins were the most frequently occurring prey item eaten by these adult mergansers, having a frequency of occurrence (FO) of 100% and a minimum number of individuals (MNI) of 1–2 sculpins per stomach. Three-Spined Sticklebacks were present in four of the five mergansers (FO, 80%). The only remains recovered from the sticklebacks were bony plates, which did not allow for the enumeration of individuals. We identified salmonids in the stomachs of four of the five merganser carcasses (FO, 80%; MNI: 1–9 individuals per stomach) from the presence of PIT tags and otoliths. We also detected PIT tags in the stomachs of two of the four mergansers captured alive between January and September 2008. Although we could not differentiate between Coho Salmon and steelhead based on otoliths because of similarities in otolith structure, all of the PIT tags recovered were from steelhead of natural origin.

We estimated the lengths of 10 steelhead recovered from the stomachs of two common mergansers using the otolith width–FL regression (equation 1; mean = 132 mm, range = 67–176, SD = 30). We obtained additional steelhead lengths from fish freshly regurgitated by mergansers while foraging (n = 3; FL = 111–118 mm). The PIT tags detected in mergansers captured alive were from fish handled more than 50 d before capture. Thus, the FL at last handling (71 and 112 mm) likely underestimate the size of the fish when eaten. We found a PIT tag from one steelhead in the stomach of a belted kingfisher that was captured via a mist net at the head of the estuary. The fish had been measured 4 d prior to the bird's capture and had a FL of 131 mm. The diet data that we present here cannot be considered a complete representation of the diets of mergansers in Scott Creek or of those foraging in the estuary because all but one merganser was collected/captured upstream of the estuary. However, all of the lengths of steelhead eaten by mergansers inferred from stomach contents and regurgitated fish (67–201 mm FL) fell within the range of steelhead captured during lagoon seining (56–280 mm FL).

DISCUSSION

We developed a bioenergetics model to estimate the proportion of juvenile steelhead that would be consumed by avian predators under varying assumptions as to the contribution of steelhead to predator diets. The model enabled estimation of the consumption of steelhead in the absence of local predator diet and energy requirement data, relying on the known abundances of predators and prey and the size distribution of prey. We assessed our model with data from Scott Creek, a small coastal watershed in central California that has been the site of much contemporary research on steelhead (e.g., Bond et al. 2008; Hayes et al. 2008, 2011). Although steelhead life history is well documented in this system, relatively little is known regarding survival and the sources of mortality during freshwater rearing. Permitting restrictions prevented the lethal capture of birds for diet analysis. Furthermore, the lethal removal of large numbers

of birds could change the predator–prey dynamics of a small system such as Scott Creek. The use of forced regurgitations to obtain stomach contents was also unlikely to be useful because we found that birds quickly learned to evade capture in mist nets in Scott Creek (Frechette, unpublished data). Our model is well suited for systems in which an indirect approach to assessing avian predation on fish is necessary because the collection of rigorous bird diet data is not feasible.

To apply our model in Scott Creek, we first conducted stream surveys to determine the identity and density of potential avian predators. Bird presence in the watershed varied spatially and temporally, with the estuary supporting the greatest number of predators (Figure 3). Although we observed several species of piscivorous birds in Scott Creek, common mergansers and belted kingfishers accounted for 62% of total sightings during the first year of the study and 70% during the second year (Table 1). Some of the less abundant species, such as great blue herons, may be effective predators (Wood 1987a), but due to their rarity likely contributed little to the total predation of steelhead in Scott Creek. For this reason, we only included mergansers and kingfishers in the bioenergetics model. We applied the model to steelhead in the lagoon habitat, where we had sufficient steelhead abundance and size frequency data. Given adequate abundance and size frequency data, this model could also be applied to the upper watershed.

Our avian predator density estimates were based on bird counts conducted within the stream corridor. Thompson (2002) discussed two main sources of bias associated with the estimation of bird populations from count data: bias that originates from the selection of sampling units and bias that originates from the counting process. The counting process may introduce bias because of the misreporting or misidentification of individuals or the failure to adjust counts when the detection probability is less than 1.0 (Thompson 2002). Our survey units (stream sections) were selected randomly using a GRTS sampling program, so that all habitat units had equal, nonzero probabilities of being selected, thus eliminating the bias resulting from nonrandom selection of sampling units. Because one of three highly trained observers identified the birds during all surveys, we believe that the bias from misreporting and or misidentification was negligible. Given our survey methods, it was not feasible for us to determine the detection probability because the calculation of that probability using a double-observer approach requires independent observations by the primary and secondary observers (Nichols et al. 2000; Thompson 2002). As noted above, in this study the secondary observer relayed all of the sightings missed by the primary observer. However, it was rare for the secondary observer to sight a bird missed by the primary observer. This could be because some birds were easy to see and both observers saw them or the birds were difficult to see and both observers missed them. Because of the narrow width of the strip and the open nature of the habitat, we believe that nearly all of the birds within the strip were observed and recorded. If many birds were not counted (detection probability was <1; Thompson 2002),

we would have underestimated predator density and thus the predation pressure on juvenile salmonids.

Prey availability and habitat features may limit the foraging of avian species, which would account for the differences in predator distribution between the estuary and the upper watershed. Common mergansers tend to be most concentrated in estuarine habitat and the lower-gradient, wider sections of rivers (Wood 1987a; Gregory et al. 1997). Such habitat is characteristic of the estuary and middle watershed in Scott Creek, where the greatest number of sightings of mergansers occurred. Belted kingfishers (the most commonly observed species in Scott Creek) typically establish territories, the size of which is limited by the availability of suitable pool habitat for foraging (Salyer and Lagler 1949). Kingfishers were more commonly observed upstream of the estuary, where pool habitat is common. Given a greater number of kingfisher-days in the upper watershed and typically smaller fish sizes (requiring more fish to meet daily energetic requirements), kingfishers are likely having an even greater impact upstream than in the estuary. More data are necessary, however, to compare steelhead predation in the upper watershed with predation in the estuary.

The prevalence of common mergansers and belted kingfishers in the lagoon was likely tied to changes in prey availability between the two years. During 2010 we recorded a greater number of bird-days in the lagoon for both species, which may have been in response to the greater initial abundance of steelhead estimated for that year. Despite the greater prevalence of kingfishers than mergansers in the lagoon during both years, mergansers had a greater effect on steelhead (Figure 4a, b) because of their greater energetic requirements.

Our finding that the annual predation on steelhead by common mergansers is much greater than that by belted kingfishers is comparable to the results of a study of predation on juvenile Atlantic Salmon in New Brunswick. Elson (1962) found that mergansers contributed significantly to Atlantic Salmon mortality while predation by kingfishers was negligible by comparison. We estimated that merganser predation in the estuary habitat removed between 6% and 54% of annual steelhead production while kingfisher predation removed 3–17% (using the range of percent contributions that we employed). Comparison with previous studies is difficult because bioenergetics approaches to estimating predation rely on parameters that must either be directly measured or borrowed from the published literature. Bird diet composition, daily food requirements, and the number of predators in the system of interest are not easy to measure, however, and different methods often are used to estimate them (Shearer et al. 1987; Wiese et al. 2008).

The use of different measures to estimate diet may change the relative importance of salmonids in predator diets. For example, in the Mad River belted kingfishers ate a variety of fish, including salmonids, sculpins, and sticklebacks. Salmonids comprised 68.9% of the kingfisher diet by live weight consumed but only 33.9% of the diet by percent frequency of occurrence (Forsell 1983). The contribution of salmonids to predator diets may also
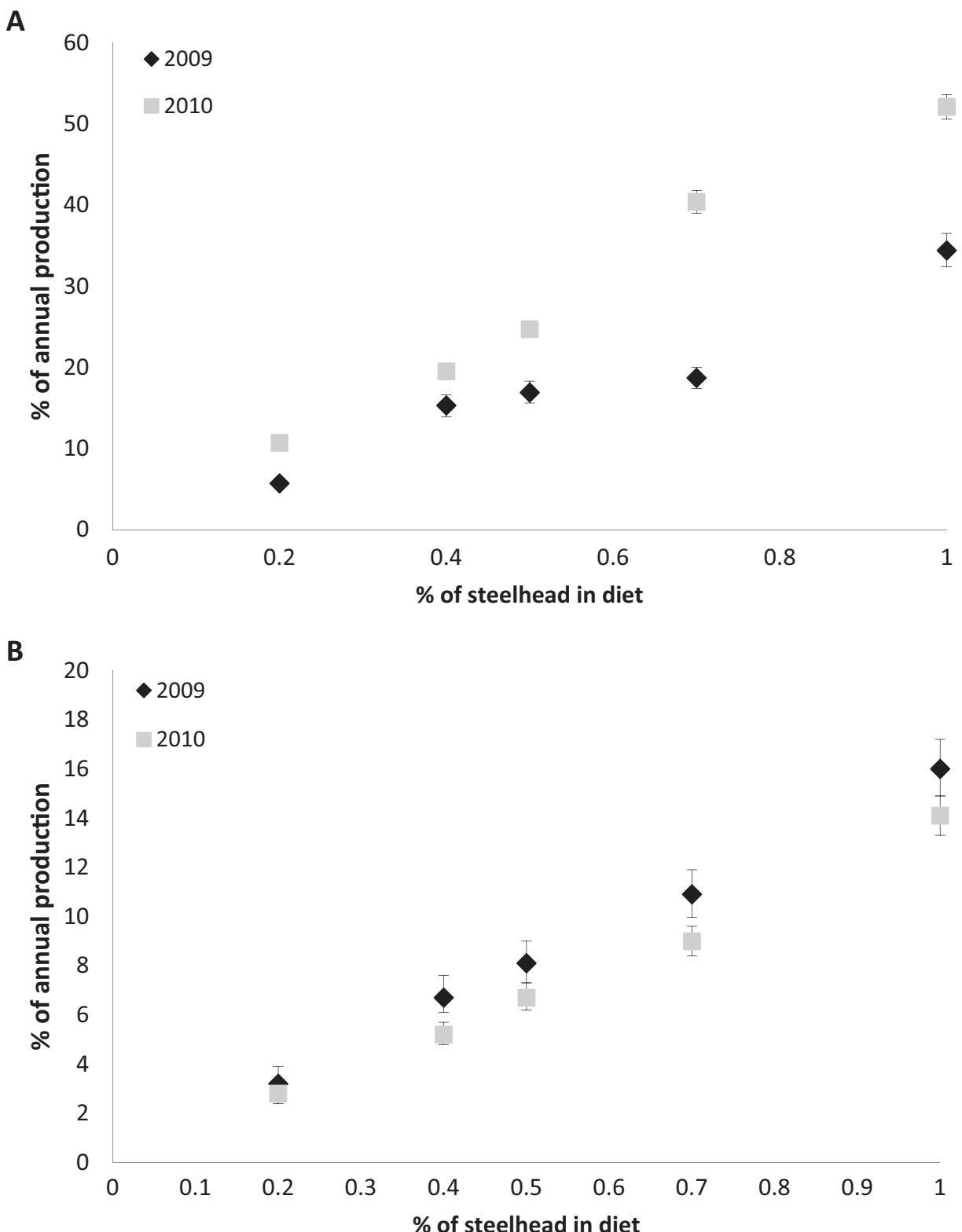
FIGURE 4.   Estimated percentages of annual steelhead production (natural and hatchery combined) eaten by **(A)** common mergansers and **(B)** belted kingfishers in the Scott Creek estuary during 2008 and 2009. The whiskers represent 95% CIs. Note the difference in the scales of the *y*-axes.

vary substantially among watersheds, possibly because of watershed characteristics or prey availability. Cairns (1998) reviewed studies of avian predation on salmonids in Canada's Maritime Provinces and reported that in major salmon rivers Atlantic Salmon comprised 9.2–90.3% of common merganser diets and 5.2–56.4% of belted kingfisher diets. Additionally, estimates from within the same system may vary considerably among years. In the mid-Columbia River, for example, salmonids comprised 12.7% of common merganser diets (mean aggregate percentage fish mass) in 2002 ($n = 7$) but 40.9% ($n = 31$) in 2004 (Wiese et al. 2008).

Estimates of predator energetic requirements introduce additional uncertainty into bioenergetics estimates of avian predation, with various methods producing estimates of daily energy intake that range from 0.21 to 0.48 kg of food per day (Elson 1962; Latta and Sharkey 1966; Wood and Hand 1985; Shearer et al. 1987; Wood 1987a). Given such variability in the estimates of diet composition and energetic requirements, we believe that our approach provides a useful solution by estimating a range of values for predator diet composition when local diet data are lacking. Models of fish consumption by birds were more sensitive to changes in the size of fish eaten and the proportion of fish in the diet than to changes in the energy requirements of birds or the energy density of fish (Feltham 1995; Madenjian and Gabrey 1995). Therefore, we believe that fixing the energy requirements of birds and the energy density of steelhead was unlikely to introduce appreciable bias into our model, relative to the unavoidable uncertainty in other parameters with higher sensitivities. We fixed the energetic requirements for common mergansers at the value published by Feltham (1995) for female mergansers. Because females have lower energy requirements than males (Feltham 1995), our model was more likely to underestimate predation than to overestimate it. For belted kingfishers, we used the daily energetic requirements estimated by Forsell (1983) for the Mad River during winter. If kingfishers have greater energetic requirements in the winter, our model may have overestimated their predation on steelhead during the summer lagoon period.

Because we had insufficient diet data with which to infer the size selectivity of avian predators, we used the most parsimonious approach: a single size-frequency distribution for the lagoon closure period from which we assumed equal probabilities of predation on all size-classes of steelhead captured during lagoon seining, given predator specific-size constraints. The size frequency of the steelhead present in the lagoon changes during the closure period, with fish increasing in size from July (mean size: 21.7 g in 2009 and 23.7 g in 2010) to November (mean size, 66.1 g in 2009 and 54.9 g in 2010). Use of a single size-frequency distribution, therefore, will overestimate the sizes of fish eaten early in the lagoon period but underestimate the sizes of those eaten in October and November. Thus, the model will underestimate the number of fish eaten early in the year and overestimate the number of fish eaten late in the year. From a population perspective, however, predation late in the year may

have a greater impact on future adult returns because some of the fish eaten early in the year might have died of other causes before attaining the lifecycle stage of those eaten later in the year. With more frequent bird surveys, we could apply the bioenergetics model to estimate predation during specific months in order to account for the change in steelhead size frequency over time.

Our model was also conditional on bird-days. Our survey approach prevented the estimation of error for bird counts. As previously discussed, we believe that there was little error in counting birds because of the open nature of the canopy in the lagoon and the narrow width of the survey transect. Because we could not estimate the error associated with bird counts, we chose not to estimate the variability in the calculation of bird-days (via linear interpolation) for inclusion in the model. Our final estimates of the consumption of steelhead by common mergansers and belted kingfishers during the lagoon period do not include any variability from either error in bird counts or error in estimating bird-days. Application of a true double-observer approach (Nichols et al. 2000; Thompson 2002) would enable estimation of the error in bird counts. The variability associated with bird counts could then be used to estimate the variability in the estimation of bird-days for incorporation into the model.

The range of values that we chose for the contribution of steelhead to bird diets (20–100%) nearly encompasses the range of values in the literature for belted kingfishers and common mergansers (Forsell 1983; Shearer et al. 1987; Kålås et al. 1993; Feltham 1995; Cairns 1998; Wiese et al. 2008). A diet of 100% steelhead was unrealistically high and was included to represent a worst-case scenario. Although we could not characterize the diet of mergansers in the Scott Creek estuary using stomach contents because the birds were collected dead and in the upper watershed, most stomachs contained the remains of sculpins, Three-Spined Sticklebacks, and steelhead. A diet of ≤20% salmonids is likely too low. Although the presence of other prey species can ameliorate the predation pressure on steelhead, mergansers and kingfishers have targeted salmonids over other species in systems where salmonids were productive (Elson 1962; Wood 1987b). There are few other prey species in the Scott Creek lagoon, and the biomass is dominated by juvenile steelhead (Beck et al. 2006); therefore, we assumed that avian predators target steelhead over Three-Spine Sticklebacks and Tidewater Gobies *Eucyclogobius newberryi* (the next most common species in the lagoon in terms of biomass). With the contribution of steelhead to merganser diets as low as 40%, mergansers would eat 15–20% of the annual production in the lagoon. Lagoon-reared fish comprise 95% of the returning adult population (Bond et al. 2008). Avian predation rates of 15–20% therefore, may have a significant effect on this imperiled steelhead population because of their disproportionate contribution to the breeding population.

Our study represents progress toward quantifying the mortality of ESA-listed steelhead from predation during freshwater rearing. A combination of stream surveys and bioenergetics modeling allowed us to identify the predators that likely

have the greatest effect on steelhead in this small coastal watershed. Rarely observed predators, such as great blue herons and pied-billed grebes, were not likely to exert significant predation pressure relative to the more common belted kingfishers and common mergansers. Furthermore, due to their smaller size and lower energy requirements, kingfishers likely affect steelhead populations to a lesser degree than mergansers. Directing resources toward understanding merganser foraging habits and better quantifying the diet of mergansers may be the most effective way to improve estimates of freshwater rearing mortality for steelhead along the central California coast.

ACKNOWLEDGMENTS

REFERENCES

Adrean, L. J., D. D. Roby, D. E. Lyons, K. Collis, and A. F. Evans. 2012. Potential effects of management on Caspian tern *Hydroprogne caspia* predation on juvenile salmonids at a colony in San Francisco Bay, California. Transactions of the American Fisheries Society 141:1682–1696.

Beck, N., E. Freund, and M. Mathias. 2006. Comparative lagoon ecological assessment project (CLEAP), Santa Cruz County, California. 2NDNATURE Ecosystem Science and Design, Santa Cruz, California. Available: www.2ndnaturellc.com/wp-content/uploads/2011/12/CLEAP-Final_reduced.pdf. (January 2013).

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242–2252.

Cairns, D. K. 1998. Diet of cormorants, mergansers, and kingfishers in northeastern North America. Canadian Technical Report of Fisheries and Aquatic Sciences 2225.

Collis, K., D. D. Roby, K. W. Larson, L. J. Adrean, S. K. Nelson, A. F. Evans, N. Hostetter, D. Battaglia, D. E. Lyons, T. Marcella, and A. Patterson. 2012. Trends in Caspian tern nesting and diet in San Francisco Bay: conservation implications for terns and salmonids. Waterbirds 35:25–34.

Elson, P. F. 1962. Predator–prey relationships between fish-eating birds and Atlantic Salmon. Fisheries Research Board of Canada Bulletin 133.

Evans, A. F., D. D. Roby, K. Collis, B. M. Cramer, J. A. Sheggeby, L. J. Adrean, D. S. Battaglia, and D. E. Lyons. 2011. Recovery of coded wire tags at a Caspian tern colony in San Francisco Bay: a technique to evaluate impacts of avian predation on juvenile salmonids. North American Journal of Fisheries Management 31:79–87.

Feltham, M. J. 1995. Consumption of Atlantic Salmon smolts and parr by goosanders: estimates from doubly-labelled water measurements of captive birds released on two Scottish rivers. Journal of Fish Biology 46:273–281.

Forsell, D. J. 1983. Predatory efficiency and energetics of belted kingfishers wintering along the Mad River. Master's thesis. Humboldt State University, Arcata, California.

Frechette, D. F. 2010. Impacts of avian predation on juvenile salmonids in central California watersheds. Master's thesis. San Jose State University, San Jose, California.

Frechette, D. M., A. M. K. Osterback, S. A. Hayes, M. H. Bond, J. W. Moore, S. A. Shaffer, and J. T. Harvey. 2012. Assessing avian predation on juvenile salmonids using passive integrated transponder tag recoveries and mark–recapture methods. North American Journal of Fisheries Management 32:1237–1250.

Gagliardi, A., A. Martinoli, D. Preatoni, L. A. Wauters, and G. Tosi. 2007. From mass of body elements to fish biomass: a direct method to quantify food intake of fish-eating birds. Hydrobiologia 583:213–222.

Good, T. P., R. S. Waples, and P. Adams, editors. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66.

Gregory, R. D., S. P. Carter, and S. R. Baillie. 1997. Abundance, distribution and habitat use of breeding goosanders *Mergus merganser* and red-breasted mergansers *Mergus serrator* on British rivers. Bird Study 44:1–12.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21:1009–1020.

Hayes, S. A., M. H. Bond, C. V. Hanson, E. V. Freund, J. J. Smith, E. C. Anderson, A. J. Ammann, and R. B. MacFarlane. 2008. Steelhead growth in a small central California watershed: upstream and estuarine rearing patterns. Transactions of the American Fisheries Society 137:114–128.

Hayes, S. A., M. H. Bond, C. V. Hanson, A. W. Jones, A. J. Ammann, J. A. Harding, A. L. Collins, J. Perez, and R. B. MacFarlane. 2011. Down, up, down and "smolting" twice? seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. Canadian Journal of Fisheries and Aquatic Sciences 68:1341–1350.

Hoeinghaus, D. J., and F. M. Pelicice. 2010. Lethal and nonlethal effects of predators on stream fish species and assemblages: a synthesis of predation experiments. Pages 619–648 in K. B. Gido and D. A. Jackson, editors. Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society, Symposium 73, Bethesda, Maryland.

Kålås, J. A., T. G. Heggberget, P. A. Bjørn, and O. Reitan. 1993. Feeding behaviour and diet of goosanders (*Mergus merganser*) in relation to salmonid seaward migration. Aquatic Living Resources 6:31–38.

Koplin, J. R. 1972. Measuring predator impact of woodpeckers on spruce beetles. Journal of Wildlife Management 36:308–320.

Koplin, J. R., M. W. Collopy, A. R. Bammann, and H. Levenson. 1980. Energetics of two wintering raptors. Auk 97:795–806.

Lance, M. M., A. J. Orr, S. D. Riemer, M. J. Weise, and J. L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. National Marine Fisheries Service, Alaska Fisheries Science Center, AFSC Processed Report 2001-04, Seattle. Available: www.afsc.noaa.gov/Publications/ProcRpt_pages/ProcRpt01.htm. (December 2012).

Larsen, D. P., A. R. Olsen, and D. L. Stevens Jr. 2008. Using a master sample to integrate stream monitoring programs. Journal of Agricultural, Biological, and Environmental Statistics 13:243–254.

Latta, W. C., and R. F. Sharkey. 1966. Feeding behavior of the American merganser in captivity. Journal of Wildlife Management 30:17–23.

Madenjian, C. P., and S. W. Gabrey. 1995. Waterbird predation on fish in western Lake Erie: a bioenergetics model application. Condor 97:141–153.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: www.R-project.org. (June 2012).

Remsen, J. V., Jr., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113:381–398.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Roby, D. D., D. E. Lyons, D. P. Craig, K. Collis, and G. H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. Canadian Journal of Zoology 81:250–265.

Salyer, J. C., II, and K. F. Lagler. 1949. The eastern belted kingfisher, *Megaceryle alcyon alcyon* (Linnaeus), in relation to fish management. Transactions of the American Fisheries Society 76:97–117.

Satterthwaite, W. H., S. A. Hayes, J. E. Merz, S. M. Sogard, D. M. Frechette, and M. Mangel. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. Transactions of the American Fisheries Society 141:781–794.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead Rainbow Trout (*Salmo gairdneri gairdneri*) and Silver Salmon (*Oncorhynchus kisutch*). California Department of Fish and Game, Fish Bulletin 98.

Shearer, W. M., R. M. Cook, D. A. Dunkley, J. C. MacLean, and R. G. J. Shelton. 1987. A model to assess the effect of predation by sawbill ducks on the salmon stock of the River North Esk. Scottish Fisheries Research Report 37.

Smith, J. J. 1990. The effects of sandbar formation and inflows on aquatic habitat and fish utilization in Pescadero, San Gregorio, Waddell, and Pomponio Creek estuary/lagoon systems, 1985–1989. California State University and the California Department of Parks and Recreation, Report 84-04-324, Sacramento. Available: worldcat.org/oclc/276359495/viewonline. (December 2012).

Spence, B. C., and T. H. Williams. 2011. Status review update for Pacific salmon and steelhead listed under the endangered species act: central California coast Coho Salmon ESU. NOAA Technical Memorandum NMFS-SWFSC-475.

Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 119:18–25.

Tollit, D. J., M. J. Steward, P. M. Thompson, G. J. Pierce, M. B. Santos, and S. Hughes. 1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. Canadian Journal of Fisheries and Aquatic Sciences 54:105–119.

Vessel, R. D. 1977. Energetics of the belted kingfisher. Doctoral dissertation. Oregon State University, Corvallis.

Wiese, F. K., J. K. Parrish, C. W. Thompson, and C. Maranto. 2008. Ecosystem-based management of predator–prey relationships: piscivorous birds and salmonids. Ecological Applications 18:681–700.

Wood, C. C. 1987a. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island: I. predation during the seaward migration. Canadian Journal of Fisheries and Aquatic Sciences 44:941–949.

Wood, C. C. 1987b. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island: II. predation of stream-resident juvenile salmon by merganser broods. Canadian Journal of Fisheries and Aquatic Sciences 44:950–959.

Wood, C. C., and C. M. Hand. 1985. Food-searching behaviour of the common merganser (*Mergus merganser*): I. functional responses to prey and predator density. Canadian Journal of Zoology 63:1260–1270.

Appendix: Daily Bird Counts and Length–Otolith Width Relationship
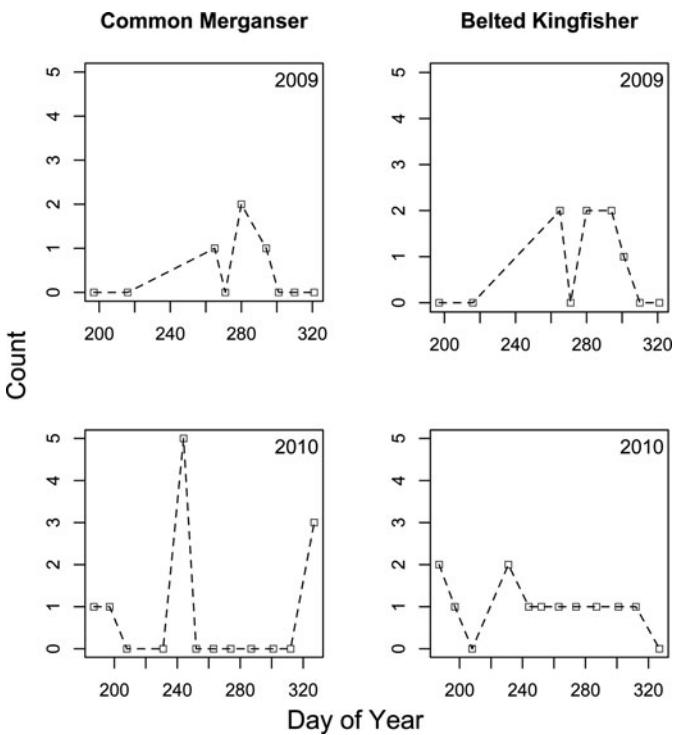
FIGURE A.1. Counts of common mergansers and belted kingfishers from stream surveys conducted in 2009 and 2010 versus day of the year. The dashed lines illustrate the linear interpolations used to estimate the number of bird-days in the Scott Creek lagoon.
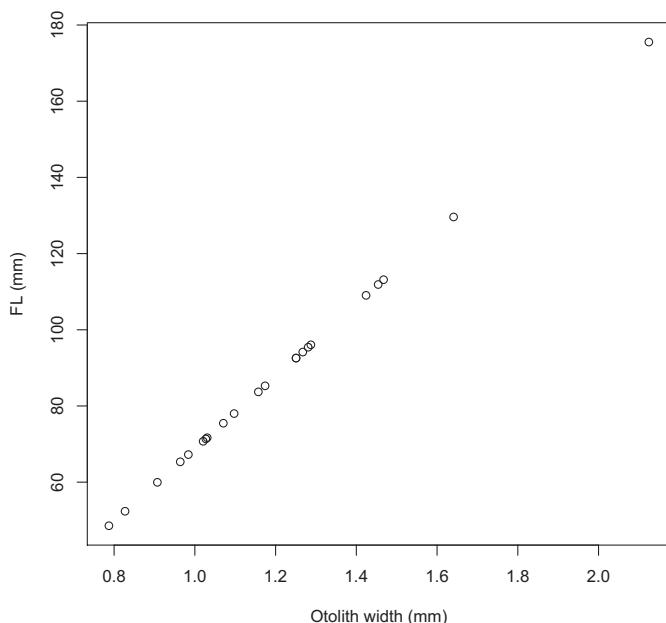
FIGURE A.2. Relationship between steelhead FL and otolith width, described by the equation FL = 115.11 · otolith width − 56.656 ($R^2 = 0.847$, $P < 0.0001$).