

Multiscale influence of climate on estuarine populations of forage fish: the role of coastal upwelling, freshwater flow and temperature

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ABSTRACT: We examined how local- and regional-scale environmental drivers affect patterns of abundance and recruitment in 2 abundant and ecologically significant forage fishes (Pacific herring *Clupea pallasii* and surf smelt *Hypomesus pretiosus*) in the Skagit River estuary (Puget Sound, Washington, USA). We identified associations between survey catch rates and environmental conditions at 2 scales: within-season distributional shifts in response to local environmental conditions, and inter-annual patterns of relative year class strength related to both local- and regional-scale drivers. Using monthly data that spanned a 9 yr period, we found that a small proportion (<2%) of the total deviance in catch rates for both species was related to within-estuary variation in surface water temperature and salinity but that a larger fraction (7 and 12% for Pacific herring and surf smelt, respectively) was explained by interannual variation in recruitment strength. Annual abundance indices for both species were uncorrelated with cumulative river discharge and regional sea surface temperature but positively correlated with an index of cumulative coastal upwelling, suggesting a linkage between regional-scale environmental conditions and age-0 recruitment. Moreover, our annual age-0 Pacific herring time series was positively correlated with a similar time series from the Strait of Georgia (~100 km north), further suggesting that age-0 recruitment in these populations is synchronized by regional upwelling as opposed to estuary-specific environmental forcing related to river flows. The present study isolates a potential key process governing age-0 forage fish abundance in this system and highlights the importance of simultaneously evaluating patterns of variability across multiple spatiotemporal scales in order to identify the primary pathways through which climate may impact estuarine populations.

KEY WORDS: Puget Sound · Pacific herring · Surf smelt · Deviance partitioning · Upwelling · Fish recruitment

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INTRODUCTION

Estuaries are highly productive habitats that play an important role as both primary and nursery habitat for a wide diversity of species. However, estuarine ecosystems are increasingly threatened by water diversions, coastal development, overfishing and pollution (Kennish 2002, Lotze et al. 2006). In addition to these stressors, the dependence of estuarine communities on

river flow and ocean conditions makes them particularly susceptible to climate change. Estuaries are dynamic systems characterized by fluctuations in both freshwater input and the intrusion of marine waters across time scales ranging from daily to interannual and inter-decadal (Mann & Lazier 2006). Because estuaries occur where freshwater runoff mixes with marine waters, climate impacts expressed either over land or in coastal marine waters can alter water circulation

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patterns, nutrient delivery, habitat availability and a range of other variables that may potentially affect population and community dynamics. Given the importance of estuaries to coastal fisheries and ecosystems (Houde & Rutherford 1993) and the strong likelihood of future climate change due to global warming (IPCC 2007), the urgency of identifying how estuarine populations respond to climate variability has increased (Scavia et al. 2002).

Climate forcing has been linked to interannual variability in estuarine fish populations (e.g. Attrill & Power 2002), but fish responses to climate change can be attributed to multiple mechanisms operating at different scales (Harley et al. 2006, Rijnsdorp et al. 2009). At local spatial and temporal scales, fish may exhibit distribution shifts in response to changes in the spatial extent of preferred water temperature and salinity fields (Kimmerer et al. 2009). Several juvenile fish species, for instance, preferentially select thermal conditions that optimize metabolic efficiency and growth (e.g. Clark & Green 1991, Mortensen et al. 2007, Portner & Knust 2007). Ultimately, the average spatial extent and availability of optimal water conditions within an estuary is limited by monthly, seasonal and interannual patterns in river flow and ocean conditions. At larger spatiotemporal scales, seasonal and interannual variation in river discharge and/or ocean conditions can influence primary production rates and the availability of zooplankton (Roman et al. 2005, Barbosa et al. 2010). These environmental drivers can influence interannual variation in fish recruitment through their effects on survivorship during critical early life history stages (Kimmerer et al. 2001, North & Houde 2003, Jung & Houde 2004). Identifying biological responses to physical drivers (either correlative or mechanistic) is an essential first step for developing simulations of estuarine responses under different climate scenarios (Meynecke et al. 2006, Hollowed et al. 2009).

In the US Pacific Northwest, climate change is expected to alter both river and coastal ocean conditions. Over the past 60 yr, increased spring temperatures have resulted in advancement of the timing of peak spring runoff (Mote et al. 2003, Stewart et al. 2005) and projections under future climate warming scenarios suggest that these trends will likely continue to cause associated changes in the magnitude of seasonal flows (Stewart et al. 2004). Ocean productivity in coastal waters along the Pacific Northwest, like other eastern boundary current ecosystems, is strongly influenced by seasonal wind-driven upwelling. In estuarine systems along the outer Washington and Oregon coasts ocean exchange is the primary source of nitrogen during the growing season (Hickey & Banas 2003). Sea surface waters are expected to warm in this region by 1°C over the next 50 yr (Snover et al. 2005) and sea-

sonal coastal upwelling may intensify but initiate later in the year (Snyder et al. 2003, Diffenbaugh et al. 2004). Despite the likelihood of future changes in river flows and oceanographic conditions, our ability to anticipate impacts on estuarine communities is limited in many systems by a poor understanding of baseline variability and the extent to which environmental variables govern population and community dynamics (Roessig et al. 2004).

In the present study, we evaluated the relationship between climate-sensitive environmental variables and fish distribution and recruitment in the Skagit River estuary (Puget Sound, Washington). The Skagit River is the third largest river in the Pacific Northwest in terms of discharge (annual mean discharge 450 m³ s⁻¹) and drains a watershed of ~8000 km² into Whidbey Basin, one of 4 sub-basins comprising Puget Sound. The river supplies half of all fresh water entering the Sound and supports a highly productive estuary; marine birds, mammals, as well as juvenile marine fish and all 5 species of Pacific salmon are among the many species that utilize the estuary. Forage fish are a particularly important component of the estuarine community as they constitute greater than half of the total pelagic fish biomass (Rice 2007) and occupy a key role in the food web by linking zooplankton to higher trophic level predators (Bakun 1996). As with other estuaries worldwide, the Skagit River estuary has been impacted by a broad suite of anthropogenic stressors including extensive loss of floodplain and salt marsh habitat due to agricultural land use (Hood 2004). In addition, a large proportion of the Skagit River watershed possesses a snowmelt-dominated flow regime that is sensitive to regional climate modes (Pacific Decadal Oscillation, El Niño Southern Oscillation; Moore et al. 2008). Under various climate warming scenarios, fall and winter precipitation patterns are expected to remain similar to historic levels, but spring and summer conditions will be drier. Moreover, the proportion of precipitation falling as snow in the winter will decline, resulting in a lower snow pack and reduced spring freshet (Snover et al. 2005). If Skagit River estuary fish populations are influenced by interannual variability in the magnitude of seasonal river flows, we would expect future changes in the fish assemblage that are linked to the cumulative effects of climate change on the Skagit River watershed.

However, if fish variability is related more strongly to marine influences like sea surface temperature (SST) or coastal upwelling, we would anticipate the largest effects of climate change to be expressed through oceanographic forcing. Winter SSTs in Puget Sound are correlated with basin-scale climate modes (Moore et al. 2008) and upwelled waters from the outer Washington coast supply most (ca. 90%) of the nitrogen

entering Puget Sound (Mackas & Harrison 1997). Despite the importance of the Skagit River estuary to the Puget Sound ecosystem, only a few studies have evaluated the importance of physical drivers on fish distributions (e.g. Rice 2007), and the relationship between climate-sensitive environmental variables and the productivity of forage fishes is unknown.

Using a 9 yr survey (2001–2009) of pelagic fishes in the Skagit River estuary, we related the distribution of pelagic forage fishes to local water conditions (surface temperature and salinity) and recruitment to regional environmental variables (Skagit River discharge, regional SSTs, and coastal upwelling indices) that are correlated with ocean basin-scale climate regimes (Mote et al. 2003, Moore et al. 2008). The time span of our survey is of particular interest because it includes years with above (2002) and below average (2001 and 2005) river flow and an extreme year in terms of ocean conditions (2005) that was marked by increased SSTs and delayed coastal upwelling throughout the NE Pacific. In the spring and summer of 2005 anomalously low primary and secondary production were observed from Baja California to British Columbia, which accompanied sharp declines in the abundance and productivity of animals higher in the food web (Brodeur et al. 2006, Barth et al. 2007, Mackas et al. 2007, Jahncke et al. 2008).

MATERIALS AND METHODS

Survey design and data collection. All data analyzed in the present study were collected as part of a larger effort to monitor juvenile salmonids in the Skagit River estuary. Data were collected via surface trawl in the Skagit River estuary at monthly intervals (June–October) from 2001 to 2009. From 2001 to 2003, 2 to 3 replicate tows were performed at 12 sites located throughout the bay (Fig. 1). Beginning in 2004, a spatially stratified random sampling design was implemented. Three distinct regions in the bay were identified (north, middle and south) based on differences in bathymetry and oceanographic conditions. The northern region possesses a complex shoreline with several small embayments and islands and the middle region contains a deep submarine canyon that widens into a broad, open seafloor in the southern region. Waters in the northern region are generally more saline than the middle and southern regions, which are closer to the river mouth. A total of 26 sampling sites (10 north, 7 middle and 9 south) were randomly selected from a pool of sites identified by superimposing a 0.6 km² grid on the survey area. One tow was conducted at each of these randomly selected sites per month. To maintain consistency with the earlier sampling design, 4 histori-

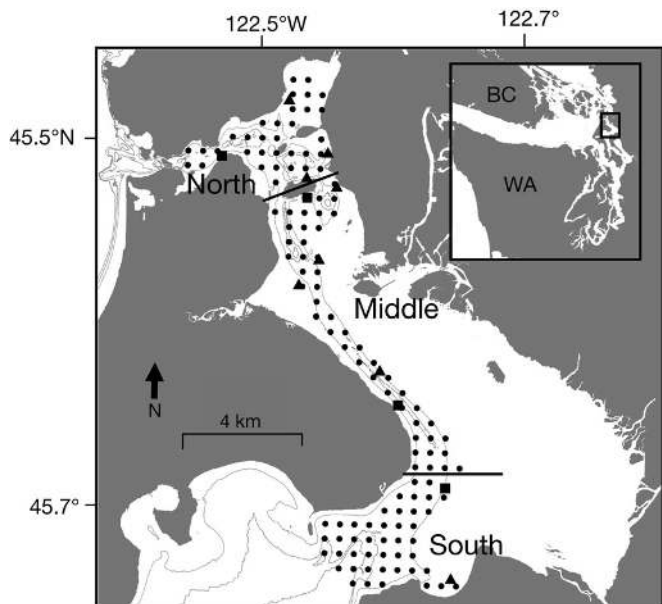


Fig. 1. Study site and survey design in the Skagit River estuary (Puget Sound, Washington, USA). ■, ▲: sampling sites that were sampled between 2001 and 2003. Starting in 2004, a sampling grid was established with sites (●) separated by 0.6 km. Ten, 7 and 9 sites were randomly sampled in the north, middle and southern regions of the survey, respectively. In addition, 4 sites from 2001 to 2003 (■) were retained in the monthly survey. BC: British Columbia, WA: Washington

cal sites (Fig. 1) from the initial survey design were also retained in the new survey (2 replicate tows each), yielding a total sampling of 30 sites and 34 tows each month. In some instances, limitations on boat time or inclement weather limited the total number of sampled sites; however, no fewer than 10 sites were sampled during any single monthly sampling event.

All sampling was performed with a 3.1 m high × 6.1 m wide Kodiak surface trawl, or 'towsnet', deployed between 2 boats, each with a 50 m tow line connected to a bridle on the net. Mesh sizes in the net ranged from 7.6 cm stretch in the forward section, and progressively reduced to 3.8 cm and 1.9 cm in the middle sections, and 0.6 cm in the codend. The net was towed at the surface for 10 min at 950 rotations per minute (RPM) on the engine of the primary vessel, for a typical towing speed of 2 to 3 knots. Catch was sorted into species, counted, weighed and sub-sampled for length measurements. At each sampling site physical data (surface water temperature and salinity) were collected using a YSI 85 environmental monitoring system (Yellow Springs Instruments).

The major forage fish species encountered in the survey included young-of-the-year Pacific herring *Clupea pallasii* and young-of-the-year surf smelt *Hypomesus pretiosus*, which combined accounted for

73% of the total catch based on numerical abundance. We therefore focused our analyses on the age-0 year class of these 2 species, which were easily separated from older age groups using length frequency data. Pacific herring spawn between February and March and deposit their eggs on substrate in shallow subtidal and intertidal habitats located along the Skagit Bay coastline. The larvae hatch 4 wk after spawning, rear in shallow nearshore waters for 2 to 3 mo and then move into deeper, open waters in the bay after metamorphosing. By June or July, post-metamorph herring appear in the survey and generally range in size between 60 and 90 mm (total length, TL). Surf smelt spawn year round with peak spawning events occurring in both the summer and winter. As with herring, surf smelt spawn on shallow subtidal and intertidal substrate and rear in nearshore waters before moving into open waters as post-metamorphs. Individuals presumed to be the result of late fall/winter spawning appeared in the spring sampling and ranged in size between 80 and 100 mm. Individuals that hatched later in the year (summer-spawned individuals) usually appeared in the survey in September or October, and were <60 mm. We categorized fall/winter-spawned individuals as age-0 and excluded summer-spawned individuals because they were too small to be caught efficiently during their first summer of life. Age-0 surf smelt occurred in all months sampled and ranged in size from 80 to 100 mm TL. Pacific herring are captured by a small commercial spawn-on-kelp roe fishery located in central Puget Sound and by recreational fishing, while mature surf smelt are only fished recreationally; age-0 fish are not harvested in Skagit Bay.

To calculate the number of age-0 individuals in a haul, we measured lengths for 25 randomly selected individuals for each species and scaled the number of individuals in the age-0 length ranges up to the total catch. Peak catches of age-0 Pacific herring and surf smelt extend up in to the thousands and were 7 and 4 times more abundant than those of older age classes, respectively. The sampling of 25 individuals was adequate for separating age-0 fish from older fish, but a slight positive bias may have been introduced to estimates of age-0 catch per unit effort (CPUE) if age-1+ fish composed a proportion of the catch that was too small to be represented by fish in the length subsample.

Statistical analysis. The analysis proceeded in 2 phases. Our first objective was to evaluate the importance of water conditions (surface temperature and salinity) on the survey catch rates at the scale of individual sampling events. From the onset we recognized that surface water conditions are just one of several possible variables that may dictate fish distributions

and that other unmeasured factors may potentially confound the effect of temperature and salinity. Fish commonly distribute across space based on fixed habitat features like bottom substrate and bathymetry (Maravelias 2001, van der Kooij et al. 2008) and exhibit seasonal ontogenetic shifts in habitat use (Clark & Green 1991, Brown 2002). In addition, climate processes operating at spatial scales matching or exceeding that of an estuary may drive interannual fluctuations in cohort strength (Attrill & Power 2002). We therefore identified 3 sets of variables in addition to water conditions that can broadly be categorized as spatial, seasonal and interannual (or 'cohort strength') predictors. Our goal was to evaluate the importance of each variable set relative to temperature and salinity and to determine whether temperature and salinity effects could be reliably isolated from the remaining variables. We therefore used deviance partitioning following Whittaker (1984). The method permits a full examination of the deviance structure underlying a response variable and provides an intuitive metric by which to compare variable importance. Because our aim was to elucidate deviance structure as well as variable importance, we did not apply standard information-theoretic methods (e.g. Akaike's information criterion (AIC) weights; Burnham & Anderson 2002). AIC weights indicate the weight of evidence in favor of including variables in a predictive model but do not convey information on the relative influence predictors have on the response variable (Murray & Conner 2009). Potential predictors were day of the year (to account for phenology), water depth, distance to shore, and spatial coordinates (for spatially fixed habitat features), year as a categorical variable (for cohort strength), and local temperature and salinity.

Preliminary analyses indicated both zero inflation in the response variables (CPUE), which is common in fish survey data, and nonlinear relationships between CPUE and day of the year and latitude and longitude. To accommodate these issues we used a 2-stage modeling approach with generalized additive models (GAMs) (Barry & Welsh 2002). In 2-stage models occurrence (presence/absence) is first modeled as a logistic function (stage one) and in cases where fish are present, the corresponding abundance (CPUE, number per tow) is modeled (stage 2) assuming a distribution appropriate for abundance (Maunder & Punt 2004). The predicted catch rate is the product of the probability of occurrence and the predicted abundance. The deviance of the complete model is simply the sum of the deviance from the first and second stage models. In GAMs, the response variable is assumed to be a sum of separate individual smooth spline functions (one for each predictor variable) with a link function that is appropriate to the distribution of the

response variable (Wood 2006). Our working full model therefore took the form:

$$\text{logit}(p) = \beta_j \text{Year} + s(\text{Day of the year}) + \beta \text{Depth} + \beta \text{Shore} + s(\text{Lat, Lon}) + \beta_i \text{Temp} + \beta_i \text{Sal}$$

$$\ln(u) = \beta_j \text{Year} + s(\text{Day of the year}) + \beta \text{Depth} + \beta \text{Shore} + s(\text{Lat, Lon}) + \beta_i \text{Temp} + \beta_i \text{Sal}$$

where p is the probability of fish occurrence linked to the predictor variables via a logit function, u is the predicted mean catch rate of a fish given its occurrence linked to the predictors via a log function and s indicates variables modeled with a spline function. The betas (β , β_i) indicate terms with linear coefficients. Interannual variation in cohort strength was accounted for using the categorical variable Year (a coefficient was estimated for each j th year) and temperature and salinity effects were estimated for each i th month to accommodate potential ontogenetic shifts in water condition preferences (e.g. Clark & Green 1991). Essentially, we estimated interaction terms between temperature and salinity with month, but instead of including the categorical variable Month in the model we used the smooth spline equivalent by modeling Day of the year. Initial analyses indicated that a smooth spline function of Day of the year outperformed Month based on deviance reduction. Latitude and longitude were modeled using a bivariate spline function. Examination of abundance histograms for each species indicated over-dispersion. Therefore we modeled the response assuming a negative binomial distribution. To limit the potential for over-fitting and simplify deviance decomposition we limited interaction terms between variables. Furthermore we avoided over-fitting by constraining the maximum number of spline knots to 4 and 8 for the univariate and bivariate spline functions, respectively (Wood 2006). The degree of nonlinearity corresponding to the spline functions in the stage 1 and 2 GAMs was optimized using generalized cross validation, which takes into account the improvement in model fit and loss of degrees of freedom that accompany increased complexity of the response curves. The routine provides an objective method for calculating the optimal flexibility of the spline (Wood 2006). In some instances, species may exhibit threshold responses to environmental variables. We ensured that our use of linear terms to model temperature and salinity was appropriate by visually inspecting plots of the raw catch data against temperature and salinity.

With 4 predictor sets (interannual: Year; seasonal: Day of the year; spatial: Latitude, Longitude, Depth, Distance to Shore; water conditions: Temperature, Salinity) the total number of unique and shared deviance components (i.e. deviance explained by a single predictor and deviance that may be explained

by 2 or more predictors, respectively) is 15. However, our main interest was in identifying the deviance components that are uniquely explained by each set of variables, and the proportion that was confounded with temperature and salinity. We therefore calculated only a subset of the total possible number of deviance components. To estimate the deviance component unique to a predictor X_1 given predictor X_2 , we calculated the deviance of a model with both and subtracted the deviance of a model that contains only predictor X_2 . To calculate the overlapping component, we summed the deviance of the models containing X_1 and X_2 separately and subtracted the deviance of the model containing both X_1 and X_2 . This general approach can be expanded to consider > 2 sets of predictor variables (Lawler & Edwards 2006).

The proportion of deviance explained (D) by generalized linear models (GLMs) and GAMs is analogous to the variance explained (R^2) in standard least squares regression (Guisan & Zimmermann 2000). The deviance of the full 2-stage model is the sum of the deviances from the individual stage 1 and 2 models (Barry & Welsh 2002). Therefore, we calculated D for each model as:

$$(\Sigma D_{\text{null}} - \Sigma D_{\text{res}}) / \Sigma D_{\text{null}}$$

where D_{null} and D_{res} correspond to null and residual deviances, respectively (Guisan & Zimmermann 2000). The null deviance is the deviance of the model with an intercept only and the residual deviance is the deviance that remains unexplained by the model after all variables have been included. In instances where water conditions explained a unique component of the deviance, we performed an F -test between a 'base' model that included spatial, seasonal, and interannual variables and a second model that possessed all base predictors as well as temperature and salinity (Wood 2006). If the model containing water conditions was a significant improvement over the base model, we extracted the temperature and salinity effect sizes from both the first and second stage models to examine seasonal patterns in water condition preference.

For the second phase of our analysis, we sought to evaluate the strength of correlations between inter-annual patterns of age-0 abundance (i.e. year class strength), with cumulative river discharge, average regional SSTs, and cumulative coastal upwelling. We obtained annual catch rate indices by first fitting full stage 1 and 2 models (base predictors + salinity + temperature). Our goal was to standardize catch in a manner that would account for spatial variation in sampling, seasonality and small-scale variation in water conditions rather than to determine which variables explain variation in CPUE (Maunder & Punt 2004); therefore, we did not perform model selection. Stan-

standardized annual catch rates were obtained by multiplying the probability of a non-zero catch in year t with the predicted catch rate for that year from the first and second stage models, respectively. We compared the standardized annual CPUE index with a simpler measure of annual abundance (the average of monthly geometric mean catches within a year) to determine the extent to which the standardized index retained patterns exhibited by the raw catch data. A correlation of 0.83 was obtained, indicating a fair degree of correspondence.

Freshwater discharge can influence the physiochemical features of an estuary as well as primary and secondary production. Cumulative river flow thus provides a time-integrated measure of these potential impacts and may be related to interannual patterns of fish abundance. We obtained daily discharge records from the US Geological Survey Mt. Vernon flow station (<http://waterdata.usgs.gov/wa/nwis/>, accessed: October 19, 2009), located ~25 km from the mouth of the Skagit River, for comparison with interannual indices of CPUE. This station closely mirrors discharge patterns in the estuary (Yang & Khangaonkar 2009). The specific season and time span when environmental conditions might be particularly important for influencing recruitment ranges widely for Pacific herring (Williams & Quinn 2000a) and is unknown for surf smelt. We therefore treated the analysis in an exploratory manner and systematically evaluated correlations between interannual abundance and a set of cumulative river discharge values that summed daily flows over a range of time spans (1 to 5 mo) across different seasons (the fall preceding sampling to the summer in which sampling occurred).

We used SST observed at Race Rocks (southern Vancouver Island) as a proxy for regional water temperature, which is well-correlated with surface temperatures within Puget Sound (Moore et al. 2008). We obtained daily SST records (www.racerocks.com/, accessed October 19, 2009) and calculated average SST values over a range of time spans and seasons in an exploratory manner as with cumulative river discharge. Cumulative upwelling provides a time-integrated measure of coastal ocean conditions that fuel primary productivity through nutrient transport. We obtained daily upwelling index values (north–south wind stress derived from sea level gridded pressure fields) located off Cape Flattery on the NW Washington coast (48° N 125° W; www.pfeg.noaa.gov/, accessed October 19, 2009). Along the US west coast, winter winds are generally southerly (downwelling-favorable), but transition to northerly winds (upwelling-favorable) occurs in early spring (Hsieh et al. 1995). We calculated cumulative upwelling by summing north–south wind stress starting from the spring transition,

which is defined as the day when winds turn to predominantly upwelling-favorable during early spring. We identified the spring transition by summing the upwelling index starting with February 1 and noting

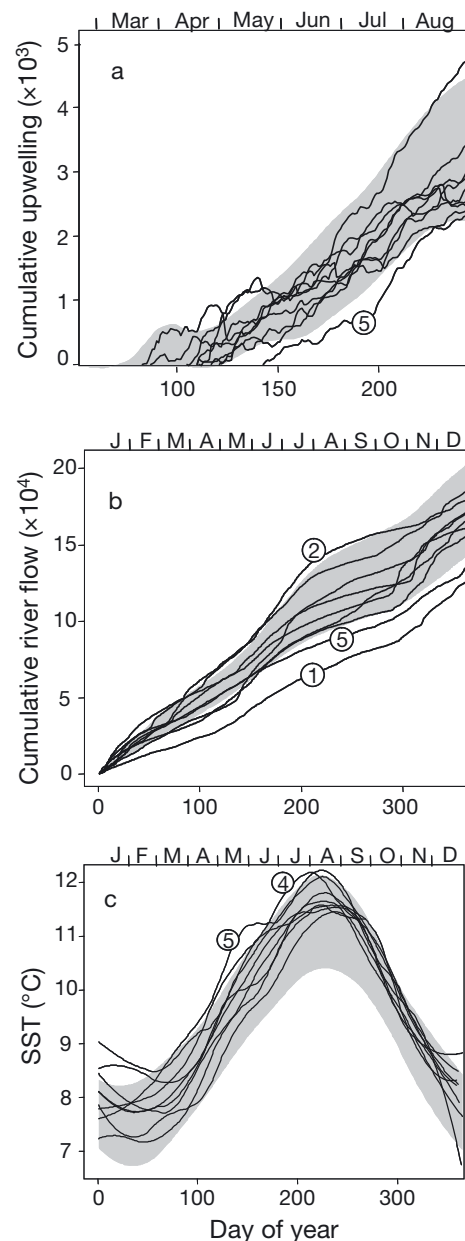


Fig. 2. (a) Cumulative upwelling, (b) Skagit River cumulative river discharge, and (c) interannual variability in sea surface temperature (SST) from 2001 to 2009. Gray bands denote the 95% range of historical values (1967–2000). Notable years that ranged outside historical variability are labeled (1, 2, 4 and 5: 2001, 2002, 2004 and 2005, respectively). For (a), the x-axis values intercepted by the cumulative upwelling curves indicate the date of spring transition. For (c), local polynomial regression smoothes (LOESS) were applied to the daily time series to clarify seasonal trends using a smoothing window of one month

the date the minimum value was achieved (Pierce et al. 2006). We examined correlations between annual abundance indices and cumulative upwelling beginning with July 1 and August 1 for both species.

If recruitment is closely linked to large-scale climate processes, separate but neighboring populations should exhibit synchronous recruitment (Williams & Quinn 2000b). To evaluate this possibility, we compared age-0 herring recruitment in Skagit Bay with data from populations ~100 km north in the Strait of Georgia. We obtained standardized annual time series of age-0 herring from a late summer surface townet survey specifically designed to monitor age-0 herring abundance (J. Schweigert, Department of Fisheries and Oceanography, pers. comm.). We considered correlations with absolute values > 0.6 as notable in all circumstances but did not calculate significance levels given the exploratory nature of the analyses (Zuur 2009). All analyses were performed using the statistical software program R version 2.9 (R Development Core Team 2009) and GAMs were implemented using the 'mgcv' statistical package (Wood 2006).

RESULTS

Over the 9 yr span of the survey (2001–2009), cumulative upwelling and cumulative river discharge varied widely in comparison to historical values (1967–2000; Fig. 2). In 2005, upwelling was delayed by ~6 wk relative to the mean spring transition date of the other 8 yr and fell outside of the 95th percentile of historical ranges (Fig. 2a). Cumulative river flow in 2002 was above average while 2001 and 2005 were below average (Fig. 2b). Winter and spring regional SST values also varied widely relative to historic values, with summer temperatures generally warmer than average, particularly in 2004 and 2005 (Fig. 2c). Within the sur-

vey area, water temperatures and salinities were most variable from June to August (Fig. 3). The monthly mean temperature rose from 12.9 to 14.1°C between June and July and then decreased to 12.0°C by October (Fig. 3). In contrast, mean monthly salinity increased consistently as the summer progressed, beginning at 17.1‰ in June and reaching 25.2‰ by October (Fig. 3). Correlations between temperature and salinity were moderate in June ($r = -0.53$), but weakened as the growing season progressed (Fig. 3), indicating that effect sizes for both variables could be estimated in the same model with little bias due to collinearity.

We obtained catch data from 1247 tows. Unlike surf smelt which were captured frequently June through October, Pacific herring were rare in June samples so we excluded June data when performing all statistical analyses for Pacific herring. Overall, surf smelt was captured most frequently (85 vs. 65% of hauls for surf smelt and Pacific herring, respectively), but the cumulative abundance of Pacific herring was ~4 times higher than that of surf smelt.

Full models for surf smelt and Pacific herring (base predictors + water conditions) explained 14 and 25% of the variability in CPUE, respectively (Fig. 4). Deviance partitioning indicated that water conditions explained 3 and 5% of the total deviance for surf smelt and Pacific herring, respectively, and that 2 and 1% of the deviance was uniquely explained by water conditions (Fig. 4). Of the remaining predictors, the largest deviance component for both species was explained by interannual or 'cohort' effects that uniquely explained 7 and 12% of the variability in surf smelt and Pacific herring CPUE, respectively. Space (3 and 5%) and season (1 and 1%) contributed comparatively less to both species' models. Inclusion of the water condition terms significantly improved the explanatory ability of the models for both species (Pacific herring: $F = 43.3$, $df =$

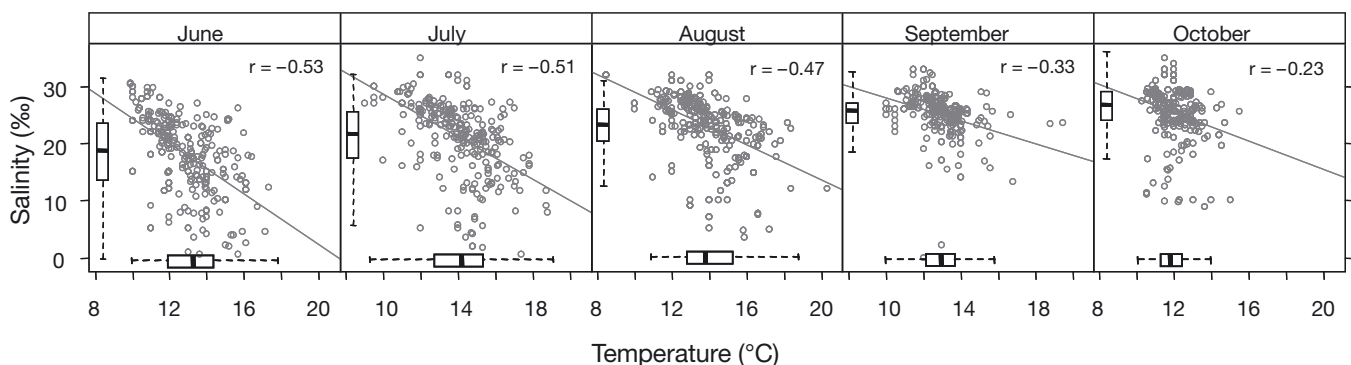


Fig. 3. Surface temperature and salinity values observed at sampling locations within the Skagit River estuary across all years (2001–2009) by month. The 99 and 95% value ranges are indicated by the vertical (salinity) and horizontal (temperature) quartile boxes. Correlations between temperature and salinity are indicated for each month

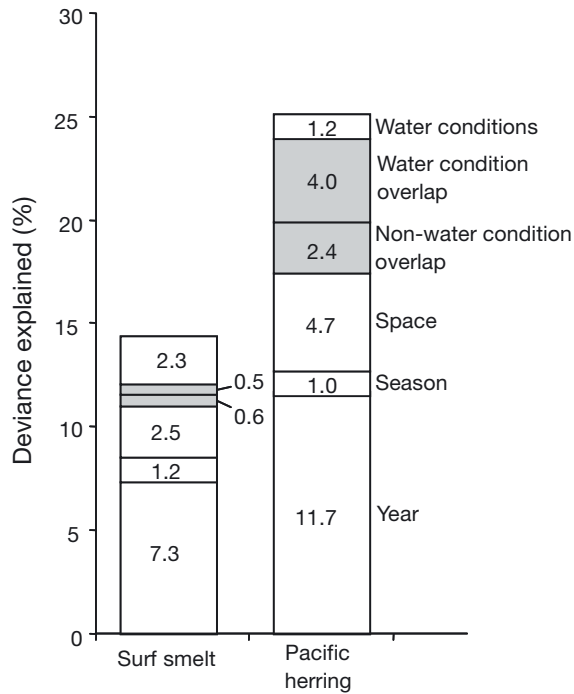


Fig. 4. Deviance decomposition of Pacific herring and surf smelt catch per unit effort. The deviance components that were uniquely explained by each predictor group are indicated (unfilled boxes). Components that were jointly explained by 2 or more non-water condition variables and those that were explained by water conditions and at least one other predictor group are depicted in the gray boxes. Variable order is identical for surf smelt and Pacific herring

15.8, $p = 0.0002$; surf smelt, $F = 101.7$, $df = 18.1$; $p < 0.0001$).

For Pacific herring, monthly effect sizes for salinity possessed confidence intervals that included zero for both the occurrence and abundance models for all months, except for July (Fig. 5). In July, abundance was positively related to salinity, but the probability of occurrence was negatively related. That is, Pacific herring were less likely to occur in high salinity waters, but when they did occur they were captured in high numbers. Of the temperature coefficients, occurrence in September and October was positively related to temperature; the remaining coefficients did not differ from zero (Fig. 5). For surf smelt, occurrence was negatively related to salinity in July, August and September (high abundance at low salinities), while coefficients corresponding to

abundance were negative in June and positive in October. Temperature on the other hand showed an overall change from a positive to a negative relationship from June to October for both occurrence and abundance coefficients (Fig. 5).

Standardized interannual catch rate indices were similar for Pacific herring and surf smelt ($r = 0.88$; Fig. 6). Both species exhibited relatively stable catch rates from 2001 to 2004 but declined in 2005 and were followed by higher interannual variability thereafter (Fig. 6). Correlations between interannual catch rate indices for both SST and cumulative river discharge were weak, with no time span–season combination yielding a correlation stronger than 0.4. In contrast, cumulative upwelling was highly correlated with both surf smelt and Pacific herring recruitment (Fig. 6). Correlations with cumulative upwelling up to August 1 were slightly higher than with cumulative upwelling up to July 1 for both species (0.70 vs. 0.73 for Pacific herring and 0.71 vs. 0.74 for surf smelt). Finally, the correlation between our age-0 herring time series and age-0 herring sampled in the Strait of Georgia was relatively strong ($r = 0.86$; Fig. 7), except for 2009 when the 2 abundance indices diverged.

DISCUSSION

Climate may impact estuarine populations of fish through a diversity of pathways and identifying popu-

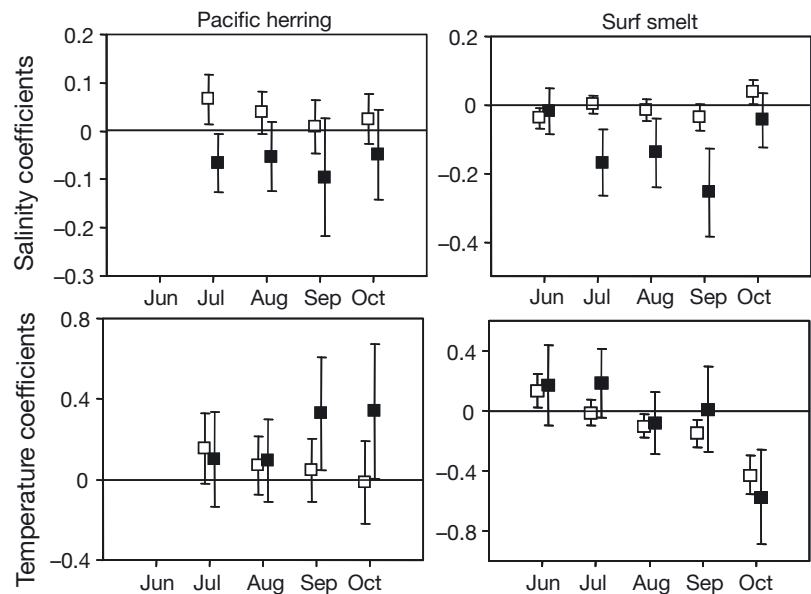


Fig. 5. Monthly temperature and salinity effect sizes for stage 1 and 2 models for Pacific herring and surf smelt catch per unit effort sampled in the Skagit River estuary. Error bars indicate 95% confidence intervals. □: abundance coefficients; ■: occurrence (presence/absence) coefficients

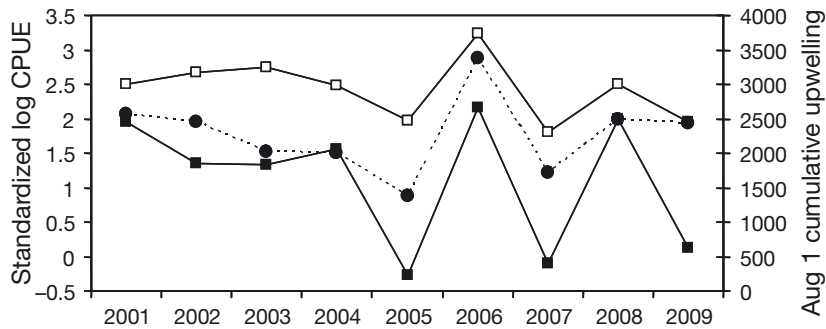


Fig. 6. *Clupea pallasii* and *Hypomesus pretiosus*. Standardized annual catch per unit effort (CPUE) of age-0 Pacific herring (■) and surf smelt (□) from the Skagit River estuary and index values of cumulative upwelling through August 1 (---●---)

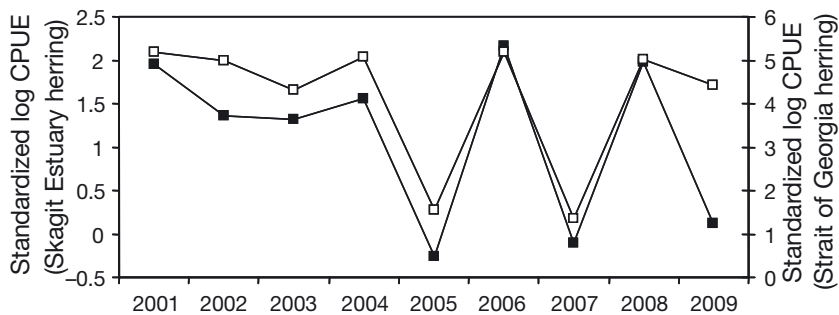


Fig. 7. *Clupea pallasii*. Standardized annual catch per unit effort (CPUE) of age-0 Pacific herring from the Skagit River estuary (this study; ■) and age-0 Pacific herring from the Strait of Georgia (□)

lation responses to physical drivers across multiple spatial and temporal scales is an essential first step towards developing models of estuarine responses to climate change. Our findings indicate that fish CPUE is partly influenced by local water conditions but that interannual effects, which are likely related to climate-mediated survivorship during early life history stages, are the largest source of variation in the catch time series. Annual age-0 Pacific herring and surf smelt abundance indices were correlated with cumulative coastal upwelling, and age-0 Pacific herring from the Skagit River estuary and Strait of Georgia covaried, which suggests that coastal upwelling may induce conditions that synchronize herring recruitment between the 2 locations.

Our results add to an emerging body of evidence that suggests that ocean climate conditions may overshadow the effects of river flow on interannual patterns of estuarine community composition (Cloern et al. 2007, 2010). In several large estuaries, interannual fish abundances have been positively correlated with river flows and these relationships were attributed to a suite of mechanisms including increased larval retention, an expansion of suitable habitat, and improved

foraging and survivorship due to enhanced primary and secondary production (Grimes & Kingsford 1996, Grimes 2001, Kimmerer 2002, Wingate & Secor 2008). The absence of a relationship between river flow and interannual CPUE for Pacific herring and surf smelt in the Skagit River estuary suggests that these mechanisms may be weak in relationship to the historical range of flows. In contrast, the positive correlation between age-0 Pacific herring and surf smelt indices with coastal upwelling indicates that ocean climate has an important influence on interannual patterns of fish recruitment in the Skagit River estuary. Unlike other estuarine systems (e.g. Oczkowski et al. 2009), Skagit River waters are nutrient-poor compared to intruding marine waters and supply only a small fraction of the nitrogen utilized by primary producers (Mackas & Harrison 1997). The significance of ocean nutrients to this estuary suggests that variation in coastal upwelling may have important consequences for survivorship during the early life history stages of age-0 Pacific herring and surf smelt through bottom-up control of the food web. A

strong relationship between ocean climate and fish and invertebrate recruitment has also recently been documented in the San Francisco estuary (Cloern et al. 2010), which further suggests that large-scale climate modes expressed through changes in ocean conditions may play a larger role in estuarine community dynamics than previously thought.

Spring and summer upwelling strongly governs primary and secondary productivity in Washington coastal waters and the overall importance of this process to forage fish in inland marine waters such as Puget Sound is partly elucidated by examining the impact of anomalous years such as 2005, which experienced a 5 wk delay in coastal upwelling (Pierce et al. 2006). Age-0 Pacific herring and surf smelt from the Skagit River estuary and Pacific herring from the Strait of Georgia declined in abundance in 2005, which paralleled negative anomalies in chlorophyll and zooplankton biomass along the Washington and British Columbia coasts (Kudela et al. 2006, Mackas et al. 2007). Moreover, reductions in salmon survivorship, rockfish recruitment and the reproductive success of marine birds were also documented in the California Current system (Brodeur et al. 2006, Sydeman et al.

2006), indicating profound ecosystem-level changes in this highly dynamic eastern boundary system (Barth et al. 2007). The sensitivity of estuarine forage fish and other species to coastal upwelling indicates that alterations in timing and intensity from climate change may have wide-ranging effects. Analyses of a 50 yr time series of wind-driven upwelling in the northern California Current ecosystem indicate an overall trend towards a later and shorter upwelling season (Bograd et al. 2009) and global climate models indicate that upwelling may intensify (Bakun et al. 2010) but initiate increasingly later in the spring (Diffenbaugh et al. 2004). Delayed upwelling disproportionately impacts species or life stages with feeding and reproductive schedules that are tuned to the seasonal availability of pelagic prey. Although uncertainty remains over the magnitude of these future changes (Mote et al. 2003, Wang et al. 2010), the prospect of years similar to 2005 reoccurring with greater frequency (Barth et al. 2007) suggests that future reductions in recruitment may occur unless populations are able to adapt (e.g. through changes in the timing of reproductive events).

Due to the limited extent of our time series, it is unclear whether the sensitivity of age-0 surf smelt and Pacific herring to upwelling is a recent phenomenon stemming from alterations in spawner age structure or is more generally characteristic of these species. A growing number of studies indicate that fish stocks that lose individuals in older age classes exhibit recruitment patterns that are more tightly coupled to climate conditions (Planque et al. 2010). For Pacific herring which spawn in late winter/early spring and can live up to 20 yr, spawn timing is closely related to body size and average winter water conditions, with larger body sizes and warmer waters favoring earlier spawning dates (Ware & Tanasichuk 1989). A loss of older, large-bodied fish results in a contraction of the time span over which spawning occurs and narrows the period during which larvae emerge, heightening the risk of a mismatch with environmental conditions (Perry et al. 2010). Over the past 3 decades, older individuals have become less numerous in British Columbian and Washington stocks (Landis & Bryant 2010), average weight-at-age has declined by as much as ca. 25% for spawners in some stocks (Schweigert et al. 2002), and the temporal window over which spawning occurs has narrowed (Therriault et al. 2009). These observations indicate that climate sensitivity may have increased over time for Pacific herring but requires further study. Considerably less is known regarding the size structure and reproductive biology of surf smelt and spawning populations are not monitored (Therriault et al. 2009), which significantly limits our ability to assess possible changes in climate sensitivity.

In systems with several forage fish species, interspecific variation in recruitment patterns can reduce inter-annual biomass variability when aggregated at the functional group level (Elmqvist et al. 2003). That is, the functional role of forage fish is maintained in the food web even though species composition may change between years. In the Skagit River estuary, however, CPUE patterns of surf smelt and Pacific herring covaried interannually, indicating similar responses to environmental conditions and fluctuations in forage fish net abundance between years. Juvenile forage fish are consumed widely by marine birds, marine mammals and a large variety of demersal and pelagic piscivorous fishes (Simenstad 1979, Therriault et al. 2009), which suggests that climate-mediated fluctuations in age-0 recruitment may indirectly impact a large array of species through the trophic web. Quantifying the impact of forage fish variability on the Puget Sound food web, however, is complicated by a lack of reliable time series for most major predators (Rice 2007). Despite these limitations, the widespread occurrence of forage fish in predator diets and their covariation with coastal upwelling suggests that continued monitoring of these species may offer a valuable metric of overall system productivity.

In estuarine systems, climate directly affects the availability and spatial extent of optimal temperature and salinity fields by influencing river flows and coastal circulation patterns that advect marine waters landward. Our results indicate that variability in temperature and salinity explained significant albeit minor proportions of the total deviance in CPUE relative to interannual effects for Pacific herring and surf smelt. These results contrast with findings from other studies, which have found strong relationships between abiotic variables and fish distributions (e.g. Kimmerer et al. 2009). Although samples in our survey spanned a range of temperatures and salinities, they likely did not exceed upper or lower threshold tolerances and therefore failed to induce strong variations in catch rates. During periods of high river flow in the summer, low-salinity water can extend across the middle and southern sampling grid areas, but rarely penetrates completely across the stations in the northern sampling section. Reduced river flow results in a contraction of the area covered by low-salinity water but the location and area covered by the plume is highly variable, changing in response to both tidal stage and surface winds (Yang & Khangaonkar 2009). With future reductions in summer river discharge (Mote et al. 2003), we might expect a reduction in the spatial extent of low salinity habitat in summer and changes in the availability of optimal water temperatures that exceed present day patterns of variability. Understanding how small-scale changes in the availability of different

water temperatures and salinities will impact fish in the Skagit River estuary is difficult to extrapolate from our study, and continued sampling is required to better resolve fine-scale relationships between forage fish and abiotic variables.

Our analyses focused on evaluating relationships between forage fish and climate-related physical variables, but biological mechanisms may also contribute to variability in catch rates. The models of fish CPUE described between 14 and 25% of the total deviance for surf smelt and Pacific herring, respectively. Although the explained deviances are comparable to other GAMs of pelagic fish distributions (e.g. Marnavelias et al. 2000), a component of the unexplained deviance may be related to mortality or distributional shifts associated with the prevalence of predators or competitors in the estuary. Similarly, fine-scale variation in prey availability that is not readily approximated by physical conditions in the water column may account for additional variation in catch rates. Lastly, the schooling behavior characteristic of these species introduces high patchiness in their distribution in both space and time that is not explainable by environmental or biological samples and effectively constrains the amount of variability that can be explained by them.

The cumulative impacts of altered ocean temperatures, river flows, ocean acidification, coastal circulation patterns and sea-level rise are still poorly understood in most coastal systems and may prove particularly challenging to uncover given the potential for synergistic interactions and nonlinear relationships with key biological response variables (Harley et al. 2006). Moreover, the indirect effects of climate change mediated through trophic interactions are particularly difficult to anticipate. Future climate conditions may redistribute prey and predator populations or increase the abundance of competitors, potentially generating novel ecological interactions with unknown outcomes. Despite the complexities associated with forecasting climate impacts on ecological systems, headway can be made by identifying critical growth and reproductive processes over the life history of a species and evaluating the potential for linkages with climate-related environmental variables (Harley et al. 2006, Hollowed et al. 2009). Our work is a first step towards evaluating the importance of climate variability by examining both small and large spatio-temporal responses of Pacific herring and surf smelt to environmental variables.

Acknowledgements. Fish collection was funded by NOAA Fisheries and the Washington State Department of Ecology's Intensively Monitored Watersheds Program. Data were conducted by the NOAA Fisheries' Northwest Fisheries Science Center with additional planning, logistical and staff support

provided by the USGS Western Fisheries Research Center and the Skagit River System Cooperative. We are particularly grateful for the field contributions of J. Chamberlin, N. Elder, A. Hall, J. Hall, A. Kagley, J. King, D. Lomax, W. Mowitt, P. Plesha, P. Polte, and D. Rudy. N. Mantua, J. Schweigert and 2 anonymous reviewers provided comments that improved earlier versions of this manuscript. J.C.P.R. was supported by funding from the University of Washington Climate Impacts Group.

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Editorial responsibility: Jana Davis,
Annapolis, Maryland, USA

Submitted: September 20, 2010; Accepted: December 14, 2010
Proofs received from author(s): February 28, 2011