



Incorporating Climate Science in Applications of the U.S. Endangered Species Act for Aquatic Species

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Abstract: *Aquatic species are threatened by climate change but have received comparatively less attention than terrestrial species. We gleaned key strategies for scientists and managers seeking to address climate change in aquatic conservation planning from the literature and existing knowledge. We address 3 categories of conservation effort that rely on scientific analysis and have particular application under the U.S. Endangered Species Act (ESA): assessment of overall risk to a species; long-term recovery planning; and evaluation of effects of specific actions or perturbations. Fewer data are available for aquatic species to support these analyses, and climate effects on aquatic systems are poorly characterized. Thus, we recommend scientists conducting analyses supporting ESA decisions develop a conceptual model that links climate, habitat, ecosystem, and species response to changing conditions and use this model to organize analyses and future research. We recommend that current climate conditions are not appropriate for projections used in ESA analyses and that long-term projections of climate-change effects provide temporal context as a species-wide assessment provides spatial context. In these projections, climate change should not be discounted solely because the magnitude of projected change at a particular time is uncertain when directionality of climate change is clear. Identifying likely future habitat at the species scale will indicate key refuges and potential range shifts. However, the risks and benefits associated with errors in modeling future habitat are not equivalent. The ESA offers mechanisms for increasing the overall resilience and resistance of species to climate changes, including establishing recovery goals requiring increased genetic and phenotypic diversity, specifying critical habitat in areas not currently occupied but likely to become important, and using adaptive management.*

Keywords: climate change, conservation planning, effects analysis, population models, recovery planning, risk assessment, vulnerability

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Incorporación de las Ciencias Climáticas en las Aplicaciones del Acta Estadunidense de Especies en Peligro para Especies Acuáticas

Resumen: *Las especies acuáticas están amenazadas por el cambio climático pero han recibido menos atención que las especies terrestres. Obtuvimos estrategias clave para científicos y administradores que buscan hablar del cambio climático en la planeación de conservación acuática a partir del conocimiento y la literatura que ya existen. Hablamos de 3 categorías de esfuerzos de conservación que dependen del análisis científico y tienen una aplicación particular bajo el Acta Estadunidense de Especies en Peligro (ESA): estudio del riesgo general para una especie, planeación de recuperación a largo plazo, y la evaluación de los efectos de acciones o perturbaciones específicas. Hay menos información para especies acuáticas disponible que apoye estos análisis y los efectos del clima sobre sistemas acuáticos están caracterizados pobremente. Por esto recomendamos a los científicos que conducen análisis que apoyan la toma de decisiones de ESA, que desarrollen un modelo conceptual que una al clima, al hábitat, al ecosistema y a las respuestas de las especies hacia las condiciones cambiantes y que usen este modelo para organizar análisis e investigaciones futuras. Recomendamos que las condiciones climáticas actuales no son apropiadas para proyecciones usadas en análisis de ESA y que las proyecciones a largo plazo de los efectos del cambio climático proporcionen el contexto temporal como un estudio extenso de especie proporciona un contexto espacial. En estas proyecciones el cambio climático no debe ignorarse solamente porque la magnitud del cambio proyectado en un tiempo particular es incierta ya que la dirección del cambio climático está clara. Identificar el probable futuro hábitat en la escala de especie indicará refugios clave y cambios potenciales de rango. Sin embargo, los riesgos y beneficios asociados con los errores en el modelado de hábitat que probablemente puedan existir en el futuro no son equivalentes. La ESA ofrece mecanismos para incrementar la resistencia general de las especies a los cambios climáticos, incluyendo el establecimiento de metas de recuperación que requieran diversidad genética y fenotípica, especificar áreas de hábitat crítico en áreas que actualmente no se encuentran ocupadas pero que pueden volverse importantes y usar el manejo adaptativo.*

Palabras Clave: análisis de efectos, cambio climático, estudios de riesgo, modelos de población, planeación de conservación, planeación de recuperación, vulnerabilidad

Introduction

The importance of addressing climate change in conservation planning is clear (e.g., Leadley et al. 2010; Groves et al. 2012). However, the management and legal context of particular efforts can place constraints on how supporting science is conducted and used. Recognizing that aquatic species and systems (here defined to include marine, diadromous, and freshwater) have been less thoroughly treated in the climate literature, particularly in the context of the U.S. Endangered Species Act (ESA), the U.S. National Marine Fisheries Service convened a working group of scientists and ESA-practitioners to explore options for considering climate change in ESA decision making.

The challenges of evaluating the effects of climate on aquatic systems relate to data availability and climate effects. Except for some aspects of coral reefs, climate studies and historical monitoring programs underrepresent aquatic species (Parmesan 2006; Rosenzweig et al. 2008), in part because they are much harder and more expensive to monitor than terrestrial systems (Richardson & Poloczanska 2008). In fact, more is known about the moon than much of the deep sea. However, conservation concerns are well founded. A review of extinctions related to climate shows a high proportion (over half of the extinct taxa for which proximate causes were identified) are of aquatic species (Cahill et al. 2013). Effects of cli-

mate on aquatic systems differ from climate effects on terrestrial systems, although both realms will be affected by increasing intensity of storm events and droughts and by rising temperatures. Oceans face acidification (Caldeira & Wickett 2005; Doney et al. 2009) that affects calciferous organisms and species that depend on them as prey or habitat. (We included ocean acidification as an effect of climate change because both arise in large part from increases in atmospheric carbon dioxide.) Greater marine stratification (Richardson & Schoeman 2004) and layered ocean circulation (Bryden et al. 2005) are anticipated. Sea level is rising, compounding pressures on near-shore and coastal ecosystems (Lowe & Gregory 2005) where many marine species rear as juveniles. Diadromous species will be affected by climate change in both freshwater and marine stages, with potentially opposing selection pressures. The marine realm is also subject to different anthropogenic pressures than the terrestrial world, with fisheries, contributions to hypoxic zones, and habitat degradation from fishing posing threats. This combination of different, less-studied effects coupled with fewer data in marine systems means that more regulatory decisions must be made in data-poor situations and with greater uncertainty about consequences of a changing climate.

The ESA is arguably the strongest conservation tool in the United States. Within legally scripted requirements for science and planning, it encompasses 3 major

categories of decisions that are common to conservation planning generally and to legislation in other countries such as Canada's Species at Risk Act and Australia's Commonwealth Endangered Species Protection Act. These laws, like most species conservation efforts, require that scientists and managers undertake at least 3 basic tasks. (1) Assess large-scale risks to or status of populations to gauge how vulnerable a species, subspecies, or population is to extinction in the near and long-term (by *species* we mean all 3 potentially listable units). In ESA implementation, listing decisions explicitly are a risk assessment. (2) Plan for the longer term by determining what courses of action will most likely lead to recovery. Under the ESA, long-term planning includes recovery planning and designating critical habitat, and alternative overarching strategies must be considered. (3) Determine whether a particular action will likely reduce species' viability and if so how to decrease adverse effects. This is a special class of risk assessment, and in the ESA regulatory context, is encompassed in Section 7 (interagency) consultations and habitat conservation plans (HCPs) under Section 10.

Climate change is another effect that must be evaluated with other threats. However, it has not typically been incorporated systematically or rigorously into ESA decision making. Reviews of both recovery plans (Povilitis & Suckling 2010) and HCPs (Bernazzani et al. 2012) show that few plans include climate change, but this proportion has increased over time. Similarly, the proportion of plans for which the effects of climate change were evaluated thoroughly, rather than the plan simply providing a general mention of it, is low but increasing.

We present conclusions gleaned from our efforts to address ESA decision making (overview in Seney et al. 2013), 2 workshops and subsequent discussions held by the working group, and a review of the literature. Although our focus is on effects of climate on aquatic species in an ESA context, many of our conclusions are also relevant for conservation planning generally and for terrestrial species.

A First Step for All Conservation Planning

All ESA and conservation decision making will benefit from a sound species- or ecosystem-specific conceptual model (Fig. 1) that describes the known and suspected drivers of species abundance, distribution, and survival (Atkinson 2001) throughout a species' life cycle. Such transparency has been recommended in formal reviews of ESA decisions (Anderson et al. 2008) and for listing decisions (Easter-Pilcher 1996) but is seldom included. Increasing the use of such models in all ESA decision making continues to be important. In a world of changing climate, clearly articulating causal and mechanistic links among climate processes, species' ecology, habitat conditions, human actions, and conservation outcomes allows

conservation scientists to describe empirical or theoretical relations that affect species status and that should inform regulatory decisions. These models are also useful tools for identifying critical knowledge gaps and key drivers of status (through either the number or intensity of links in the model). Flooding frequency and intensity appears to affect the quality of habitat for anadromous salmonids in California, for instance (Boughton & Pike 2013). Applications of models should thus not only consider changes in mean climate conditions, but also variability around the mean. Knowing key areas of climate sensitivity for listed or otherwise imperiled species is especially important for determining appropriate sources of climate information and for selecting a subset of future climate scenarios for analysis (Snover et al. 2013) and may be particularly important for aquatic species, for which links between climate change and upwelling, circulation patterns, other ocean characteristics, and productivity are currently poorly understood (Stock et al. 2011).

Conceptual models can be very simple when little is known, but a range of effects, both climate and non-climate related, should be considered when possible. Because climate change frequently affects species both directly and indirectly, useful models incorporate specific paths through which climate affects a species' distribution, abundance or survival, habitat quality, and other drivers of population status across all stages in its life cycle. Other elements to include are drivers of survival and fecundity at each life stage and climate interactions with ecosystem processes that maintain and connect those habitats (Fig. 1) (Healey 2011). Conceptual models establish a basis for quantitative models, such as population viability analyses (PVAs). Different decisions may require models focused at different spatial and ecological scales. Listing decisions ideally require a large-scale, full-range model because the likely future of the entire species is being assessed. Evaluations for Section 7 or similar consultations may require a much more local or mechanistically detailed model in addition to a species-wide model (e.g., Walters et al. 2013).

Large-Scale Risk Assessment

The first ESA decision to make is whether a species merits protection under the act and, if so, whether it should be considered threatened or endangered. This requires evaluating whether the species is in danger of extinction or likely to become so in the foreseeable future (Seney et al. 2013). Assessing degree of risk to an organism or system is common to all conservation planning. Typically, it includes a PVA or other extinction-risk analysis coupled with an evaluation of threats to the species (e.g., Brainard et al. 2013). Climate-vulnerability assessments are therefore an important component of the overall risk assessment. The conceptual model should form the basis

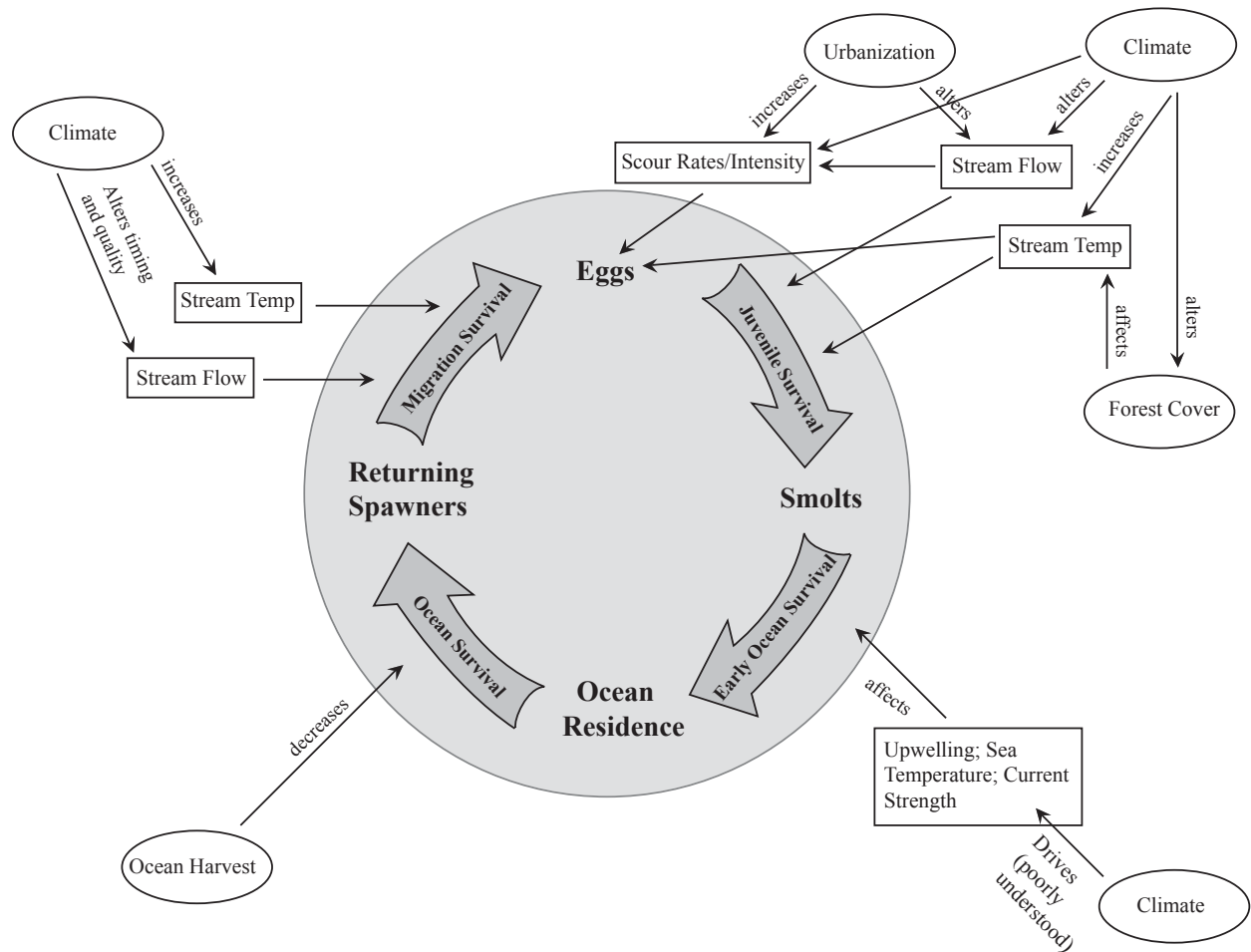


Figure 1. A conceptual model of potential links between climate, anthropogenic perturbations, habitat condition, and life-stage survival for stream-type Chinook salmon (*Oncorhynchus tshawytscha*) in the interior Pacific Northwest. The salmon life-cycle is included in the circle and broken into life stages sensitive to different environmental factors (ovals, large-scale drivers of survival; rectangles, more proximate and local drivers of survival). Unlabeled arrows indicate that the effect of the driver can be positive or negative, depending on its magnitude or the direction of change.

of identifying a species' sensitivity, exposure, and adaptability to climate change by identifying the pathways by which climate might affect the species. Climate should also be incorporated in the PVA to the extent practicable. Risk assessment for ESA listing in a changing climate, however, requires selecting appropriate climate projections and model simulations and a period over which to evaluate risks, determining whether risk occurs in a significant portion of the species' range, and managing data-poor situations.

There is no easy answer to the challenge of choosing the most appropriate scenarios of future environmental conditions (i.e., combinations of climate models, emission scenarios, downscaling methods, and models of intermediary effects) for projections of climate effects. In the current Intergovernmental Panel on Climate Change

(IPCC) AR3&4 projections, there are over 20 global climate models (GCMs), and each is based on different assumptions. The AR5 projection will have over 50 models (Meehl et al. 2012; Taylor et al. 2012). Rather than base scenario selection on attempts to select the best of each type of input, Snover et al. (2013) argue that selection and application of climate scenarios be shaped by the biological and management context of the analysis, beginning with the conceptual model development outlined above.

Using extreme scenarios to bracket a particular parameter of interest can help elucidate the range of potential species' exposure. For example, in an analysis of stream-flow effects on anadromous salmonids, Walters et al. (2013) used one GCM that predicts high precipitation and another that predicts much lower rain and snowfall to capture a range of possible outcomes under climate

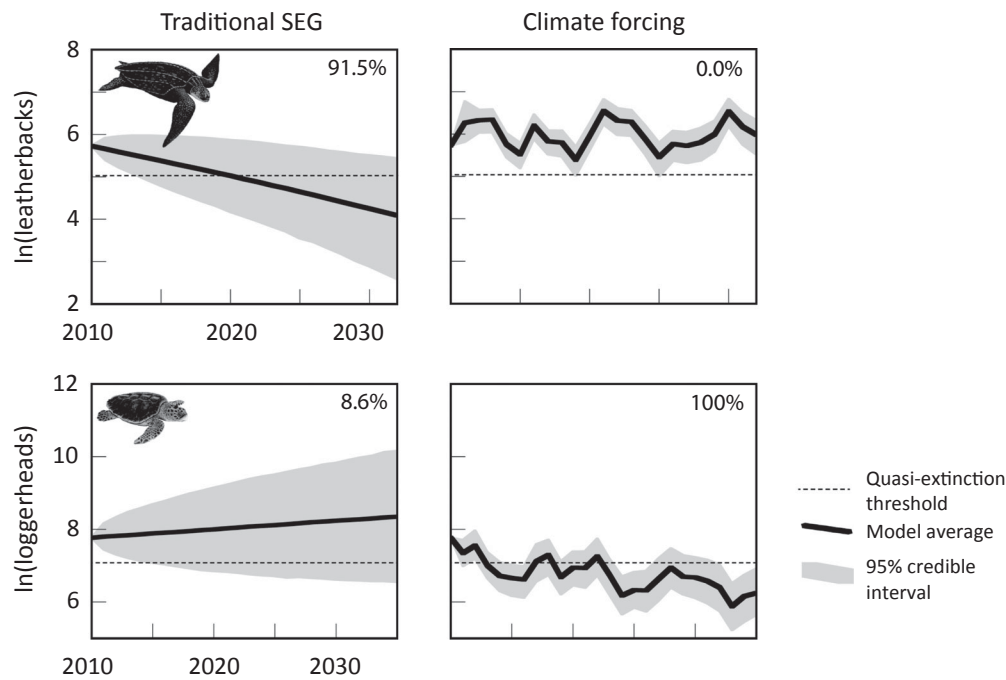


Figure 2. Results of population viability analyses (PVA) for leatherback (*Dermochelys coriacea*) and loggerhead (*Caretta caretta*) sea turtle populations in northern Pacific Ocean. Left panels show model forecasts of traditional stochastic exponential growth (SEG) and projects future population changes from the distribution of observed population growth rates. Right panels show forecasts from the fitted relations of climate-forcing models that account for nesting changes from bottom-up oceanographic processes (Van Houtan & Halley 2011). Solid lines are the average of 10,000 model runs, shaded area is the 95% credible interval, and listed percentage is the quantified extinction risk which is defined here as the runs below a 50% population decline (dotted line, quasi-extinction threshold). Illustrations by César Landazábal/State of the World's Turtles Report (used with permission).

change in a particularly relevant and uncertain climate variable. The conceptual model for the species or system will be a critical tool in identifying which factors (e.g., changes in temperature, sea level, carbonate chemistry) are most important to bracket.

Risk assessments for listing decisions should be conducted assuming that climates will change, rather than assuming an extension of current conditions or past conditions. Although projections under current climatic conditions may serve useful comparative purposes, they can no longer be considered credible pictures of the future (Solomon et al. 2009) and may misrepresent risk. Projections of leatherback (*Dermochelys coriacea*) and loggerhead (*Caretta caretta*) sea turtle population status, for example, are very different when climate change is incorporated (Fig. 2) (Van Houtan & Halley 2011).

Choice of emission scenario is also important in climate projections. Global climate models apply several alternative scenarios that describe greenhouse gas trajectories over the next century in response to possible social, economic, and technological developments. Although the scenarios exhibit sizeable differences in the second half of the 21st century, the steady increase in atmospheric concentrations of greenhouse gasses is similar among scenarios before approximately 2050 (Moss et al. 2010).

Over these decades the emission scenario is not an extremely critical choice. However, available information suggests that currently realized emissions are exceeding all but one of the AR4 scenarios (Manning et al. 2010). Although we cannot know how emissions will unfold in the long term, given the challenges associated with stabilizing emissions (Davis et al. 2013), it is prudent to consider the plausibility of future scenarios when choosing among them for ESA purposes. Other risk-averse approaches include preparation for the worst outcomes and assuming greater urgency when even optimistic scenarios project negative outcomes.

Time frames for assessing risk—in an ESA listing decision, the “foreseeable future” (Seney et al. 2013)—should be determined on a case-by-case basis, founded on how far into the future science can meaningfully predict the species’ status. Overall, there is a trade-off between certainty in results (longer-term climate and population projections are more variable than shorter projections) and likelihood of detecting an effect. Magnitude of climate effects increases with time, and likelihood of extinction in the short-term is always very small, unless a species has exceptionally low abundance and productivity. Quantitative PVAs typically use time frames in the 100-year range. Use of long assessment periods is especially important

for species with long generation times so that the real demographic risks are captured; long-lived individuals can mask deteriorating conditions for reproduction or recruitment. The window of time used for assessing future climate effects is also important. Generally, it is necessary to average GCM output over several decades in order to separate the effects of decadal climate variability from the long-term trend in climate change (Santer et al. 2011).

When choosing a period for climate-scenario or population-response projections, it is important not to confuse the uncertainty in rate or magnitude of change with uncertainty in directionality. Although the precision of estimates of global temperature increase is low, for example, an increase in mean global temperature increase is virtually certain (IPCC 2007). When the direction of change is clear, projections of species status under climate change should not be discounted solely because the magnitude of projected change at a particular time is highly variable. Nothing precludes conducting projections over 2 or more time frames. In fact, multiple projections can be used to gain a greater understanding of a single projection by showing the range of potential responses to directional effect or describing the pattern of response through a range of climate conditions. Both pieces of information can provide perspective on consequences of a particular course of action (Hare et al. 2012).

The geographic scope of a listing analysis—the species' future status over a "significant portion of its range" (SPOIR)—poses a novel scientific and policy challenge. Already, aquatic and other species are shifting their distributions as climates change (Nye et al. 2009; Wassmann et al. 2011). Evaluating extinction risk within SPOIR under climate change includes comparing species' habitat requirements with likely future environmental conditions and habitat availability (e.g., Wenger et al. 2011) and yields a hypothesis of likely future distribution (Fig. 3) (Hare et al. 2012). Species vary in their colonization abilities (Hiddink et al. 2012), and species-specific characteristics should also affect benefits assumed for species when novel habitats are projected.

As species' ranges change, determining current range, likely future range, and what constitutes a significant portion of either area becomes more difficult and more uncertain. However, the type and direction of uncertainty in projections of future range may have an important bearing on risk tolerance because the consequences of error are not equivalent to the species. For example, areas of new habitat modeled under climate change are beneficial only if models are correct and those areas are colonized successfully. If occupancy of those areas does not materialize, then any assumed benefit is also not realized, at cost to the species. If habitat gained is greater than projected, then obviously, the species benefits. The direction of error also matters if habitat is projected to be lost. If less habitat is lost than projected, the species

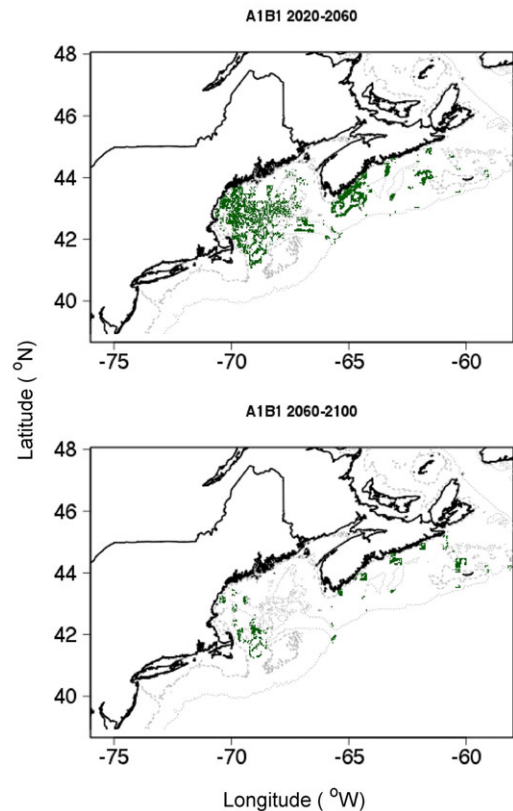


Figure 3. Potential habitat for adult cusk from a statistical niche model coupled with an ensemble of atmospheric ocean general circulation models used in the AR4 Report: (a) A1B scenario in 2020–2060 and (b) A1B scenario in 2060–2100 (green, area of projected potential habitat; dotted lines, 40- and 200-m isobaths).

benefits. If more is lost than projected, the species will likely be in poorer condition. The scale of the projection also matters. For a species-wide review, offsets in both directions might render the error neutral. On the smaller scale of most Section 7 consultations, however, offsets are unlikely to materialize. Thus, when making decisions based on anticipated ranges rather than current ranges, a precautionary approach would assume less benefit to the species for anticipated future habitat and work to ensure that the disadvantage of potential losses of current habitat are not underestimated.

Conservation planners must often evaluate risk for species for which there is little information even when they ignore climate change. In these cases, assessors must rely on general ecological principles coupled with available species or taxon-specific information. One helpful way to frame this analysis is by considering a species' sensitivity and exposure to climate changes as well as its adaptive capacity to those changes (Glick et al. 2011). For example, an evaluation of extinction risk for corals, with little species-specific information, combined information

Table 1. Characteristics of organisms and populations and mechanisms that affect likely response to climate change.

<i>Characteristic</i>	<i>Mechanism</i>	<i>Reference</i>
Dispersal potential (high mobility, broad larval distribution)	Confers resilience by reversing local extinction, confers ability to colonize new habitat	Williams et al. 2008
Population- and species- level diversity	Provides adaptive capacity by promoting evolutionary adaptation	Williams et al. 2008
Phenotypic plasticity	Confers resilience by allowing phenotypic response to environmental changes	Williams et al. 2008
Generation time	Long generation times limit rate of demographic response to changing conditions but may also buffer population during extreme events	Laidre et al. 2008
Small geographic range	Increases vulnerability through greater proportional loss of current habitat, but species may gain new habitat elsewhere	Thuiller et al. 2005
Habitat or niche specialization	Increases vulnerability through greater proportional loss of current habitat but new habitat may be gained elsewhere	Thuiller et al. 2005
Near the warm or dry edge of its geographic range	Increases vulnerability through greater proportional loss of current habitat	Thuiller et al. 2005
Dependent on pack ice (reproduction, resting, etc.)	Increases sensitivity to polar warming with little refuge	Laidre et al. 2008

about ocean acidification rates and distribution (exposure) with information about general calcification rates (sensitivity) (Brainard et al. 2013). Many factors affect a species' adaptive capacity (Table 1), although the predictive power of any single trait for range shifts in an individual species without relevant natural history information appears at this time to be low (Angert et al. 2011). This suggests that understanding the links between climate, its secondary effects, and a species' ecology will be very important, even if that understanding is only qualitative. The range of approaches can also include a hybrid approach involving quantitative (e.g., climate change) and qualitative (e.g., species effect) assessments. Expert opinion can also be used in climate-change vulnerability assessments (Glick et al. 2011). Finally, climate assessment for one species can provide a useful framework to aid in assessing effects on other species (e.g., Nye et al. 2012).

Recovery Planning and Critical Habitat Designation

Species have 3 primary avenues to persist in the wild, given climate change: adapt to novel conditions, shift to new habitat made available by climate change, or exist within the historical range in refugia that have retained conditions appropriate for the species (Dawson et al. 2011). Long-term planning, which in an ESA context includes recovery planning and critical habitat designation, should foster conditions supporting the species' ability to follow at least one of these paths. Plans offering all 3 have the greatest chance of success (Schindler et al. 2008). Such climate-adaptation planning should be incorporated into all ESA recovery plans (NFWPCAP 2012).

The general approaches to climate adaptation include building resistance (forestalling effects and protecting valued resources), cultivating resilience (improving ca-

capacity of the system to return to desired conditions after perturbation), facilitating response (allowing the system to transition to a new condition), and realigning degraded environments for transition to future, climate-appropriate state (Millar et al. 2007). These approaches focus more on the ecosystem than on individual species, and there are several ESA requirements that can be integrated with an ecosystem approach to improve species persistence. These include establishing appropriate recovery goals for the species, designating critical habitat that considers climate change, maintaining or improving species' condition as much as possible in the near term, and using strategies that are robust to a variety of future climate conditions.

The ESA requires that, to the extent practicable, a recovery plan include "objective, measurable criteria" that describe conditions under which a species could be deemed recovered (Section 4f). Most recovery plans focus on abundance as a recovery goal. However, a more comprehensive framework for viability developed for salmonids includes abundance, productivity, spatial structure, and phenotypic and genetic diversity (McElhany et al. 2000). Recovery goals that include these 4 elements generate population-level traits that foster all 3 pathways for long-term persistence. Ecoevolutionary adaptive response and resilience to climate change is tied to the genetic variability within a population, including variability in norms of reaction for plasticity (Reed et al. 2011). Ensuring diverse populations thus provides the foundation from which species can adapt to novel conditions. Increased diversity also provides a buffer from extinction by reducing demographic synchronization in variable environments (Moore et al. 2009). Practically, it may not be possible to sample population traits frequently or widely enough to monitor this diversity; ensuring that a wide range of high-quality habitat types

are available and accessible may serve as a proxy (see Jorgensen et al. [2013] for consideration of habitats tied to life-history diversity). In terrestrial environments, soil type, topography, and geology may be relevant proxies (Brost & Breier 2012; Groves et al. 2012). In marine and lacustrine environments, depth, temperature, and bottom substrate may be similarly indicative. Spatial-structure goals for recovery that clearly articulate and define the distribution of individuals and populations across current and future high-quality habitat patches needed for recovery are most useful for policy makers. The distribution of patches should support natural movement between populations, ensure persistence of source populations, and promote potential movement to emerging habitats. Such spatial goals foster resilience and resistance by promoting both migration and the long-term occupancy of refugia; they support longer persistence of species with distributions that are projected to become patchier under climate change.

The ESA allows areas outside habitat occupied at the time of listing to be designated as critical habitat if they are essential to the conservation of the species. This provides opportunities to be proactive in regard to climate change, and hypotheses of future likely habitat (e.g., Abdul-Aziz et al. 2011; Isaak et al. 2012) can inform such efforts. Designation of critical habitat should support movement to emerging habitats and maintenance of key populations. Although corridors have received much attention for terrestrial species that migrate (Williams et al. 2005; Brost & Beier 2012), their relevance for marine species is somewhat different, given that many species' dispersal occurs over large scales at the larval phase. In addition, drivers of movement, such as currents and gyres, may change in unpredictable ways due to climate change (Bryden et al. 2005). Maintaining connectivity, particularly for migratory species, may involve targeting restoration, preservation, or other conservation activities in areas not currently used but likely to become important to the species, such as streams at higher elevations now blocked to passage or coastal areas blocked by tide gates. Diadromous species have the advantage of being able to use the ocean as a corridor between freshwater habitats; strictly riverine species are more constrained by lack of aquatic connections to move between watersheds. Some authors recommend translocation and other active management be considered as higher elevation, cooler habitats are exhausted (Olden et al. 2011).

The distribution of critical habitat is also relevant. Novel habitats that are contiguous with existing habitats (such as deeper habitats for pelagic fishes [Dulvey et al. 2008]) for at least one life stage are more likely to be colonized than those separated by areas with no or highly altered habitat. Areas that are currently occupied and likely to remain occupied are also a main component of seascape management and are critical for species that may need to rely on refugia for long-term persistence.

For example, the deeper parts of a species' depth range (Hare et al. 2012) or higher elevation areas with already cooler temperatures (Isaak & Rieman 2013) may become the only part of a species' distribution with suitable temperatures for one or more life stages (Ruesch et al. 2012). Protecting or improving these areas can be a key aspect of ensuring long-term persistence of a species. These concepts should be incorporated in current and future efforts in coastal and marine spatial planning. However, situations where there is high confidence that a currently occupied area will become unsuitable for a species, such as habitats at the highest end of a species' temperature tolerance, should be identified to inform decisions about appropriate use of limited resources.

Two remaining components of long-term planning are primarily common sense but are still critical for increasing the likelihood of recovery. First, populations or species that are more robust initially will have greater likelihood of enduring the additional challenges of climate-related change (Table 1). Improving a species' status in the near-term may be an important investment in species recovery. These populations can also provide migrants to other areas, and linking robust and emerging populations strategically with corridors can enhance the likelihood of migration. Second, one should expect to be surprised by the consequences of climate change. Thus, strategies and actions that are useful in the face of more than one potential future will improve the likelihood of success. The developing focus on restoring ecosystem-level processes, rather than engineering (Beechie et al. 2012) is likely to be extremely beneficial in this regard.

Risk Assessment for Individual Activities

Predicting the effects of human actions on a species is an enduring challenge. Section 7 of the ESA requires consultation with the listing agency for activities with a federal (U.S.) government nexus, and Section 10 requires a permit from the listing agency for nonfederal activities that might take a listed species (Bernazzani et al. 2012; Seney et al. 2013). In consultation or permitting, the regulatory agency analyzes effects of the activity on the survival and recovery of the species. If negative effects are great, the consultation may prescribe mitigating actions. Although many scientific aspects of these analyses are established, climate change introduces novel concerns about projecting future species status, the environmental baseline (the conditions projected to exist in the future without the proposed action) (Seney et al. 2013), and the consistency of the action with survival and recovery of the species.

Formerly, effects analyses implicitly used historical climate conditions as the environmental baseline (usually by not considering climate) and projected these forward. Now, however, risk assessments should assume climate change as the more certain future (Solomon et al. 2009).

Projections should use anticipated climate conditions as the environmental baseline and add the action's effects for comparison with desired species status (e.g., recovery goals). As with risk assessments for listing decisions, bracketing climate outcomes, choosing appropriate time frames for analysis, and linking selection of future scenarios to biological-effect pathways are important techniques for describing anticipated climate consequences. For more local actions, some sort of spatial downscaling usually must be done to reconcile the difference in spatial scale of GCMs and the finer scales at which these human actions occur and natural resource management decisions are made (e.g., Battin et al. 2007). The appropriate scale of projection depends on the scale of the climate drivers.

A long-term projection of species status is important in risk analyses for all species and consultations, regardless of the time frame of the action, to comprehensively describe the species' status and more accurately evaluate its influence on the likelihood of recovery. In a static environment, a project or action might have a discrete, short-term effect on population abundance or other attribute from which a population can rebound. In a rapidly changing environment, however, the status of the species is likely to change independent of the action. The effect of the action on the species might be worsened when coupled with climate-induced change to the degree that achieving conservation targets becomes less likely, or, in fortunate cases, improved such that greater effects might be permissible. Again, the direction of risk must be considered in evaluations. A thorough risk analysis thus includes an evaluation of aggregate effects of the action, climate change, and direct and indirect links between climate drivers and the action. Of particular importance when considering indirect links will be the differential colonization abilities and vulnerabilities of different organisms (Hiddink et al. 2012), given that one of the best documented causes of climate-related extinctions is species interactions and particularly loss of prey species (Cahill et al. 2013).

A proposed action may limit the ability of a species or habitat to respond to the effects of climate change. For example, removing trees from an area might make streams that are suitable for cold-water fishes, and likely to remain so under climate change, unsuitable. Armoring coastlines may prevent beaches and marshes from moving with rising sea levels through deposition or erosion or otherwise affect important habitats (Jorgensen et al. 2013). Especially important in evaluating an action and proposed mitigation is ensuring that population parameters that promote resilience and adaptation, such as diversity, are not unwittingly compromised. For example, many species are subject to age selection in marine fisheries. This selective pressure and reduction in diversity can have negative effects on adaptive capacity, and the loss of older age classes appears to reduce resilience

to climate change (Rouyer et al. 2011). Columbia River sockeye salmon (*Oncorhynchus nerka*) appear to have changed migration timing in response to changing river temperatures both through adaptive genetic change and plastic response (Crozier et al. 2011). Evaluating proposed and mitigation actions, such as mandated spill timing or cold-water releases from dams, must also consider these changes and how best to maintain similar buffering or adaptive capacity.

For all consultations, both the action and any mitigation included as part of an HCP or a biological opinion's "reasonable and prudent alternative" (i.e., legally specified changes, if it is required) should be consistent with the recovery plan and climate adaptation measures incorporated into it. A first step is to consider the location of the action and gauge it against all recovery goals for the species to determine what role the location and individuals occupying it are intended to play in overall recovery of the species. For instance, does the effect occur in an area that is anticipated to be high quality habitat in the future? Or, is the location of the action expected to become unsuitable for the species as climate change progresses? Does it negatively affect a population that has unique or unusual life-history characteristics likely to play a key role in recovery? These questions should help managers and other decision makers determine what level of risk-tolerance is appropriate. A second consideration is whether a proposed action or HCP precludes the ability to implement or realize the climate adaptation strategy developed during long-term planning. For example, an action might disrupt a migration corridor leading to potential critical habitat or modify an area of hyporheic flow important for cooling a stream in the future. Because Sections 7 and 10 consultations involve both risk assessment and mitigation, it will be key to assess the reversibility of actions and the potential to change course if needed. Section 10 consultations are constrained by the no-surprises rule, which precludes additional mandatory mitigation after the plan is approved and may affect the initial level of risk tolerance. Adaptive management within the plan provides another approach to anticipating and addressing effects of climate change.

Moving Forward

Climate-related changes of the magnitude anticipated are unknown in recorded human history. Consequently, the best approaches for evaluating their effects and developing strategies for the persistence of species and ecosystems are continually being improved. There is no single best way to deal with climate change in all conservation contexts, and the uncertainty associated with our future will not go away. The onus, then, for conservation scientists and managers, is to address that uncertainty as substantively as possible in communication and in

approaches to recovery and restoration, research prioritization, and refinement of decision-making processes.

To reduce risk, conservation planners need to boldly consider the unprecedented nature of climate-related changes. For example, a recovery plan might emphasize measures to abate historic sources of mortality unrelated to climate that can be used to offset reduced survival attributable to climate change. Planners might choose to establish recovery criteria that are greater than the estimated biological minimum or encourage conservation actions beyond those typically taken in the past. They may also include in recovery plans and critical habitat designations areas not currently occupied by the species to support anticipated range shifts. Time frames covered by HCPs or other consultations could be shortened, given the uncertainty of future climate and the pace at which understanding of climate effects is changing.

Scientific uncertainty can make managers hesitant to act. Scientists can help by being clear about what is known—directionality of temperature change, for example, as opposed to magnitude of that change. Biologists can be more rigorous in identifying climatic sensitivities of systems of species of interest and be more probabilistic in presentations of extinction risk and other analysis results (e.g., McClure et al. 2003), which gives managers more information about the likelihood of various outcomes. Finally, scientists and managers can work together to implement conservation actions in ways that reduce uncertainty and allow management approaches to be altered as necessary. Executing management actions as experiments has the added benefit of increasing understanding of relevant ecological systems and reducing overall uncertainty. Conservation decisions are made under uncertain conditions, and level of risk-tolerance is a policy and societal choice. Decisions related to the ESA are bounded by the societal choices encoded in the law, although the acceptable level of risk tolerance is not explicit. Maximizing efforts that allow species to move, adapt evolutionarily, and use refugia will provide the greatest opportunities for species to persist. In addition, increasing individual, population, and species status improves resilience and resistance to climate change and other stressors such as habitat modification, changes in species composition, and bycatch. When implementing conservation actions, greater-than-minimal efforts are likely to strengthen species' status, as will actions that are robust to multiple future climate scenarios or that allow alternative strategies to be pursued.

Agencies implementing the ESA must grapple with a variety of policy issues. In particular, risk tolerance is an issue that pervades all conservation planning and the scientific analyses supporting those decisions (e.g., in determining extinction risk tolerances). Ongoing communication between stakeholders and managers about the degree of risk or caution that is acceptable will be an important component of decision making. Adaptive management, with rigorous monitoring and explicit trig-

gers and responses at defined decision points, provides an opportunity for risk management that can be built into most types of consultations or HCPs. In addition, conducting frequent reviews and updates of status, recovery plans, and critical habitat designations is likely to be prudent, given the rapid pace of change in the understanding of climate effects. Ensuring that evaluations of specific actions are closely tied to longer-term plans and regularly updated can prevent the inadvertent damage of resources that are important for the future, as can proactive designation of unoccupied habitat as critical habitat in appropriate situations.

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Literature Cited

- Abdul-Aziz, O., N. Mantua, and K. Myers. 2011. Potential climate change impacts on thermal habitats of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and adjacent seas. *Canadian Journal of Fisheries and Aquatic Sciences* **68**:1660–1680.
- Anderson, J., P. Duffy, K. Rose, and P. Smith. 2008. Independent Review of the 2008 NMFS Analytical Framework for its OCAP Biological Opinion. California Bay-Delta Authority Science Review Panel, Sacramento. Available from http://www.science.calwater.ca.gov/events/reviews/review_ocap.html (accessed January 2013).
- Angert, A., L. Crozier, L. Rissler, S. Gilman, J. Tewksbury, and A. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? *Ecology Letters* **14**:677–689.
- Atkinson, I. 2001. Introduced mammals and models for restoration. *Biological Conservation* **99**:81–96.
- Battin, J., M. Wiley, M. Ruckelshaus, R. Palmer, E. Korb, K. Bartz, and H. Imaki. 2007. Projected impacts of climate change on salmon habitat restoration. *Proceedings of the National Academy of Sciences of the United States of America* **104**:6720–6725.
- Beechie, T., et al. 2012. Restoring salmon habitat for a changing climate. *River Research and Applications* DOI: 10.1002/rra.2590.
- Bernazzani, P., B. Bradley, and J. Opperman. 2012. Integrating climate change into habitat conservation plans under the U.S. Endangered Species Act. *Environmental Management* **49**:1103–1114.
- Boughton, D., and A. Pike. 2013. Floodplain rehabilitation as a hedge against hydroclimate uncertainty in a threatened steelhead migration corridor. *Conservation Biology* **27**:1158–1168.
- Brainard, R., C. Birkeland, C. Eakin, P. McElhany, M. Miller, M. Patterson, G. Piniak, M. Dunlap, and M. Weijerman. 2013. Incorporating climate change and ocean acidification into 368 extinction risk assessments for 82 coral species. *Conservation Biology* **27**:1169–1178.
- Brost, B., and P. Beier. 2012. Use of land facets to design linkages for climate change. *Ecological Applications* **22**:87–103.

- Bryden, H., H. Longworth, and S. Cunningham. 2005. Slowing of the Atlantic meridional overturning circulation at 25 degrees N. *Nature* **438**:655–657.
- Cahill, A., et al. 2013. How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* **280**:20121890, DOI:10.1098/rspb.2012.1890.
- Caldeira, K., and M. Wickett. 2005. Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research-Oceans* **110**:C09S04, DOI:10.1029/2004JC002671.
- Crozier, L., M. Scheuerell, and R. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: a case study of a shift toward earlier migration date in sockeye salmon. *American Naturalist* **178**:755–773.
- Davis, S. J., L. Cao, K. Caldeira, and M. Hoffert. 2013. Rethinking wedges. *Environmental Research Letters* **8**, DOI:10.1088/1748-9326/8/1/011001.
- Dawson, T., S. Jackson, J. House, I. Prentice, and G. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**:53–58.
- Doney, S., W. Balch, V. Fabry, and R. Feely. 2009. Ocean acidification: a critical emerging problem for the ocean sciences. *Oceanography* **22**:16–25.
- Dulvy, N., S. Rogers, S. Jennings, V. Stelzenmuller, S. Dye, and H. Skjoldal. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**:1029–1039.
- Easter-Pilcher, A. L. 1996. Implementing the Endangered Species Act: selecting species to list as endangered or threatened. *BioScience* **46**:1–26.
- Glick, P., B. Stein, and N. Edelson, editors. 2011. Scanning the conservation horizon: a guide to climate change vulnerability assessment. National Wildlife Federation, Washington, D.C.
- Groves, C. R., et al. 2012. Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation* **21**:1651–1671.
- Hare, J. A., et al. 2012. Cusk (*Brosme brosme*) and climate change: assessing the threat to a candidate marine fish species under the U.S. Endangered Species Act. *ICES Journal of Marine Science* **69**:1753–1768.
- Healey, M. 2011. The cumulative impacts of climate change on Fraser River sockeye salmon (*Oncorhynchus nerka*) and implications for management. *Canadian Journal of Fisheries and Aquatic Sciences* **68**:718–737.
- Hiddink, J., F. Lasram, J. Cantrill, and A. Davies. 2012. Keeping pace with climate change: what can we learn from the spread of Lessepsian migrants? *Global Change Biology* **18**:2161–2172.
- IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R. K. and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 pp.
- Isaak, D., C. Muhlfeld, A. Todd, R. Al-Chokhachy, J. Roberts, J. Kershner, K. Fausch, and S. Hostetler. 2012. The past as prelude to the future for understanding 21st-century climate effects on rocky mountain trout. *Fisheries* **37**:542–556.
- Isaak, D., and B. Rieman. 2013. Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. *Global Change Biology* **19**:742–751.
- Jorgensen, J., M. McClure, M. Sheer, and N. Munn. 2013. Combined effects of climate change and bank stabilization on shallow-water habitats of Chinook salmon. *Conservation Biology* **27**:1201–1211.
- Laidre, K., I. Stirling, L. Lowry, O. Wiig, M. Heide-Jorgensen, and S. Ferguson. 2008. Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecological Applications* **18**:S97–S125.
- Leadley, P., et al. 2010. Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 50, 132 pages.
- Lowe, J., and J. Gregory. 2005. The effects of climate change on storm surges around the United Kingdom. *Philosophical Transactions of the Royal Society A* **363**:1313–1328.
- Manning, M., et al. 2010. Misrepresentation of the IPCC CO2 emission scenarios. *Nature Geoscience* **3**:376–377.
- McClure, M., B. Sanderson, E. Holmes, C. Jordan. 2003. A large-scale, multi-species status assessment: salmonids in the Columbia River Basin. *Ecological Applications* **13**:964–989.
- McElhany, J. P., M. Ruckelshaus, M. Ford, T. Wainwright, and E. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionary significant units. U.S. Department of Commerce, NOAA Technical Memorandum, **156**.
- Meehl, G., et al. 2012. Climate system response to external forcings and Climate Change Projections in CCSM4. *Journal of Climate* **25**:3661–3683.
- Millar, C., N. Stephenson, and S. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* **17**:2145–2151.
- Moore, S., N. Mantua, B. Hickey, and V. Trainer. 2009. Recent trends in paralytic shellfish toxins in Puget Sound, relationships to climate, and capacity for prediction of toxic events. *Harmful Algae* **8**:463–477.
- Moss, R., et al. 2010. The next generation of scenarios for climate change research and assessment. *Nature* **463**:747–756.
- National Fish, Wildlife and Plants Climate Adaptation Partnership (NFW-PCAP). 2012. National fish, wildlife and plant climate adaptation strategy. Association of Fish and Wildlife Agencies, Council on Environmental Quality, Great Lakes Indian Fish and Wildlife Commission, National Oceanic and Atmospheric Administration, and U.S. Fish and Wildlife Service. Washington, D.C. Available from <http://www.wildlifeadaptationstrategy.gov> (accessed January 2013).
- Nye, J., J. Link, J. Hare, and W. Overholtz. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology-Progress Series* **393**:111–129.
- Nye, J., P. Lynch, M. Alexander, C. Stock, and J. Hare. 2012. Results of Preliminary Analyses of the Effect of Climate Change on River Herring. Fisheries and the Environment (FATE) Annual Report 2012.
- Olden, J., M. Kennard, J. Lawler, and N. Poff. 2011. Challenges and opportunities in implementing managed relocation for conservation of freshwater species. *Conservation Biology* **25**:40–47.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**:637–669.
- Povilitis, A., and K. Suckling. 2010. Addressing climate change threats to endangered species in US recovery plans. *Conservation Biology* **24**:372–376.
- Reed, T., D. E. Schindler, and R. Waples. 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology* **25**:56–63.
- Richardson, A., and E. Poloczanska. 2008. Under-resourced, under threat. *Science* **320**:1294–1295.
- Richardson, A., and D. Schoeman. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* **305**:1609–1612.
- Rosenzweig, C., et al. 2008. Attributing physical and biological impacts to anthropogenic climate change. *Nature* **453**:353–357.
- Rouyer, T., G. Ottersen, J. Durant, M. Hidalgo, D. Hjermann, J. Persson, L. Stige, and N. Stenseth. 2011. Shifting dynamic forces in fish stock fluctuations triggered by age truncation? *Global Change Biology* **17**:3046–3057.

- Ruesch, A., C. Torgersen, J. Lawler, J. Olden, E. Peterson, C. Volk, and D. Lawrence. 2012. Projected climate-induced habitat loss for salmonids in the John Day River Network, Oregon, USA. *Conservation Biology* **26**:873–882.
- Santer, B., et al. 2011. Separating signal and noise in atmospheric temperature changes: the importance of timescale. *Journal of Geophysical Research-Atmospheres* **116**:DOI:10.1029/2011JD016263.
- Schindler, D., X. Augerot, E. Fleishman, N. Mantua, B. Riddell, M. Ruckelshaus, J. Seeb, and M. Webster. 2008. Climate change, ecosystem impacts, and management for Pacific salmon. *Fisheries* **33**:502–506.
- Seney, E., M. McClure, M. Rowland, R.A. Lowery, and R. Griffis. 2013. Overview of climate change, marine environments, and the U.S. Endangered Species Act. *Conservation Biology* **27**.
- Snover, A., N. Mantua, J. Littell, M. Alexander, and M. McClure. 2013. Choosing and using climate-change scenarios for ecological-impact assessments and conservation decisions. *Conservation Biology* **27**:1147–1157.
- Solomon, S., G. Plattner, R. Knutti, and P. Friedlingstein. 2009. Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences of the United States of America* **106**:1704–1709.
- Stock, C., et al. 2011. On the use of IPCC-class models to assess the impact of climate on living marine resources. *Progress in Oceanography* **88**:1–27.
- Taylor, K., R. Stouffer, and G. Meehl. 2012. An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society* **93**:485–498.
- Thuiller, W., S. Lavorel, and M. Araujo. 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography* **14**:347–357.
- Van Houtan, K. S., and J. Halley. 2011. Long-term climate forcing in loggerhead sea turtle nesting. *PLoS ONE* **6** DOI: 10.1371/journal.pone.0019043.
- Walters, A., K. Bartz, and M. McClure. 2013. Interactive effects of water diversion and climate change for juvenile Chinook salmon in the Lemhi River Basin (U.S.A). *Conservation Biology* **27**:1179–1189.
- Wassmann, P., C. Duarte, S. Agusti, and M. K. Sejr. 2011. Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology* **17**:1235–1249.
- Wenger, S., et al. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America* **108**:14175–14180.
- Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araujo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape proteaceae. *Conservation Biology* **19**:1063–1074.
- Williams, S., L. Shoo, J. L. Isaac, A. Hoffmann, and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* **6** DOI:10.1371/journal.pone.0019043.

