

Climate forcing and the California Current ecosystem

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The Climate Forcing and Marine Ecosystem (CFAME) Task Team of the North Pacific Marine Science Organization (PICES) was formed to address climate forcing impacts on ecosystem structure and productivity of marine species. For the California Current system, the Task Team described the physical processes, built an overview of species across trophic levels, and described how the population dynamics of these species have changed over time. Based on the synthesis work, conceptual models were developed describing the potential pathways linking climate forcing, oceanography, and species' responses. The resultant empirical data scenarios draw on ecosystem histories to provide a synopsis of expected change given global climate change. The multidisciplinary team faced challenges and limitations in their attempt to draw connections between the outputs from global climate models (GCMs), the physical processes, and the subsequent impacts on species via the identified pathways. To some degree, there was a mismatch of variables that fishery scientists identified as important in determining species' response to climate and physical forcing and the variables that current GCMs can now resolve at the regional level. These gaps will be important for researchers to consider as they begin to develop higher-resolution climate and regional oceanographic models for forecasting changes in species' productivity.

Keywords: blue shark, California Current, Chinook salmon, climate change, Dover sole, empirical scenarios, mechanistic models, Pacific hake, Pacific sardine.

Introduction

The Climate Forcing and Marine Ecosystem (CFAME) Response Task Team was established under the Climate Change and Carrying Capacity Program of the North Pacific Marine Science Organization (PICES) to integrate hypotheses and data that forecast the consequences of climate variability on the ecosystems of the Subarctic Pacific. A broad complement of trophic levels and species was considered by the Task Team, including commercially important fish species, seabirds, and marine mammals. For each species, conceptual pathways were developed that link the physical features of the California Current system (CCS) to biological impacts for various life stages. However, for brevity, this paper focuses on only five fish species that were selected to cover a range of life-history strategies.

Two approaches are used to forecast the impacts of climate change on the five fish species: (i) scenarios based on empirical observations of population dynamics in warm years and (ii) statistical downscaling from the outputs of global climate models (GCMs). To forecast impacts, first we selected species representing different life strategies and identified potential common physical

oceanographic features that were hypothesized to mediate climate change impacts onto population responses. Then, we examined the GCM outputs to find forecasted changes in these key physical features. Unfortunately, the spatial and temporal resolutions of the GCMs for the variables identified as key forcing mechanisms for the species in question were not amenable to the development of these forecasts. Nevertheless, the work presented here allowed us to develop species-specific conceptual pathways and empirically based response scenarios and to identify key physical features of the CCS that we suggest will have impacts on ecosystem structure. This paper provides a solid foundation for climatologists, oceanographers, and biologists for building future links between GCM outputs, regional climate models (RCMs), and ecosystem models. It also outlines the challenges and limitations inherent in any attempt to forecast the response of species to climate change.

CCS overview

The CCS is associated with the California Current (CC), a surface boundary current that forms the eastern limb of the Central Pacific Gyre (Figure 1). There are three principal circulation

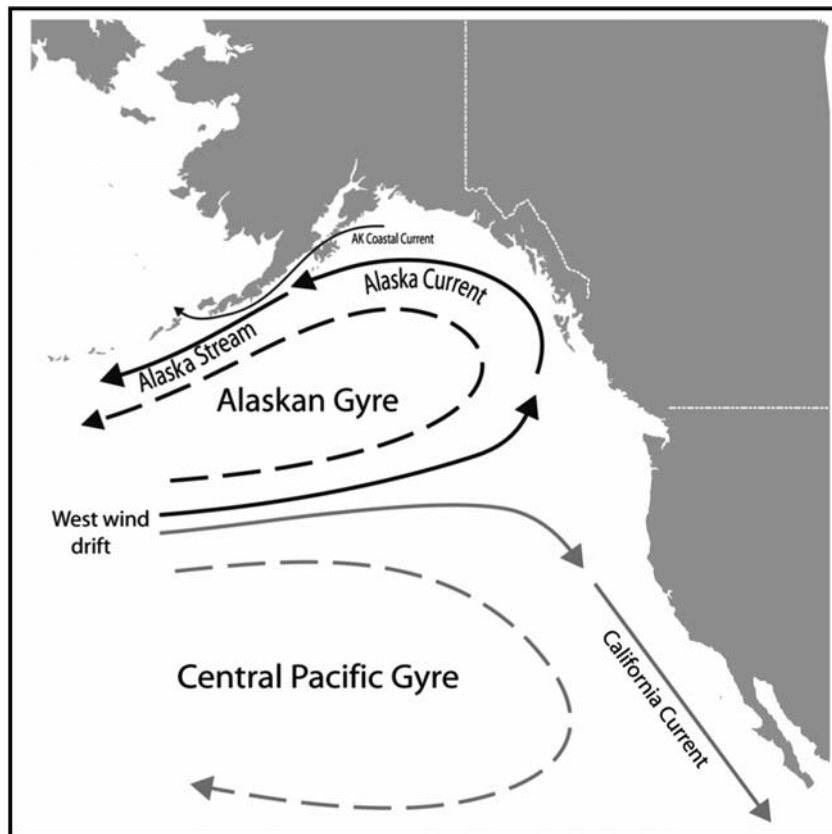


Figure 1. Generalized representation of circulation in the North Pacific (from Agostini, 2005).

features in the CCS: the equatorward CC, the poleward California Undercurrent (CU), and the seasonal poleward Davidson Current (DC) along the continental slope. The CC is a slow, broad (from 50 to 1000 km offshore), shallow (upper 50 m) year-round flow of cool, low-salinity, and nutrient-rich water from the North Pacific (Figure 2). South of Point Conception ($\sim 35^\circ\text{N}$), a portion of the CC turns north to become the Southern California Countercurrent; however, in summer, this flow does not make it completely north and recirculates in the Southern California Bight to become the Southern California Eddy (Figure 2). This poleward flowing current is matched at depth by the CU, which flows along the continental slope carrying warm, high-salinity, low-oxygen water from Baja California to at least Vancouver Island ($\sim 50^\circ\text{N}$). The CU is relatively narrow (10–40 km) and strongest at depths of 100–300 m. Additional surface poleward flow originates close to Pt Conception in winter as the DC and travels northward past Vancouver Island. On average, the CC is strongest in spring and summer and the DC dominates the flow over the shelf and beyond the shelf break throughout winter.

The CCS exhibits great spatial diversity in physical and biological processes (Strub *et al.*, 1990; Mendelssohn *et al.*, 2003), and it can be divided into three subareas: the region north of Cape Blanco, the region between Cape Blanco and Pt Conception, and the regions south of Pt Conception (Figure 3). In the northern and coastal regions, spring and summer upwelling results in considerable cooling at depth and penetration of Subarctic water causes additional cooling of surface (and possibly deep) waters (Mendelssohn *et al.*, 2003). The southern and offshore regions, dominated by subtropical water and associated species, reveal

very little annual thermocline variability and reduced summer and autumn stratification in the seasonal mixed layer.

Physical forcing

On seasonal time-scales, the CCS is forced by two dominant atmospheric pressure regimes: the Aleutian Low (AL) pressure system during winter and the North Pacific High pressure system during summer (Emery and Hamilton, 1985). North of 48°N , local winds are primarily poleward and strongest in winter (Hickey, 1998). Local winds in the south ($\sim 25\text{--}35^\circ\text{N}$) are equatorward on average and reach a maximum in late spring. Local winds at midlatitudes ($35\text{--}48^\circ\text{N}$) have a strong seasonal cycle: persistent and equatorward in summer and intermittent and poleward in winter. Spring and summer equatorward winds drive the offshore Ekman transport of surface waters, causing upwelling of deep, cool, nutrient-rich waters.

On interannual and decadal time-scales, the CCS is affected by two patterns of large-scale ocean climate variability referred to as the Pacific Decadal Oscillation (PDO; Mantua *et al.*, 1997) and the North Pacific Gyre Oscillation (NPGO; Di Lorenzo *et al.*, 2008). The PDO, defined as the first mode of North Pacific sea surface temperature (SST) variability, is driven by a strengthening and southward shift of the AL sea level pressure (SLP) system (Figure 4a). During the positive phase of the PDO, the AL pressure system is deeper and displaced south, causing stronger than usual coastal downwelling winds along the northern CCS and the Gulf of Alaska (Figure 4a). These stronger downwelling conditions generate a local convergence of water masses at the coast that result in higher than usual sea level height (SSH) and warmer SSTs along



Figure 2. Schematic diagram illustrating mean seasonal circulation of large-scale boundary currents off the US west coast. Surface currents in white, subsurface in black (Femia, 2003, based on Hickey, 1998).

the eastern boundary (Figure 4b and c). The higher coastal SSH anomalies (SSHa) drive an anomalous poleward circulation along the eastern boundary resulting in a weakening of the CCS and strengthening of the Alaskan Gyre (AG; Figure 4b, red arrows). There is some evidence (Gargett, 1997; Logerwell *et al.*, 2003) that the extent of spring/summer upwelling in the CCS is influenced by the AL/PDO variability, in particular north of $\sim 38^{\circ}\text{N}$ (Figure 4a), where the alongshore projection of the AL wind anomalies is strongest (Chhak and Di Lorenzo, 2007). The NPGO, defined as the second mode of Northeast Pacific SSH, is forced by a north–south dipole pattern in atmospheric SLP anomalies (SLPa; Figure 4d) associated with the North Pacific Oscillation (Rogers, 1981; Chhak *et al.*, 2009). This dipole pattern in SLPa and its associated windstress curl drive changes in the large-scale Ekman pumping that result in upwelling conditions in the centre of the AG (negative SSHa) and downwelling conditions in the subtropical gyre (positive SSHa; Figure 4e). These SSHa project positively on the mean circulation of the gyres by strengthening the North Pacific Current, the CCS, and the AG (Figure 4e, blue arrows). In the central and southern

CCS (south of $\sim 38^{\circ}\text{N}$), the alongshore windstress anomalies of the NPGO exert a stronger control on coastal upwelling than the AL/PDO (Di Lorenzo *et al.*, 2008; Figure 4, compare alongshore windstresses in panels a and d). Importantly, the NPGO tracks the dominant decadal fluctuations of nutrients, salinity, and chlorophyll *a* in both the Gulf of Alaska and the central/southern CCS (Di Lorenzo *et al.*, 2009; Figure 5).

The CCS is also influenced by the *El Niño* Southern Oscillation (ENSO; Trenberth, 1997), as reported in various studies (Chelton *et al.*, 1982; Hollowed, 1992; Hickey, 1998). The ENSO signature in the CCS is similar to the PDO (Figure 4a–c) in that ENSO influences the winter variability of the AL (Alexander, 1992), which drives the oceanic response of the PDO. ENSO also excites coastally trapped waves that propagate poleward along the North Pacific eastern boundary (Clarke and vanGorder, 1994) and result in strong depressions of the thermocline, higher SSH, and warmer SST anomalies (SSTa) in the southern CCS (Bograd and Lynn, 2003). Although the canonical ENSO drives the interannual power of the PDO (Newman *et al.*, 2003) through the atmospheric and the oceanic teleconnections, a different flavour of ENSO,

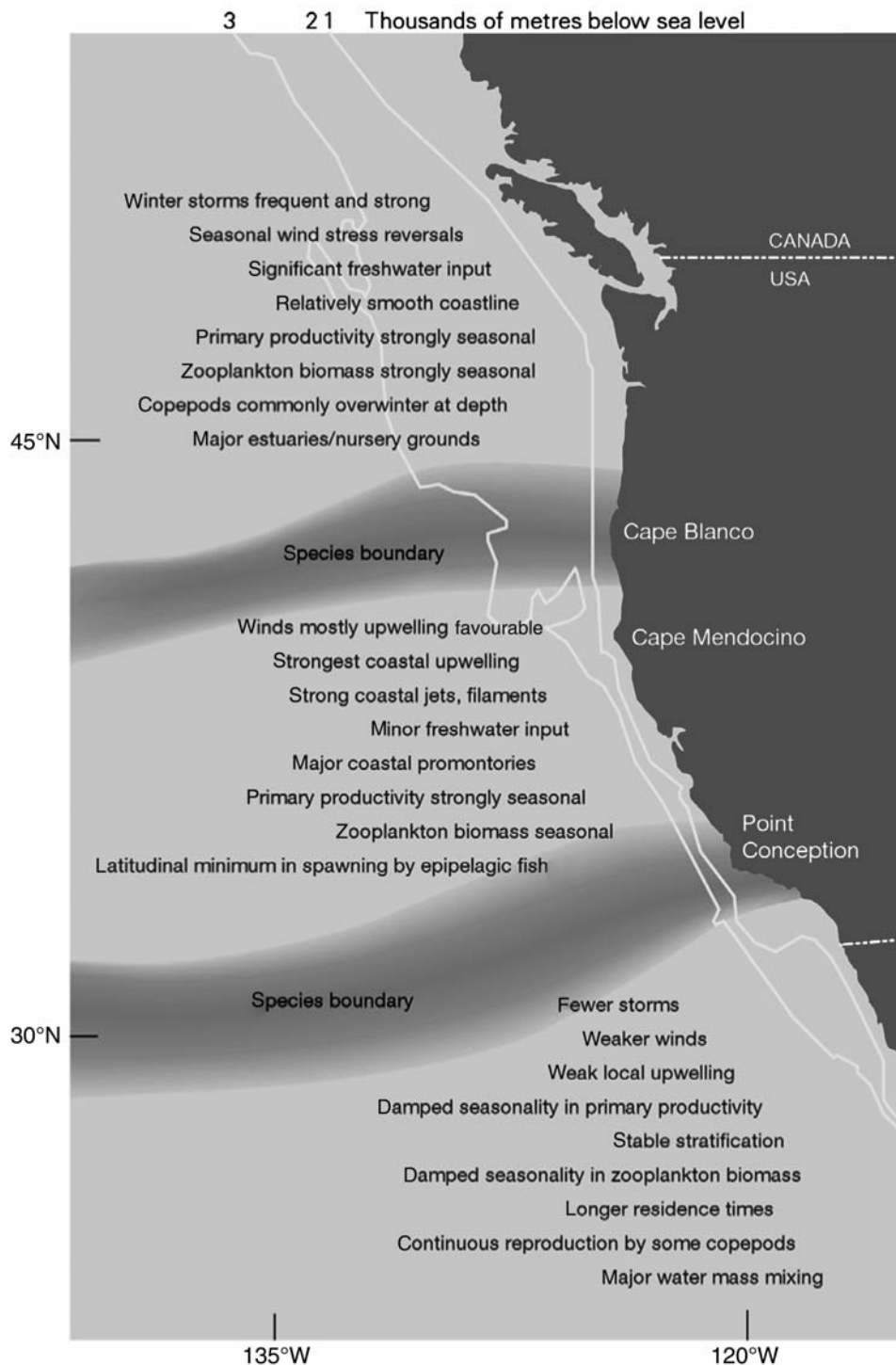


Figure 3. Generalized regional variations in physical and biological processes within the CCS. The boundaries between regions are only approximate and vary over time (from Agostini, 2005).

referred to as the central tropical Pacific warming *El Niño* (Kug *et al.*, 2009), drives the dominant decadal scale fluctuations of the NPGO (Di Lorenzo *et al.*, 2010), implying that a large fraction of the interannual and decadal power of the CCS originates from the tropical Pacific.

Superimposed on the variability driven by the large-scale climate fluctuations, local wind variability along the eastern

boundary has been demonstrated to excite coastally trapped waves, which propagate into the CCS from the south, affecting the coastal variability (Battisti and Hickey, 1984).

Primary productivity

Seasonal variability of primary production in the CCS can be divided into three periods, based on prevailing wind patterns.

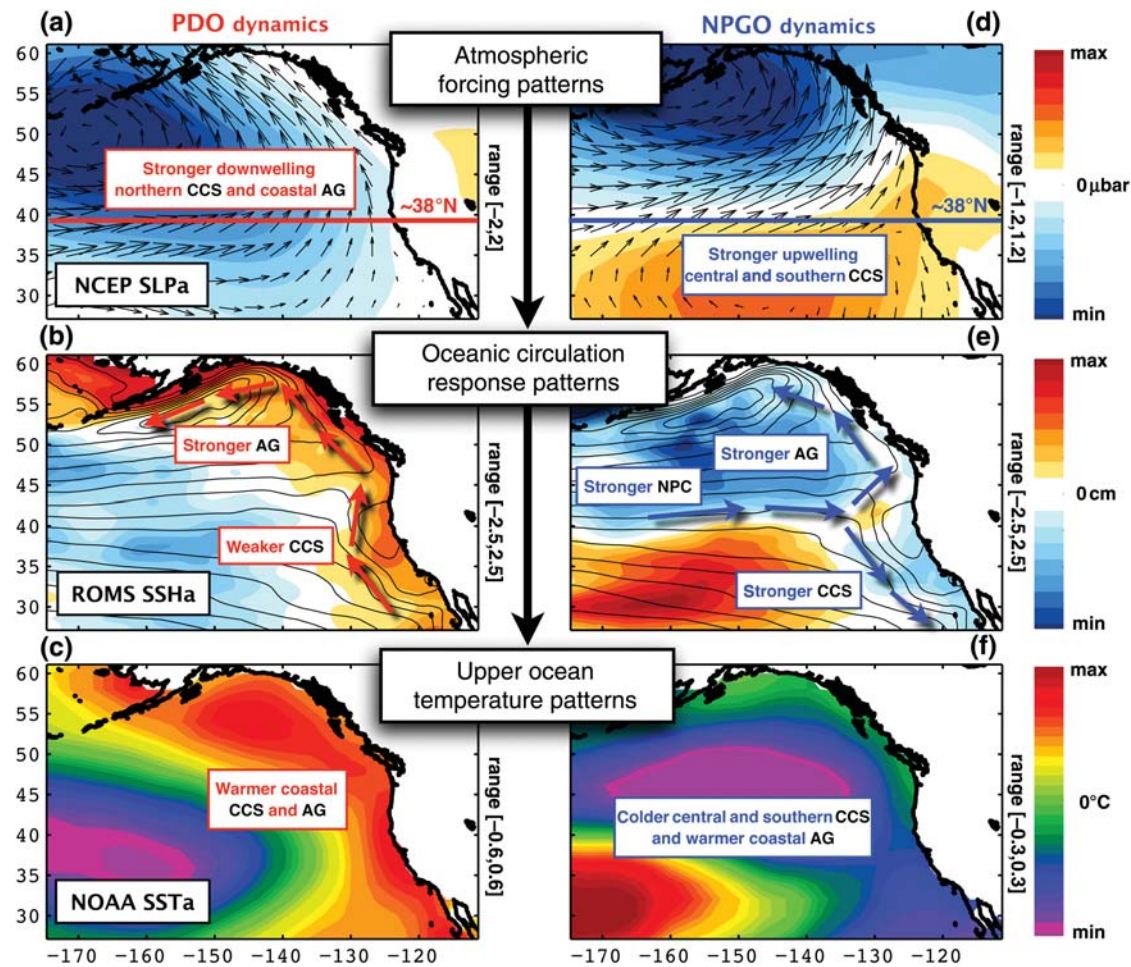


Figure 4. The atmospheric forcing and oceanic response of the Northeast Pacific during the positive phases of the PDO and NPGO. The patterns are obtained by regressing the PDO (left column) and NPGO (right column) indices with (a and d) the NCEP SLPa and windstresses (black vectors; b and e) the ROMS SSHa used in Di Lorenzo *et al.* (2008, 2009), and (c and f) the NOAA SSTa. In the SSHa (b and e), the black contours correspond to the long-term mean SSH (1950–2008), so that it is possible to visualize how the PDO and NPGO SSHa project on the mean circulation—the bold vectors in the SSHa panels indicate the direction of the PDO (red vectors) and NPGO (blue vectors) contributions to the circulation.

Northwesterly winds characterize the upwelling season (February–September). These winds force surface waters south and offshore, allowing nutrient-rich water to ascend and hence support increased phytoplankton stocks inshore. The short oceanic season (September–October) is characterized by decreased windstress, stopping upwelling. During this period, phytoplankton sink below the surface layer, where reduced light levels decrease the primary production rate (Ware and McFarlane, 1989). Southerly winds dominate in winter (November–February), creating the downwelling season, where oceanic water flows into the coastal region following a poleward path along the continental shelf (Ware and McFarlane, 1989).

Whereas primary productivity in oceanic systems typically averages between 50 and 100 $\text{gC m}^{-2} \text{year}^{-1}$, upwelling systems support much higher levels, typically $\sim 300 \text{gC m}^{-2} \text{year}^{-1}$ (Ware and McFarlane, 1989). Ware and Thomson (2005) reported that primary productivity, as corroborated by chlorophyll *a* measurements, varies with latitude, being approximately twice as high in the northern CCS as in southern areas. Factors responsible for these differences include variability of seaward export of

phytoplankton, local enhanced upwelling, and supply of land-derived nutrients (Hickey and Banas, 2008). Strong interannual variability of chlorophyll concentrations within the CCS happens in response to *El Niño* events, as well as forcing through advection of Subarctic water into the system (Thomas and Strub, 2001). For example, the sudden transition from cool to warm SSTs during the strong 1957–1958 *El Niño* event caused a substantial decline in phytoplankton biomass in the coastal California region (McGowan *et al.*, 1998). Analysis of data spanning several decades reveals that primary productivity in the CCS has responded to several regime shifts in the previous century, particularly the 1977, 1989, and 1998 regime shifts (King, 2005).

Secondary productivity

Secondary productivity within the CCS is characterized by low species diversity and high biomass per unit volume (Ware and McFarlane, 1989). Herbivorous copepods and euphausiids dominate the zooplankton communities, whereas carnivorous species make a small contribution (Bernal and McGowan, 1981). Copepods can be categorized into three groups. “Boreal shelf”

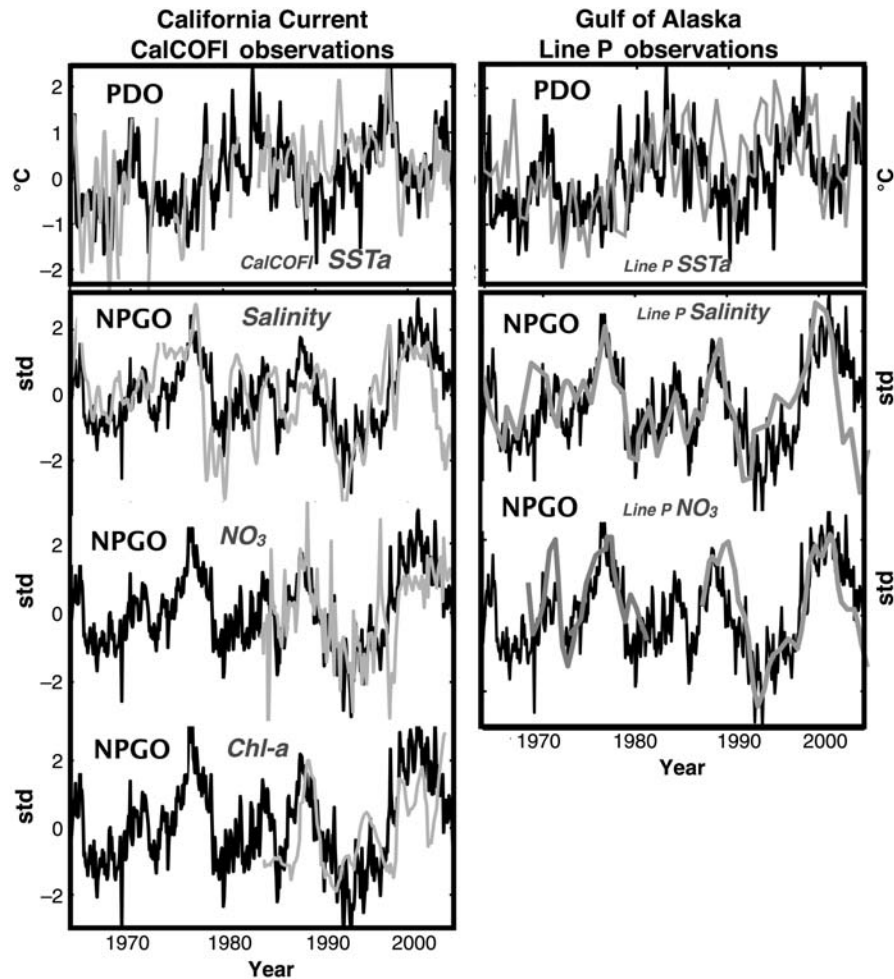


Figure 5. Observed low-frequency fluctuations of temperature, salinity, and nutrients connected to large-scale climate patterns. The time-series of SSTa inferred from the *in situ* CalCOFI (left column) and Line P (right column) observations are significantly correlated with the PDO index. In contrast, the dominant decadal fluctuations in surface salinity, nitrate at 150 m and surface chlorophyll *a* are significantly correlated with the NPGO index. The figure is an extract of the analysis presented in Di Lorenzo *et al.* (2009).

copepods (*Calanus marshallae*, *Pseudocalanus mimus*, *Acartia longiremis*, and *Acartia hudsonica*) dominate the cooler waters extending north from 40°N (Mackas *et al.*, 2004). The “southern copepod” group (*Ctenocalanus vanus*, *Paracalanus parvus*, *Clausocalanus* spp., and *Mesocalanus tenuicornis*) is endemic to the California coast (Mackas *et al.*, 2004). Third, “Subarctic oceanic” copepods (*Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii*) have a brief upper ocean residence during spring and early summer, where they mix onto the shelf of British Columbia. The two major euphausiid taxa found in the northern range of the CCS are *Euphausia pacifica* and *Thysanoessa spinifera* (Mackas *et al.*, 2004). Off Central California and farther south, four euphausiid species are important: *Nematoscelis difficilis*, *Euphausia gibboides*, *Euphausia recurva*, and *Thysanoessa gregaria* (Brinton, 1981).

Variation in secondary production likely reflects changes in primary production in response to nutrient availability through upwelling events or shifts in currents (Chelton *et al.*, 1982). As a rule, increased zooplankton biomass is associated with increased southward flow of cool, nutrient-rich water from the northern CCS (Chelton *et al.*, 1982). Decadal regime shifts have been correlated with major step-like changes in zooplankton composition.

For example, north of Cape Blanco, the 1989 regime shift was characterized by significant reductions in biomass of “boreal shelf” and “Subarctic oceanic” copepods, as well as increased year-round “southern copepod” biomass (Mackas *et al.*, 2004). The *El Niño* events of 1982–1983, 1987–1988, 1991–1992, and 1997–1998 produced the same trend. The strong and cumulative shift to dominance of “southerly” zooplankton fauna in the northern CCS throughout the 1990s reversed sharply in 1999. The cold 1999 *La Niña* event prompted the recovery to average or above average biomass of “boreal shelf” and “Subarctic oceanic” copepod groups, dominance of Subarctic euphausiid species, and a concurrent decline in the “southern copepod” group (Brinton and Townsend, 2003; Mackas *et al.*, 2004).

Fish species

Five fish species were selected to represent distinct life-history strategies described by King and McFarlane (2003; Table 1). Opportunistic strategists (e.g. Pacific sardine, *Sardinops sagax*) have relatively low fecundities, but their short generation time, coupled with high intrinsic population growth rates, allow their abundance to rebound rapidly from depletion. These fish are surface and midwater pelagic species that occupy low trophic

Table 1. Life-history traits and ecological requirements and roles of selected fish species in the CCS.

Species	Fecundity	Max. age	Age at first maturity	Marine habitat	Spawning season	Spawning area	Nursery area	Feeding area	Major prey	Major predators
Pacific sardine	200 000	12	2	Epipelagic	January–September (peaks April–June)	Mainly off southern California in 15–18°C water	Inshore inlets and shallow coastal waters	Coastal waters from Mexico to Canada	Diatoms; copepods; euphausiids	Fish
Dover sole	1 514 000	50	4	Demersal on shelf and upper slope	December–February	Deep water beyond the shelf break	Pelagic larvae for up to 2 years	Soft sediments continental shelf and slope	Benthic invertebrates	Pinnipeds, seabirds, demersal fish
Blue shark	25–50	20	4–6	Epipelagic	May–June (parturition)	Offshore areas	Offshore and coastal areas	Offshore and coastal areas	Bony fish, squid, seabirds; marine mammal carrion	Shortfin mako, white sharks, and sea lions
Chinook salmon	9 500	5	4–5	Epipelagic	August–October	Rivers	Rivers	Fry: rivers; smolts: nearshore areas; juveniles – adults: coastal waters	Euphausiids; small fish	Fish prey on smolts, marine mammals, and salmon sharks
Pacific hake	1 147 000	16	3	Bathypelagic (50–200 m)	January–February	Mainly off California	50–100 m	North and central regions	Euphausiids, shrimp, and small fish	Cannibalistic, sharks, and marine mammals

levels. Periodic strategists (e.g. Dover sole, *Microstomus pacificus*) are long-lived, slow-growing, and have high fecundity. They are piscivores that typically inhabit shelf or slope benthic habitats. Equilibrium strategists (e.g. blue shark, *Prionace glauca*) are dominated by elasmobranchs, which are slow-growing, have extremely low fecundity, are large with large eggs, and exhibit a great degree of parental investment. These fish are higher-order carnivores that inhabit a range of habitats. Salmonid strategists (e.g. Chinook salmon, *Oncorhynchus tshawytscha*) are similar to opportunistic strategists, in that they are not extremely fecund and are short-lived. In contrast, however, they are fast-growing, larger, anadromous, and semelparous. Finally, intermediate strategists (e.g. Pacific hake, *Merluccius productus*) are midrange in their life-history traits compared with the suite of marine fish. Details on the distributions and life histories of the representatives are given in Table 1.

Downscaling for the CCS

As part of the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (AR4; IPCC, 2007), simulation results from more than 20 GCMs were made freely available on an ftp archive at the Lawrence Livermore Laboratory. Unfortunately, the spatial resolution of most of these GCMs was greater than 100 km, meaning that smaller scale features such as the CCS would not be adequately captured, thereby making their change and impact analyses more difficult. Two approaches are often used to overcome this resolution problem: statistical and dynamical downscaling. The former establishes relationships between GCM results over the 20th century and local observations; then, assuming they also apply in future, it uses them to infer estimated values for the 21st century. These relationships can be as simple as spatial interpolations or involve much more complicated statistical techniques. The problem with this approach is that if the dynamics underlying the variable(s) of interest are not well represented in the global models, statistical relationships with local observations cannot be established. Summer SST in the CC region is a good example. Global models do not have sufficient resolution to distinguish adequately the shelf and slope and, therefore, do not capture upwelling SST patterns accurately.

The alternative approach, dynamic downscaling, attempts to overcome this problem by embedding an RCM with grid size of 10 km or smaller to resolve better the relevant physics inside one or more of the GCMs. The lateral boundary conditions for the RCM are taken from the GCM, and forcing mechanisms, such as wind, heat flux, and river discharge, are provided on finer spatial scales. To date, only one RCM has been developed and run for the CCS (Auaud *et al.*, 2006), though at least two others are in development. Because the Auaud *et al.* (2006) RCM only covers the southern CCS and their analysis only addresses upwelling, we have to rely on statistical downscaling procedures to infer other relevant GCM results for both the southern and the northern portions of the CCS.

Methods

Conceptual pathways

Climate change impacts on the five representative fish species will likely be mediated through mechanisms where key ecological processes or life-history traits are substantially influenced by physical forcing and primary or secondary productivity. For each species, we reviewed the literature to inventory life-history and ecological

mechanisms that link physical features and lower trophic productivity to biological responses or population dynamics. The pathways primarily linked oceanography and productivity to the species' spatio-temporal distribution, spawning behaviour, spawning success, larval survival, feeding and growth, and adult survival. The inventory of pathways provides a basis for anticipating the effects of climate changes projected, either using empirically informed climate scenarios or using climate models.

Empirical data scenarios

Based on the species' conceptual pathways, scenarios for impacts of climate change on population dynamics were hypothesized based on warming trends in recent decades. Empirical data from the latter half of the 20th century indicate warmer surface and near-surface waters; an increase in upwelling-favourable winds in spring and summer, particularly in the north; a deepening thermocline in coastal waters, particularly in the north; increased coastal stratification, particularly in the south; and increasing incidence of hypoxia in shelf waters (Bakun, 1990; Mendelssohn *et al.*, 2003; Palacios *et al.*, 2004; Chan *et al.*, 2008). The increase in upwelling may have been counteracted by the increase in stratification, such that nutrient-rich upwelled waters did not reach the euphotic zone and spur primary and secondary production (McGowan *et al.*, 2003; Palacios *et al.*, 2004). The few available RCM simulations of coastal CCS waters project a continuation of these observations.

In scenarios where atmospheric CO₂ nearly doubled over the 21st century, upwelling-favourable winds also increased substantially off northern California and peak upwelling happened nearly a month later than in contemporary conditions (Snyder *et al.*, 2003). Another study predicted increased water temperature, upwelling, stratification, and offshore surface transport in the mid-21st century off central and southern California, assuming a 36% increase in CO₂ (Auad *et al.*, 2006). The model projected increases in near-surface temperature, upwelling, stratification, and offshore surface transport. The predicted changes were particularly strong in the northern portion of the model domain.

In addition, in the last half of the 20th century, there have been more frequent and intense *El Niño* events (An and Wang, 2000). If future warming resembles these events, the result would be a higher degree of warming of surface waters directly along the coast (through a combination of direct heating and influx of warmer southern waters), an increase in upwelling-favourable winds, increased stratification, and a deeper thermocline in coastal waters. Strong *El Niño* events have been associated with substantial declines in phytoplankton biomass in the southern region of the CCS. If increased stratification results in warmer, nutrient-poor upper waters, phytoplankton will also decrease in northern regions. There will likely be a decrease in secondary productivity in the southern region and an overall northward shift of the "southern" zooplankton community, replacing and, thereby, reducing the biomass of "boreal shelf" and "Subarctic oceanic" copepods in the northern regions.

Statistical downscaling

Alternatively, we could view the conceptual pathways of the representative species in the context of statistically downscaled climate-change model outputs. Information on the future climate of the CCS was available from IPCC-AR4 simulations by coupled atmosphere–ocean GCMs carried out for a variety of greenhouse-gas-emission scenarios over the period 2000–

2100 (IPCC, 2007). The most common ones for impact analyses are A2, a business-as-usual scenario with steadily increasing emissions. However, the moderate scenario A1B, with emissions levelling off around and dropping slightly after 2050, was used in this project. These GCMs have been proven reasonably faithful in characterizing the broad-scale features of the observed climate of the last half of the 20th century (Reichler and Kim, 2008). Overland and Wang (2007) revealed that 12 of the 22 GCMs reproduce the spatial and temporal character of the PDO. We examined this subset of 12 models regarding their forecasts to 2050.

Three physical forcing elements were considered by the above model runs: eastern North Pacific SST, upwelling along the central Oregon coast, and nearshore zonal wind. The SST reflects the basin-scale climate; the upwelling and zonal wind represent two examples of the regional atmospheric forcing. Upwelling along the Oregon coast can be related to large-scale pressure patterns, such as the AL (Logerwell *et al.*, 2003), which in principle the GCMs can simulate. As a proxy for the upwelling on the Oregon coast, we used the SLP averaged over a box extending from 42.5 to 52.5°N 142.5 to 127.5°W for the summer season (June–August). Zonal winds, through their forcing of meridional Ekman transports, ultimately affect the latitude of the transition between subtropical and Subarctic lower-trophic level communities. Wang *et al.* (2010) demonstrate that the GCMs poorly characterize these winds in the immediate vicinity of the coast; therefore, a nearshore region of 40–50°N 135–125°W was examined.

Results

Pacific sardine

Conceptual pathways

Pathways that link Pacific sardine ecology and population biology to environmental forcing are summarized in Supplementary Table S1. Temperature, circulation patterns, and regional productivity drive their distribution and the timing and location of spawning. Pacific sardine are usually abundant during warm years, because of lowered predation pressure (Agostini *et al.*, 2007). Year-class success is critically important to Pacific sardine population biology: in stage-based models, the largest changes in Pacific sardine population growth came from changes in the mortality rate of eggs and larvae (Lo *et al.*, 1995). Some authors believe that year-class success is related to ocean temperature (Kawasaki and Omori, 1988; Lluch-Belda *et al.*, 1992); others suggest that temperature is a secondary correlate (McFarlane and Beamish, 2001; Agostini *et al.*, 2007). Agostini *et al.* (2007) could not find a distinct link between increased zooplankton abundance and change in Pacific sardine year-class success, likely because of change in plankton species composition (not abundance). Alternatively, year-class strength could be related to changes in stratification or properties of coastal flow (meanders) that concentrate food organisms for larvae (Logerwell *et al.*, 2001; MacCall, 2002). Moreover, low food concentrations characteristic of *El Niño* years may be overcompensated by reduced predation pressure on Pacific sardine larvae, possibly resulting in bursts in recruitment (Agostini *et al.*, 2007). Pacific sardine are omnivorous filter-feeders, with diets composed of regionally abundant copepods, diatoms, a variety of other zooplankton, and occasionally fish larvae. It is generally believed that decadal-scale changes in stratification and upwelling are related to changes in species

composition of phytoplankton, particularly diatoms that improve the growth and survival of Pacific sardine (McFarlane and Beamish, 2001).

Empirical data scenario

The Pacific sardine that feed off British Columbia were produced in the south, off the coasts of California and Mexico. There is some spawning off British Columbia, but it is minor. The period before 1947 was favourable for Pacific sardine production and the regime from 1948 to 1976 was not favourable. The Pacific sardine population increased off California from 1977 to the early 1990s, indicating that periods of intense ALs (positive PDO and stormy winters) resulted in improved Pacific sardine production. If greenhouse-gas-induced climate change increases the frequency of periods of intense ALs and increased mid-ocean, winter upwelling (Mote *et al.*, 1999), Pacific sardine population fluctuations should continue, possibly with more frequent favourable periods. Off British Columbia, Pacific sardine will still fluctuate in abundance, but warmer coastal waters may result in greater abundance, possibly with resident populations being established. However, periods of collapse will still happen.

Dover sole

Conceptual pathways

Pathways linking Dover sole ecology and population biology to environmental forcing are presented in Supplementary Table S2, with the most substantial links relating to spawning and early survival. Circulation patterns are critical for transport and retention of Dover sole eggs and pelagic larvae during their protracted pelagic phase. Little evidence was found of directed movement by larval sole from spawning areas to settling areas in the Gulf of Alaska; instead, larvae moved with currents and displayed diel vertical movements in the water column (Bailey *et al.*, 2008). These movements may allow larvae to use alternately surface currents and subsurface countercurrents to remain in areas that are suitable for eventual settlement. Adult Dover sole in the Gulf of Alaska may select spawning grounds near features, such as canyons, where directed flows will transport eggs and larvae to regions of optimal retention and settlement (Bailey *et al.*, 2008). Some Dover sole spawning grounds have been identified in the CCS, such as the Willapa Deep grounds at 300–500-m depths off Willapa Bay, Washington (Sampson, 2005). According to Toole *et al.* (1997), Dover sole settlement peaks during midwinter in deep continental shelf waters. Settlement timing is correlated with strong onshore Ekman transport, positive vertical velocity, and relatively warm bottom temperatures (7.4–10.3°C) between January and March. In spring, newly settled juveniles move inshore to depths of 100–120 m (Toole *et al.*, 1997). Markle *et al.* (1992) hypothesized that Dover sole move inshore to nursery habitat by making night-time vertical ascents off the bottom, allowing onshore Ekman transport to push them up the shelf; they continue this hopping behaviour until they encounter desirable habitat. Adult Dover sole, which move into progressively deeper waters as they age, are especially well adapted to relatively low dissolved oxygen conditions (Drazen, 2007).

Empirical data scenario

Climate-mediated changes in currents, particularly currents around the spawning grounds in the winter spawning season and the currents and countercurrents that control the dispersal and retention of eggs and larvae, will likely affect Dover sole,

although some aspects of their life history (e.g. batch spawning throughout the spawning season) may act to lessen the impacts of environmental mismatches. Climate change effects on late winter onshore Ekman transport may affect the ability of juvenile Dover sole to move up the shelf into suitable nursery habitat. After the juveniles reach favourable habitat, the key influence of climate (and, hence, of climate change) may be through temperature and upwelling, which respectively influence metabolic rates and productivity of prey resources.

The depths where adult Dover sole live may buffer them from the direct impact of temperature increases associated with climate change. However, if Dover sole reproductive success is indeed linked to spatial associations between particular spawning grounds and specific circulation patterns, the distribution of suitable spawning habitat may shift if climate change alters circulation in the CCS. If climate change affects the size or seasonal dynamics of the oxygen minimum zone off the North American west coast, the total habitat available to adult Dover sole would be expected to change.

Blue sharks

Conceptual pathways

Compared with the other species examined, we found few obvious pathways that link blue shark ecology and population biology to environmental forcing (Supplementary Table S3). Blue sharks are pelagic apex predators that generally feed indiscriminately on smaller fish, swarms of seasonal crustaceans, and squid (Nakano and Seki, 2002). Some blue shark distribution and movement patterns appear linked to feeding habits. In the central North Pacific, young-of-the-year sharks occupy the more productive waters of the northern Transition Zone and Subarctic Boundary, where a large food base is available (Nakano and Seki, 2002). Nakano (1994) speculated that food availability in the region might dictate the location of the nursery grounds. Water temperature plays a significant role in determining the patterns of catch and distribution observed by researchers in different areas (Nakano and Seki, 2002). Most blue sharks have been caught in a water temperature range of 15.6–18.9°C, with females preferring cooler water than males.

Empirical data scenario

Impacts of climate change on blue sharks may be limited to changes in food resources (e.g. abundance and distribution of schooling pelagic species) and temperature. Little information is available on changes in blue shark distribution or other biological parameters in relation to prior decadal-scale climate events. It is likely that blue sharks (and other large open ocean pelagics) would be affected regarding their distribution and growth, with more sharks entering the CCS and moving north following food resources. However, given the strong affinity of female blue sharks for specific water temperatures, a warming climate may induce a major shift in spawning or parturition area and nursery ground.

Chinook salmon

Conceptual pathways

Characteristics of freshwater regimes are tightly linked to migration, spawning, hatching, and early rearing phases of Chinook salmon (Supplementary Table S4). Adequate freshwater flows during spawning migrations permit passage upstream and provide suitable temperatures, as well as dissolved oxygen levels.

Adequate flow throughout summer and autumn months provides juveniles with rearing habitat, drifting prey and refuge from predators (Crozier *et al.*, 2008). Both summer and winter temperatures are linked to growth and mortality of juvenile salmon during their extensive freshwater incubation and nursery phases. With extremes from 3 to 20°C, preferred temperatures for most Pacific salmon in freshwater range from 7 to 16°C (Reiser and Bjornn, 1979). Upper lethal temperatures are 25–26°C. In the marine phase of the life history of salmon, there are critical temperatures of 9–10°C that restrict feeding areas for salmon to areas cooler than these temperatures (Welch *et al.*, 1995). In addition, Chinook salmon exhibit a marine growth response to large-scale forcing (Supplementary Table S4), although the response depends on stock origin. Wells *et al.* (2008) found that marine growth of ocean-type Chinook salmon from the central CCS responded positively to a strong CC, cool temperatures, strong upwelling, and a strong North Pacific High pressure system. In contrast, Chinook salmon originating in northern CCS streams responded negatively to a strong CC, although their overall response was complex, possibly related to age- and race-specific movements across the transition zone into the Alaska Gyre.

Empirical data scenario

Because Chinook salmon are anadromous, impacts from climate change will happen in both freshwater and ocean habitats. Levy (1992) hypothesized that a warmer climate will increase river temperatures and decrease flows during spawning migrations, increasing prespawning mortality, and reducing egg deposition. A warmer climate will increase water temperatures during egg incubation stages, increasing fry-to-smolt mortality at the same time as increasing the severity and frequency of winter floods, thereby reducing egg-to-fry survival rates (Battin *et al.*, 2007). Reduced snowpack will result in lower flows and higher juvenile mortality in autumn (Beechie *et al.*, 2006; Crozier *et al.*, 2008). Extreme temperatures may kill eggs, juveniles, or adult salmon, potentially extirpating some populations (Crozier *et al.*, 2008); less extreme temperatures can affect growth, reproduction, and movement. Early marine mortality, a major determinant of population growth rates via food availability and bioenergetics, is expected to become more variable and more extreme (Beamish and Mahnken, 2001), and poor growth in freshwater may contribute to increased mortality in the ocean. Populations that experience lower marine growth because of a weakened CC will experience greater mortality or lower fecundity upon maturation (Wells *et al.*, 2008). Predation may increase as more pelagic predators move north (e.g. Pacific hake and mackerel). Ocean warming, particularly in winter, could favour northern areas for marine rearing of salmon.

Pacific hake

Conceptual pathways

The major linkages between Pacific hake and environmental drivers involve recruitment and the extent of the annual migrations (Supplementary Table S5). The prevailing hydrographic conditions related to recruitment success of Pacific hake can be grouped into two categories: those that affect transport of larvae and those that concentrate prey. Cold years with intense upwelling present significant advection offshore and south away from favourable inshore nursery areas, which results in lower growth rates, lowered prey abundance, and higher predation mortalities (Bailey, 1980; Bailey and Francis, 1985; Hollowed and

Bailey, 1989). During warmer years (e.g. *El Niño*), reduced upwelling intensity produces reduced offshore advection, which may favour larval survival (Hollowed and Bailey, 1989; Hollowed, 1992; Smith *et al.*, 2001). Eddies (both offshore and nearshore), jets, and meanders are also the areas of increased larval survival for Pacific hake, possibly because of increased prey availability and retention in favourable habitats.

Pacific hake spawning activity shifts equatorward during cold periods and poleward during warm periods (Bailey and Francis, 1985; Horne and Smith, 1997; Saunders and McFarlane, 1997). The migratory behaviour of Pacific hake is influenced by a number of physical processes (Supplementary Table S5). Overall, feeding grounds extend farther north during *El Niño* years (Bailey *et al.*, 1982). Generally, these are the years of stronger poleward flow, decreased CC flow, weak upwelling, and warm coastal SSTs (Hollowed, 1992). Warmer temperatures and weaker upwelling result in lower nutrient enrichment, resulting in low zooplankton availability in southern waters (Horne and Smith, 1997), especially for younger fish whose diet is primarily euphausiids. Reduced prey availability may motivate older Pacific hake, which can migrate, to seek better conditions farther north. Strong poleward flow might also aid migration by reducing energy expenditure (Agostini *et al.*, 2006). Limited northern migration years result in higher spatial overlap between adult and juvenile Pacific hake, which increases the probability of cannibalism (Buckley and Livingston, 1997).

Empirical data scenario

Stratification, upwelling, and nutrient changes might reduce primary productivity and, therefore, Pacific hake year-class success. In addition, spawning and rearing areas off California could shift north. This could result in an overall decrease in abundance off California and southern Oregon. Increased upwelling will also concentrate euphausiids at the shelf break where Pacific hake feed, thereby increasing growth. Because adult migration patterns shift north in warm years, it is likely the projected increases in temperature will result in a greater percentage of the existing coastal stock moving farther north into Canadian and Alaskan waters. The establishment of a resident portion of this stock in the northern regions of the CCS could be possible with a northward shift in spawning grounds, coupled with available northern feeding grounds. If the distributions of potential predators (e.g. jumbo squid, *Dosidicus gigas*) shift into the CCS, Pacific hake may experience greater predation mortality or altered foraging behaviour related to predator avoidance (Holmes *et al.*, 2008).

Statistical downscaling

In the projections to 2050, natural variability overshadowed any climate signals in SST, SLP, or near zonal winds for most of the time-scale until ~2040. All outputs based on the A1B (moderate) greenhouse-gas-emission scenarios resulted in only mild SST warming and minor increases in zonal winds and the upwelling proxy (SLP).

Eastern North Pacific SST

Figure 6 indicates for the far eastern North Pacific an increase in SST of 1.2°C by the decade of 2040–2049 relative to a baseline period of 1980–1999, based on ten IPCC AR4 models (right panel). The left panel illustrates the year when the expected warming because of climate change will exceed the magnitude of the natural variability (i.e. noise). This year is defined by dividing

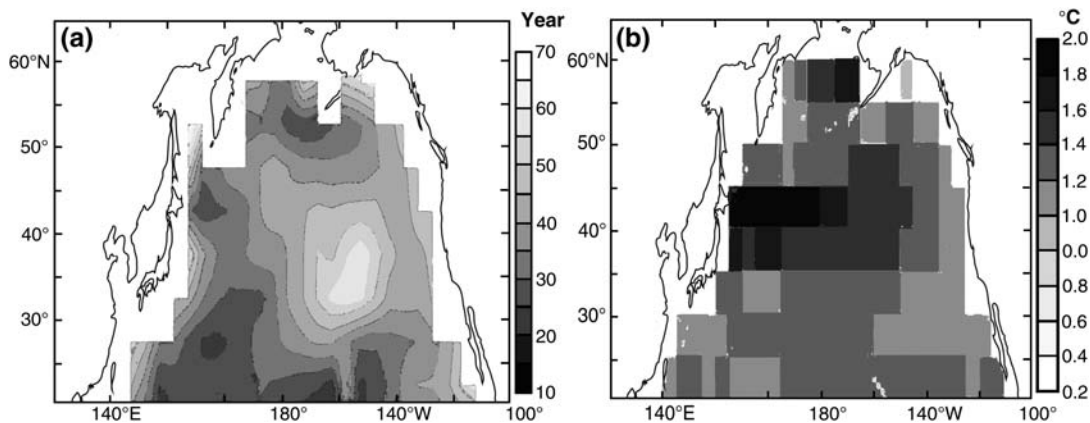


Figure 6. (a) Estimated year (+2000) when the net warming will exceed the magnitude of natural variability. (b) Projected winter SST change for 2040–2049 minus 1980–1999 (from Overland and Wang 2007).

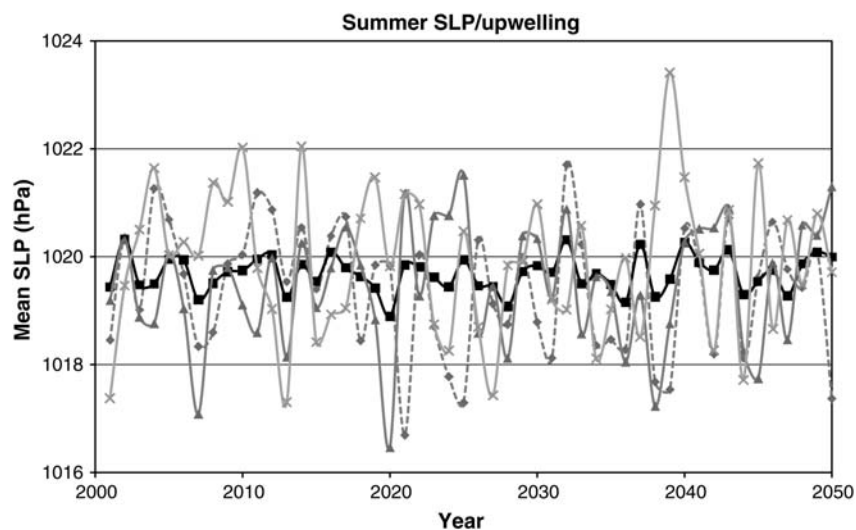


Figure 7. Projected SLP in June–August for the region 42.5–52.5°N 142.5–127.5°W. The squares with solid black line represent the ensemble weighted mean; the other traces represent individual GCM simulations.

twice the standard deviation of the modelled SST by the modelled temperature trend. This threshold is reached for the far eastern North Pacific near the middle of the 21st century.

SLP proxy for Oregon coast upwelling

Time-series of the weighted ensemble-mean projections of SLP and some selected individual GCM projections are illustrated in Figure 7. The SLP in the study area is projected to remain nearly constant, implying little change in summer upwelling over the first half of the 21st century. The uncertainty in the projection for any particular year, based on a combination of intramodel and intermodel variance, is ~ 1.5 hPa (for a standard deviation). This magnitude is comparable with the amplitude of the major swings in the predicted SLP from the individual model runs.

Nearshore zonal winds

The weighted ensemble-mean projection for the nearshore zonal winds (Figure 8) indicates little in the way of any trend and hence change in the mean meridional transports compared with the current climate forcing. There is a hint that years of strongly

positive zonal wind anomalies may become less frequent. The uncertainty in the projection for any particular year is ~ 0.6 m s⁻¹. As with SLP, the combination of the natural variability and uncertainty in the model projections dominate any systematic changes.

Discussion

The development of conceptual models for different life-history strategists highlighted some common physical features of the CCS that affect fish population distribution or abundance. Overall, the recurring physical features that were important to some component of most species were stratification intensity and depth of the mixed layer; upwelling intensity and timing; temperature (at surface and at depth); strength of the northward undercurrent; and eddies and meanders at the upwelling front (Supplementary Tables S1–S5). However, IPCC-AR4 GCMs could not resolve these features in sufficient detail to produce a true forecast, and higher resolution RCMs are still under development. The development of quantitative scenarios of species'

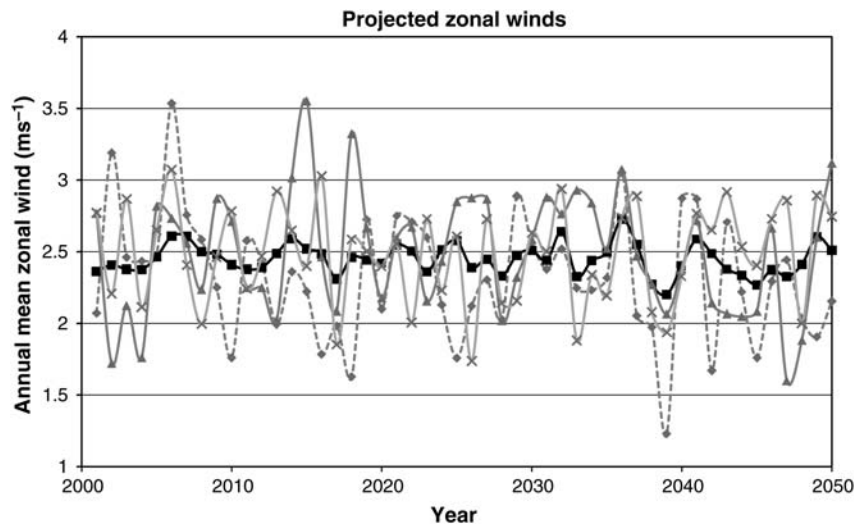


Figure 8. As in Figure 7, but for projected annual average zonal winds for the region 40–50°N 135–125°W.

Table 2. Empirical scenarios under increased warming (with references for conceptual pathways or observations) for trophic levels and additional fish species considered for the larger CCS project (captured in Figure 9), but not discussed in detail here.

Trophic level	Empirical scenario	References
Phytoplankton	Declines in phytoplankton biomass in the southern region In the northern region, increased stratification resulting in warmer, nutrient-poor upper waters with decreased phytoplankton biomass	Chelton <i>et al.</i> (1982) and McGowan <i>et al.</i> (1998)
Zooplankton	Decrease in secondary productivity in the southern region An overall northward shift of the “southern” zooplankton community, replacing and, thereby, reducing the biomass of “boreal shelf” and “Subarctic oceanic” copepods in the northern regions	Brinton and Townsend (2003) and Mackas <i>et al.</i> (2004)
Fish		
Albacore tuna (<i>Thunnus alalunga</i>)	More albacore tuna closer to shore and northwards in summer with warmer surface waters, increased water clarity because of reduced primary productivity Could be mitigated by decreased dissolved oxygen because of warmer water	Kimura <i>et al.</i> (1997) and Laurs (1983)
Rockfish (<i>Sebastes</i> spp.)	Overall northward shift in distribution and with concomitant decreases in maximum age and size, age and maturity, and fecundity Increased larval predation with influx of predators because of warmer water Decreased larval survival due to a mismatch with earlier phytoplankton blooms Decreased adult reproductive output Longevity with periodic strong year classes maintains biomass	Berkeley <i>et al.</i> (2004), Harvey (2009), King and McFarlane (2003), and Woodbury (1999)
Sablefish (<i>Anoplopoma fimbria</i>)	Loss of southern range with warm-water impacts on larvae In the north, decreased year-class success with reduced spring productivity and copepod production for larvae Longevity with periodic strong year classes maintains biomass	King <i>et al.</i> (2000), King and McFarlane (2003), and Schirripa and Colbert (2006)
Seabirds	Declines in cool-water species (sooty shearwaters, alcids) and shift in dominance to warm-water species Decline in nesting and fledgling success of species, such as Cassin’s auklet and tufted puffin	Gjerdrum <i>et al.</i> (2003), Hyrenback and Veit (2003), Lee <i>et al.</i> (2007), and Wolf <i>et al.</i> (2009)
Marine mammals	Marine mammals will respond with plasticity in diet and movement to follow prey availability Northward movement of warm-temperate species, such as California sea lions, common dolphins, harbour seals; decline in cool temperate species, such as Dall’s porpoise	Benson <i>et al.</i> (2002), Sydeman and Allen (1999), and Weise <i>et al.</i> (2006)

responses will depend on resolving these features in GCMs and being able to link to RCMs.

Of the variables currently available from GCMs, one (SST) is a recurring feature in our conceptual models and two others (upwelling winds and nearshore zonal winds) are closely related to other recurring features. The statistical downscaling approach, based on a moderate greenhouse-gas-emission scenario (A1B), suggests only moderate oceanographic changes: mild surface warming accompanied by relatively minor increases in upwelling-favourable winds in northern portions of the CCS. Natural variability overshadows climate signals for many important metrics (Overland and Wang, 2007; Wang *et al.*, 2010). Our downscaling results agree with the basic findings of Mote and Mantua (2002) that drastic changes in upwelling are unlikely over the next few decades. They are at odds with Bakun (1990) and Snyder *et al.* (2003), who posited that upwelling was liable to strengthen. Although the regional atmospheric forcing may not change dramatically over the next few decades, it may be acting on an ocean with different physical properties. For example, the warming at depth will presumably be less than that for the SST, which will result in an increase in upper-ocean static stability (assuming vertical gradients in salinity are unchanged or also increasing). The analysis carried out here suggests no systematic trends in upwelling or nearshore meridional transport for the CCS because of anthropogenic effects by midcentury, but continued large year-to-year and decadal variability. Increases in SST could result in an increase in upper-ocean static stability.

Under a scenario based on the statistical downscaling outlined above, resource managers might anticipate relatively minor changes rooted in mild warming and small, localized increases in upwelling. Impacts across all trophic levels will mainly be distributional, resulting in changes in community structure in the various CC regions. Although there are few studies on the potential changes in phytoplankton community structure, another possible impact might be a shift in the timing of maximum phytoplankton concentrations from current (April–May) to March–April, with cascading effects on higher trophic levels. Decreased zooplankton abundance and changes in community composition have been associated with an increase in water temperature, inferring that a moderate warming will result in decreased zooplankton abundance. For the northern CCS, the shift in community composition observed in warmer years has resulted in lower-quality copepods that are typically found in regions that are more southern. For the fish species we examined, moderate warming will be reflected in distributional changes for all life-history strategists. Species such as Pacific sardine and Pacific hake, which are typically associated with warm water and spawn in the southern region of the CCS, will expand their range northward. Conversely, salmonids, which prefer cooler waters, may move north out of the CCS. Moderate warming may not greatly affect deep demersal species, such as Dover sole. Pelagic migratory species, such as blue sharks, may shift their range shoreward and north following migratory pelagic finfish on which they predate. With changing temperatures or latitudinal distributions, some fish may experience mild changes in energetic demands and in characteristics, such as growth, age at maturity, and fecundity (Harvey, 2009). Despite the minor changes that a moderate scenario produces, a precautionary approach to managing fisheries and marine ecosystems mandates that resource managers also consider more extreme climate change scenarios. Future changes may be extensions of trends in recent decades and the empirical data

scenarios developed here offer more extreme climate change scenarios than the moderate scenario suggested by the statistical downscaling approach.

As noted in the introduction, the CFAME Task Team considered a larger suite of finfish, including albacore tuna (*Thunnus alalunga*), rockfish (*Sebastes* spp.), and sablefish (*Anoplopoma fimbria*), as well as seabirds and marine mammals (Table 2). As with the fish species presented here, we used a synthesis of information available from the literature to develop conceptual pathways and forecast the climate change impacts under the empirical data scenarios. Figure 9 is a synthesis of all the forecast impacts; the process involved in producing this kind of synthesis helped the CFAME Task Team clarify links and obtain a whole-system view. The upper panels of Figure 9 graphically represent current conditions in the three regions of the CCS (north, central, and south). The empirical data scenarios project warmer surface and near-surface waters; an increase in upwelling-favourable winds in spring and summer, particularly in the north; a deepening thermocline in coastal waters, particularly in the north; increased coastal stratification, particularly in the south; reduced snowpack and stream flows; and increasing incidence of hypoxia in shelf waters (lower panels, Figure 9). The increase in upwelling might be counteracted by the increase in stratification, such that nutrient-rich upwelled waters do not reach the euphotic zone, with subsequent lower primary productivity (Figure 9).

The overall impacts forecast with the empirical data scenario include changes in species distribution, with either northward extension of species, such as zooplankton (Table 2), Pacific sardine, and Pacific hake, or inshore extension of blue shark and albacore tuna (Table 2, Figure 9). Other forecast responses include impacts on year-class (recruitment) success. For example, Pacific hake (intermediate strategist) may experience reduced recruitment, unless they exhibit migratory ability with the potential for relocating spawning grounds to waters that are more productive. Historically, recruitment failure in opportunistic and intermediate strategists has resulted in dramatic declines in population abundance within a generation (3–5 years; King and McFarlane, 2003). Conversely, long-lived, highly fecund species (periodic strategists), such as Dover sole, sablefish, and rockfish (Table 2), can withstand many years of poor recruitment by taking the substantial advantage of interannual variability that periodically favours good recruitment. These demersal species might be able to move offshore to deeper waters to preferred thermal habitats, if other conditions (e.g. dissolved oxygen) are suitable. Finally, salmonid strategists, such as Chinook salmon, would have additional impacts in their freshwater environments. Warmer freshwater temperatures and decreased flows in summer and autumn will reduce juvenile survival, survival of migrating adults, and egg deposition. Warmer water temperatures will increase fry-to-smolt mortality, at the same time increasing the severity and frequency of winter floods, thereby reducing the egg-to-fry survival rate. Early marine and growth-based mortality will become more variable and extreme. We also hypothesized that the biomass and abundance of cool-water seabirds, such as alcids and shearwaters, will decrease (Table 2, Figure 9). Marine mammals will initially respond with plasticity in diet (switching to alternative prey) and movement corresponding to prey availability (Table 2). Eventually, the quality of prey items will affect the pup and calf survival rate. Prolonged starvation, or diet composed of lower-quality prey, will eventually result in the

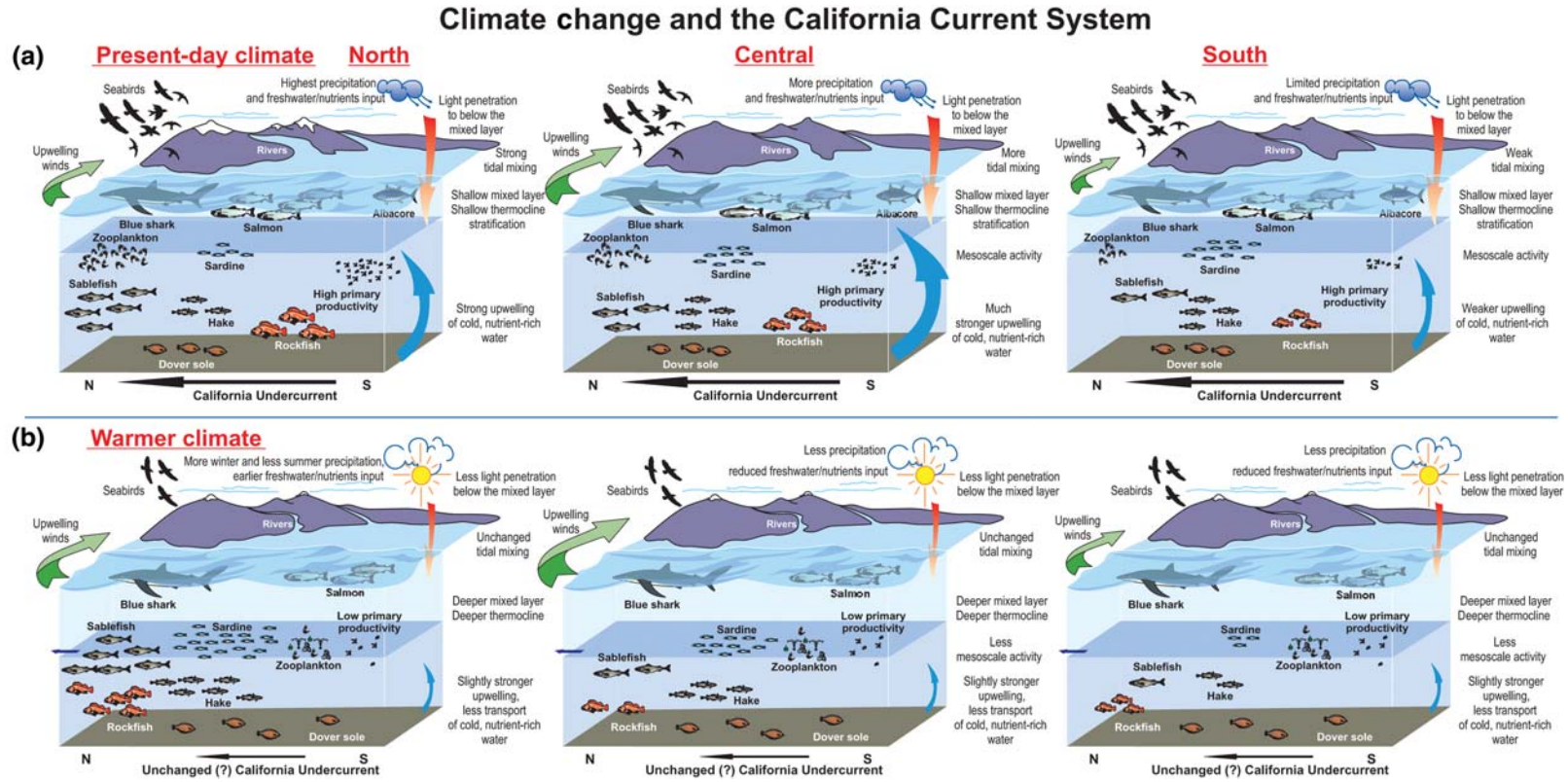


Figure 9. Schematic representations of the current climate and ecosystem conditions (a) of the three regions of the CCS (north, central, and south). Under the empirical data scenarios developed here, forecast climate and ecosystem conditions (b) would be represented with warmer surface waters; increased upwelling-favourable winds; a deepening thermocline; increased coastal stratification that may counteract upwelling and reduce nutrient enrichment and lower primary productivity. This scenario is associated with changes in distribution, northwards or inshore, of species such as Pacific sardine, Pacific hake, blue shark, and albacore tuna. Poor freshwater conditions and early marine survival may decrease Chinook salmon abundance. Long-lived, highly fecund species, such as Dover sole, sablefish, and rockfish may be able to withstand prolonged periods of poor recruitment, which coupled with northward shift in distribution, may result in higher biomass in the northern region. However, seabirds may exhibit a decline in abundance because of poor hatchling survival.

metabolizing of fat-stored toxins and disruption of endocrine, reproductive, and immune systems.

One of the most important outcomes of this process was the dialogue between fishery scientists and the physical oceanographers and climatologists. This allowed for clearer formulation of potential links between the biology and the physics of the CCS and identification of challenges involved when attempting to forecast ecosystem state quantitatively. One clear challenge that emerged was that many of the recurring physical features in conceptual pathways of the fish species (see Table 2 and Supplementary Tables S1–S5, and depicted in Figure 9) could not be projected at appropriate spatial scales by GCMs. However, the pathway tables offer climatologists and physical oceanographers a basis for analysing climate change impacts on population dynamics once outputs from higher-resolution models become available.

Clearly, any forecast has a degree of uncertainty. In our study, two aspects contribute to uncertainty: the uncertainty in the physical prediction from climate model projections; and the uncertainty of our ecological scenarios from the species' conceptual pathways. Uncertainty of GCM projections has been discussed in the literature and its treatment is beyond the scope of this paper. Any future research that attempts to treat species' responses quantitatively should address uncertainty in community-scale interactions, such as competition, predation, and spatio-temporal mismatches with the climate-driven changes proposed here. Meeting that challenge may begin with tools, such as foodweb models of the CCS. Finally, we have essentially ignored the demands of fisheries that rely on these species and related impacts that fisheries in turn will have on the stocks. If climate change results in substantial changes in patterns of recruitment, distribution, growth, and production, fishery management will clearly have to adjust therefore to maintain sustainable catch rates.

With the increased awareness of and interest in understanding climate change impacts, forecasting ecosystem and species status have become the central focus of many research initiatives. Although this is an important activity, an awareness of the limitations of current tools available is essential. To continue to make progress towards forecasting biological status under climate change scenario, robust dialogue between biologists, oceanographers, and climatologist will be important. This effort highlights some of the challenges involved in achieving biological forecasts given the current state of our science and the value of true dialogue between disciplines.

Supplementary material

The following supplementary material is available at *ICESJMS* online. Table S1: Conceptual pathways linking physical features and productivity processes to Pacific sardine biology and population dynamics; Table S2: Conceptual pathways linking physical features and productivity processes to Dover sole biology and population dynamics; Table S3: Conceptual pathways linking physical features and productivity processes to blue shark biology and population dynamics; Table S4: Conceptual pathways linking physical features and productivity processes to chinook salmon biology and population dynamics; Table S5: Conceptual pathways linking physical features and productivity processes to Pacific hake biology and population dynamics.

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