Climate-induced primary productivity change and fishing impacts on the Central North Pacific ecosystem and Hawaii-based pelagic longline fishery

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Abstract An existing Ecopath with Ecosim (EwE) model for the Central North Pacific was updated and modified to focus on the area used by the Hawaii-based pelagic longline fishery. The EwE model was combined with output from a coupled NOAA Geophysical Fluid Dynamics Laboratory climate and biogeochemical model to investigate the likely ecosystem impacts of fishing and climate-induced primary productivity changes. Four simulations were conducted based on 2 fishing effort and climate scenarios from 2010 to 2100. Modeled small and large phytoplankton biomass decreased by 10 % and 20 % respectively, resulting in a 10 % decline in the total biomass of all higher trophic level groups combined. Climate impacts also affected the Hawaii longline fishery, with a 25-29 % reduction in modeled target species yield. Climate impacts on the ecosystem and the fishery were partially mitigated by a drop in fishing effort. Scenarios with a 50 % reduction in fishing effort partially restored longline target species yield to current levels, and decreased longline nontarget species yield. These model results suggest that a further reduction in fishery landings mortality over time than the 2010 level may be necessary to mitigate climate impacts and help sustain yields of commercially preferred fish species targeted by the Hawaii longline fishery through the 21st century.

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1 Introduction

The Central North Pacific Ocean is an important ecosystem and a valuable area for a number of fishing fleets, including the Hawaii-based pelagic longline fishery. In recent decades, the Central North Pacific (CNP) has appeared to undergo changes in its environment and ecosystem composition and function due to both anthropogenic and natural forcing (Kitchell et al. 2002; Polovina et al. 2008, 2009). More than 50 years of fishing pressure have led to observed decreases in apex predators and corresponding increases in fastergrowing prey species (Cox et al. 2002; Essington et al. 2002; Polovina et al. 2009). While there is debate on the magnitude of apex predator removals from fishing (Myers and Worm 2003; Sibert et al. 2006), there is agreement on the importance of managing and rebuilding fish stocks (Worm et al. 2009) and understanding possible effects of fishing pressure and climate change on the ecosystem (Polovina et al. 2008, 2009). In the face of these changes, a growing number of calls have been issued to develop ecosystem-based approaches to fisheries management (Ruckelshaus et al. 2008; Tallis et al. 2009; Link et al. 2011). Unlike traditional management approaches that focus on single species, activities, or concerns, ecosystem-based management considers cumulative natural and anthropogenic impacts on different species or sectors to maintain healthy, productive and resilient ecosystems (McLeod et al. 2005). This approach requires tools that can synthesize and combine data from models, in-situ studies, and single-species stock assessments into a larger framework to understand dynamics at the ecosystem level.

Ecopath with Ecosim (EwE) is a modeling software used worldwide as a tool to understand system dynamics and 'visualize' responses of an ecosystem to human and naturally induced pressures (Christensen et al. 2009). The EwE framework has been used for hindcasting to understand historic fishing pressure in the North Pacific Ocean (Cox et al. 2002; Essington 2006), and also for future projections to recognize the likely impacts of climate change and fishing pressure on ecosystems (Griffiths et al. 2010). From an ecosystem standpoint, it is important to understand the potential combined effects from top-down fishing pressure and possible bottom-up variations introduced by climate change to select effective and sustainable management strategies for the future.

The goal of the present study was to use the EwE framework to explore the effects of climate change (i.e., changes in primary productivity) and fishing pressure over time on the CNP ecosystem. Previous studies have used similar model simulations to explore possible individual and combined climate effects within different ecosystems in the Eastern Tropical and Northeast Pacific Ocean (Watters et al. 2003; Ainsworth et al. 2011), and the coastal regions around Australia (Brown et al. 2010; Griffith et al. 2011), and elsewhere (Mackinson et al. 2009). For this study, an existing EwE model of the CNP (Kitchell et al. 1999; Cox et al. 2002) was updated and combined with climate model outputs to create four scenarios with varying fishing and climate pressures from 1991 to 2100. This experimental design is similar to recent studies that have combined climate model outputs with ecosystem models (Watters et al. 2003; Griffith et al. 2011), yet our study design differs from previous work in two distinct ways. First, we used the output from a coupled physical-biological climate model to directly represent the changes in biomass of two phytoplankton size classes through 2100. Second, to our knowledge such model analysis has not been performed for the area of the CNP used extensively by the Hawaii-based pelagic longline fishery. Results from these model runs were used to understand how climate-induced phytoplankton biomass changes and top-down fishing pressure might affect CNP ecosystem structure, biomass of target and non-target species, and what impacts these pressures may have on the yields by the Hawaii-based pelagic longline fleet through the remainder of the 21st century.

2 Methods

The following sections contain a synopsis of the methods used to obtain the EwE model input data and scenarios developed in this study. A more detailed description of data sources, as well as results and discussion of the Ecopath model and baseline Ecosim scenario are available in the electronic supplemental material (ESM).

2.1 Ecosystem boundaries and study area

This study focused on the area of the CNP used by the Hawaii-based pelagic longline fishery (hereafter referred to as Hawaii longline; from 170°E to 150°W and 10° to 40°N (Fig. 1)). Specifically, we subset the larger study area used by Kitchell et al. (2002) and Cox et al. (2002). Our Hawaii Longline Fishing Grounds model (HLFG1) covered a surface area of 13,275,700 km² encompassing the region where more than 95 % of the Hawaii longline sets occur. This static area estimate was used to convert biomass estimates to biomass per area units, as required by Ecopath.

2.2 Ecosystem modeling approach and initialization

The HLFG1 ecosystem model was built using EwE version 6.2.0.714 (Christensen and Walters 2004; Christensen et al. 2008). The Ecopath (snapshot in time) with Ecosim (dynamic simulations) approach and underlying equations are well documented (Walters et al. 1997; Pauly et al. 2000; Christensen and Walters 2004). The HLFG1 Ecopath model contained 28 functional groups (ESM Table 1) and was parameterized to represent the annual average situation of this region in 1991, which was the first available year for logbook information for the Hawaii longline. The biological parameters required by Ecopath for each functional group (diet; biomass (B); production to biomass (P/B); consumption to biomass (Q/B); and an "ecotrophic efficiency" term (EE), representing production consumed within the system or removed by fishers) were obtained from field studies, stock assessments, fishery data and reports, the literature, and/or FishBase (www.fishbase.org) (see



Fig. 1 Map of the Central North Pacific and model study area. The box represents the model's eastern, western, and southern domain. The lines indicate the position of the GFDL-modeled 17 $^{\circ}$ C sea surface temperature contour used as the dynamic northern boundary for the model domain

ESM for details). All input values were assigned confidence intervals based on the origin of the data using the "Pedigree" routine (Pauly et al. 2000), with interval size relating to the degree of uncertainty in the data sources (e.g., data obtained from field studies versus data obtained from FishBase).

Three fishing fleets were created in Ecopath based on fishing gear type representing the international longline, international purse seine, and US. albacore troll fisheries. The Hawaii longline effort was split according to depth range and target species of the fishery, resulting in shallow (billfish) and deep (tuna) fleets. Catch-and-effort time series for all fleets were constructed for later use in Ecosim from all available years between 1991 and 2010. Only a small fraction of the purse seine fishery operated north of 10°N in our study area. However, recent analyses have attributed declines in adult bigeye biomass landed by longliners to the purse seine fishery (Harley et al. 2009; Davies et al. 2011), which removes small bigeye from the stock before they can reach maturity. To account for this effect, we assigned a purse seine fishing mortality for juvenile tuna species and effort time series based on fishery data from the area south of the HLFG (170°E-150°W, 10°S-10°N).

2.3 Fisheries data

Fisheries data were used to obtain fishing mortality estimates for input into Ecopath, and to construct biomass, catch, and effort time series used in Ecosim. Fisheries catch, effort, and species length/weight information was obtained from several sources depending on the fleet and the country of origin. For the U.S. domestic Hawaii longline, data were obtained from federal logbook information collected by the National Marine Fisheries Service (NMFS) Pacific Islands Fisheries Science Center (PIFSC) Fisheries Research and Monitoring Division. U.S. albacore troll fishery data were obtained from the NMFS Southwest Fisheries Science Center (SWFSC). Non-confidential international longline and purse seine fishery data were obtained from the Secretariat of the Pacific Community (SPC) Ocean Fisheries Programme.

Biomass time series were constructed from the most recent available stock assessments (ESM Table 1). Only stock assessment estimates from regions overlapping the study area were used. Catch-per-unit effort (CPUE) time series scaled to initial biomass provided by the EwE mass balance analysis (ESM) were used when biomass time series were not available from a stock assessment. For mid-trophic level species (skipjack, mahi mahi, lancetfish, snake mackerel, escolar, opah, and wahoo), nominal CPUE time series were constructed from federally mandated vessel and observer logbook data (as shown in Polovina et al. (2009) for the 1996–2006 period).

2.4 Climate data

Climate-induced changes during the study period were represented by modeled phytoplankton biomass time series as obtained from the NOAA GFDL prototype Earth System Model (ESM2.1) integrated with a biogeochemical model [Tracers of Phytoplankton with Allometric Zooplankton (TOPAZ)]. A complete description of the model initialization, parameters, and outputs is available in Polovina et al. (2011). The TOPAZ model contains four phytoplankton groups based on two size classes. These groups were combined to create one large (>5 μ m) and one small (<5 μ m) class of phytoplankton for input into Ecopath. An annual time series of both phytoplankton groups from 1991 to 2010 was created over the study area. To account for north–south seasonality in the fishery (Howell et al. 2010), a dynamic northern boundary was defined as the geographic location of the 17 °C isotherm, a typical northern limit for the Hawaii longline fishery (Fig. 1 and detailed method description in ESM).

2.5 Ecosim model fitting and sensitivity analysis (1991–2010)

An initial Ecosim scenario (1991–2010) was constructed to fine-tune the model and derive vulnerability parameters. Vulnerability is one of the most important parameters in Ecosim and represents the degree to which a large increase in predator biomass will affect predation mortality of a given prey. Vulnerabilities were computed by fitting the model-estimated biomass to the reference species biomass or CPUE time series using the "Fit to Time Series" tool. The option to maintain consistent vulnerabilities across each predator's arena (i.e., by predator column) was chosen during the fitting process to avoid possible over-parameterization of the model, which could happen by allowing independent vulnerability values for each predator–prey interaction.

The Monte Carlo routine in Ecosim was applied to examine uncertainty in Ecopath input parameters. Confidence intervals for each parameter were increased or decreased from the default values within the Monte Carlo module based on their "Pedigree" as defined in Christensen and Walters (2004). Results from 500 Ecosim simulations (each involving up to several thousand iterations to find a balanced model) were used to construct 95 % confidence intervals for the Ecosim-derived biomass time series.

2.6 Ecosim model scenarios through 2100

Four Ecosim scenarios projected through the year 2100 were constructed based on 2 fishing and 2 climate time series:

- (1). Scenario 1 (F + CC): a "business as usual" fishing scenario with climate change, where fishing effort for all fleets was held constant at 2010 effort levels through 2100, and Ecosim-derived small and large phytoplankton values were replaced with the GFDL model-based phytoplankton values to represent climate change.
- (2). Scenario 2 (F): the "business as usual" fishing scenario as above, but where the first 20 years of GFDL data (1991–2010) were repeated through 2100 to represent a continuation of 1991–2010 climate conditions into the future (i.e., no climate induced changes in productivity).
- (3). Scenario 3 (0.5F + CC): the climate time series as in (1) but with a 50 % reduction in fishing effort from 2010 levels for all fleets.
- (4). Scenario 4 (0.5F): a climate time series as in (2) coupled with a 50 % reduction in fishing effort from 2010 levels for all fleets.

All four scenarios were run to obtain biomass and catch estimates for all functional groups. Ecological indicators were calculated to understand possible changes in ecosystem structure over time from top-down and bottom-up pressures (Fulton et al. 2005; Shin et al. 2010). These indicators included the total ecosystem biomass, ecosystem biomass diversity (using the Kempton's Q index derived from the Ecopath Network Analysis Plugin), and the ratio of high trophic level species in the fishing yield to the total yield. The total ecosystem biomass and diversity indices represent ecosystem characteristics that are most visible and readily identified by interested sectors of society, namely what trophic groups comprise the ecosystem and how much of each group is available. The ratio of higher trophic level species in the catch is of importance to fishery managers to monitor changes in landings of commercially preferred higher-trophic level fish.

3 Results

3.1 Initial Ecopath and Ecosim (1991–2010) model fits

The final HLFG1 Ecopath model was balanced with only minor adjustments (<5 %) to input parameters (see ESM Table 1). Primary producers represented 23 % of the total biomass, while apex predators (e.g., sharks, tunas, and billfish) accounted for less than 1 % of total biomass. ESM Figure 1 illustrates the food web and trophic flows for the HLFG1 model, with major trophic pathways through either the invertebrate or epi-fish groups.

The initial Ecosim model fit was satisfactory for mid-trophic and apex functional groups (ESM Figs. 2a–h). The model captured a previously reported decline in tuna and billfish species, and concurrent rise in blue sharks and mid-trophic level species (Kleiber et al. 2009; Polovina et al. 2009). Additionally, modeled catch for the Hawaii longline fit the reported landings from federal logbooks for the year 2010 ($r^2=0.99$, p<0.01). The 95 % confidence intervals constructed using the Monte Carlo routine showed that modeled predictions for most species were not towards either extreme of the simulation's 500 runs (ESM Figs. 2a–h).

3.2 TOPAZ model climate trends

The SST output showed a 300–400 km northern shift in the average 17 °C isotherm latitudinal position from the period 1991–2010 to 2080–2100 (Fig. 1). TOPAZ-derived small and large phytoplankton biomass trends were negative over time, with sharper declines during the initial 40-year period and from 2060 to 2100 (Fig. 2a). Biomass of the small phytoplankton class remained an order of magnitude greater than the large phytoplankton class throughout the time series, yet the ratio between small and large classes decreased sharply after 2050 (Fig. 2a). Overall, by the end of the 21st century, model results showed a 10 % and 22 % reduction in the small and large phytoplankton biomass from the average 1991–2010 values, respectively (Fig. 2a).

3.3 Ecosim scenarios (1991–2100)

The impacts of bottom-up climate forcing and top-down fishing pressure were seen across many dimensions of the ecosystem, with clear interactions between these effects. Bottom-up climate forcing was observed across all ecosystem groups, with 7–20 % declines in biomass levels for autotroph, heterotroph, small fish, and mollusk groups by 2100 (Fig. 2c). Modeled biomass and catches by the Hawaii longline were pooled into 2 subgroupings to represent longline target (bigeve, yellowfin, albacore tuna, and all billfish groups including swordfish) and non-target species (skipjack tuna, all sharks, and mid-trophic level fish as defined above) (ESM Table 1). Note that the non-target category includes skipjack tuna, the mainstay of the purse seine fishery. Tuna and billfish groups responded similarly to climate and fishing effects, with biomass declines due to climate change and fishing pressure, and biomass increases under reduced fishing pressure and when climate change was removed. The non-target shark and mid-trophic level fish groups both registered increases under "business as usual" fishing pressure, and biomass declines under a reduced fishing scenario. Fishing pressure had a larger effect than climate on biomass for both of these groups, yet climate had an equal or greater effect on target species yield, with a



Fig. 2 a GFDL TOPAZ model large (*grey*) and small (*black*) phytoplankton time series from 1991 to 2100, **b** total biomass estimates from the four fishing and climate Ecosim scenarios, and **c**) model-estimated average biomass values of trophic groups from the four model scenarios during the period 2080–2100 period relative to their average 1991–2010 values

projected 26–29 % decline by 2100 (Table 1, Fig. 3a–b). Both shark and mid-trophic level fish groups responded to a 50 % reduction in fishing pressure, with a large decrease in non-target yield, including the yield most important to the purse seine fishery. There were corresponding increases in longline target species yield equal to the loss by climate change, or enough to bring the yield level up to 90 % of that during the 1991–2010 period in the absence of climate change (Table 1, Fig. 3a–b).

Overall, fishing pressure had a greater impact on higher trophic levels, yet these groups represented less than 5 % of the total ecosystem biomass. Bottom-up forcing as a result of climate-induced changes in primary productivity had a direct effect on lower trophic levels, and tended to exacerbate top-down forcing effects in the model (e.g., species diversity, and tuna biomass). Scenarios including climate change showed

% change from 1991-2010 within scenario			Biomass		Yield	
			2050	2100	2050	2100
	Group	Scenario	%	%	%	%
	Target ^a	F + CC	-39.6	-49.4	-43.9	-61.8
		F	-31.9	-36.3	-30.6	-32.4
		0.5F + CC	26.0	2.6	-20.7	-35.1
		0.5F	41.5	35.9	-9.1	-9.4
	Non-target ^b	F + CC	51.4	41.5	58.2	44.8
		F	62.3	61.1	71.0	73.5
		0.5F + CC	-55.5	-47.2	-67.0	-67.0
		0.5F	-58.1	-56.4	-66.1	-66.1
% change between scenarios			$\Delta Biomass$	5	Δ Yield	
			2050	2100	2050	2100
Effect						
Lineet	Group	Scenario Change	%	%	%	%
Climate	Group Target	Scenario Change F to F + CC	% -7.7	% -13.1	% -13.2	% -29.4
Climate	Group Target	Scenario Change F to F + CC 0.5F to 0.5F + CC	% -7.7 -15.4	% -13.1 -33.4	% -13.2 -11.6	% -29.4 -25.6
Climate	Group Target Non-target	Scenario Change F to F + CC 0.5F to 0.5F + CC F to F + CC	% -7.7 -15.4 -11.0	% -13.1 -33.4 -19.5	% -13.2 -11.6 -12.9	% -29.4 -25.6 -28.7
Climate	Group Target Non-target	Scenario Change F to F + CC 0.5F to $0.5F$ + CC F to F + CC 0.5F to $0.5F$ + CC	% -7.7 -15.4 -11.0 2.7	% -13.1 -33.4 -19.5 9.2	% -13.2 -11.6 -12.9 -1.0	% -29.4 -25.6 -28.7 -0.9
Climate	Group Target Non-target Target	Scenario Change F to F + CC 0.5F to $0.5F$ + CC F to F + CC 0.5F to $0.5F$ + CC F + CC to $0.5F$ + CC	% -7.7 -15.4 -11.0 2.7 65.6	% -13.1 -33.4 -19.5 9.2 52.0	% -13.2 -11.6 -12.9 -1.0 23.2	% -29.4 -25.6 -28.7 -0.9 26.7
Climate	Group Target Non-target Target	Scenario Change F to F + CC 0.5F to $0.5F$ + CC F to F + CC 0.5F to $0.5F$ + CC F + CC to $0.5F$ + CC F to $0.5F$	% -7.7 -15.4 -11.0 2.7 65.6 73.3	% -13.1 -33.4 -19.5 9.2 52.0 72.3	% -13.2 -11.6 -12.9 -1.0 23.2 21.5	% -29.4 -25.6 -28.7 -0.9 26.7 22.9
Climate	Group Target Non-target Target Bycatch	Scenario Change F to F + CC 0.5F to $0.5F$ + CC F to F + CC 0.5F to $0.5F$ + CC F + CC to $0.5F$ + CC F to $0.5F$ F to $0.5F$ F + CC to $0.5F$ + CC	% -7.7 -15.4 -11.0 2.7 65.6 73.3 -106.8	% -13.1 -33.4 -19.5 9.2 52.0 72.3 -88.7	% -13.2 -11.6 -12.9 -1.0 23.2 21.5 -125.2	% -29.4 -25.6 -28.7 -0.9 26.7 22.9 -111.8
Climate	Group Target Non-target Target Bycatch	Scenario Change F to F + CC 0.5F to $0.5F$ + CC F to F + CC 0.5F to $0.5F$ + CC F + CC to $0.5F$ + CC F to $0.5F$ F + CC to $0.5F$ + CC F to $0.5F$ F + CC to $0.5F$ + CC F to $0.5F$	% -7.7 -15.4 -11.0 2.7 65.6 73.3 -106.8 -120.5	% -13.1 -33.4 -19.5 9.2 52.0 72.3 -88.7 -117.5	% -13.2 -11.6 -12.9 -1.0 23.2 21.5 -125.2 -137.1	% -29.4 -25.6 -28.7 -0.9 26.7 22.9 -111.8 -139.6

 Table 1
 Effects of climate and fishing pressures on target and non-target species model biomass and Hawaii

 longline fishery yield in 2050, and 2100, relative to the average 1991–2010 period

^a Target species include the Swordfish, Blue Marlin, Striped Marlin, other billfish, Bigeye, Yellowfin, and Albacore Ecopath groups

^b Non-target species include the Blue shark, other shark, Skipjack, Mahi mahi, Lancetfish, and Mid-trophic level fish Ecopath groups

a 10–20 % reduction in phytoplankton, equivalent to a 10 % decrease in total ecosystem biomass. This was largely based on declines in lower trophic levels, accounting for more than 90 % of total biomass. Mid-trophic level species were the most variable across runs, being affected by both bottom-up and top-down forcing. Scenarios with no reduction in fishing pressure saw major changes in biomass, shifting the apex species in the ecosystem from tunas and billfish to sharks and mid-trophic level fish species, with additional biomass declines from climate change. Observed changes in billfish biomass were mainly driven by fishing pressure on swordfish and striped marlin, with blue marlin and other billfish biomass steadily declining over time due to prey biomass reduction from bottom-up climate forcing.

3.4 Ecosystem indicators

Ecosystem indicators were plotted for each model scenario to summarize changes in total ecosystem biomass, ecosystem biomass diversity, and commercially preferred fishing yields across the 4 scenarios (Fig. 3c). "Total biomass", which included the phytoplankton groups, primarily captured the bottom-up climate forcing on the high



Fig. 3 Model-estimated fishing yields by the Hawaii longline fishery for target (**a**) and non-target (**b**) species. *Dashed lines* represent scenarios with climate change effects removed, while colors represent scenarios with business as usual (*black*) or reduced (*grey*) fishing. The *shaded areas* represent the change in fishing yield from climate change effects. **c** Percent change in the model's ecosystem indicators during the 2080–2100 period relative to the 1991–2010 period

biomass, lower trophic level groups in the ecosystem. Climate change led to an overall 10 % drop in biomass by 2100 (Fig. 3c). Fishing impacts on total biomass were negligible, with only a slight increase in the indicator under a reduced fishing scenario. The ecosystem "biomass diversity" indicator represented changes in the midand higher-trophic level groups and responded to both top-down fishing and bottomup climate effects. Biomass diversity declined in the "business as usual" fishing scenario and increased in the reduced fishing scenario. "Percentage of high trophic level species in the catch" primarily captured the top-down fishing effects on the ecosystem. Climate effects were not observed, yet a 50 % reduction in fishing pressure resulted in a 53 % increase in this indicator, yielding a greater percentage of high trophic level species in the catch relative to the 1991–2010 period (Fig. 3c).

4 Discussion

4.1 Ecosystem responses to fishing pressure and climate change scenarios

Results from the 4 scenarios provided insights into the effects of climate and fishing, individually and together, on the HLFG ecosystem from 2010 to 2100. The effects of fishing pressure were observed from the higher trophic levels in the ecosystem down through the mollusk groups. This is not surprising, as intensive fishing pressure may lead to large-scale restructuring of communities (Fulton et al. 2005). Tuna groups reacted to changes in fishing pressure across scenarios, with simulations suggesting that they can adapt to increased prey availability from mid and lower trophic levels in scenarios without climate change. As tunas were modeled as multi-stanza groups, any climate-related changes in the lower trophic level juveniles propagated up to the adult groups. In reduced fishing scenarios with climate, tuna species biomass declined gradually over time until 2060, when the declining biomass trend accentuated. This declining trend in biomass by the end of the 21st century was also found in a coupled ecosystem-population dynamics and climate modeling results for bigeye tuna in the Pacific Ocean (Lehodey et al. 2010). Despite differences in study methodologies, their results indicated that climate impacts could be seen in high trophic level tuna species. Topdown and bottom-up effects were also observed in billfish biomass across our scenarios. Both swordfish and striped marlin were able to take advantage of prey increases under the reduced fishing scenario with no climate change, yet only swordfish biomass followed the trajectory of increased prey in the "business as usual" scenario as fishing pressure continued to have a stronger impact on the striped marlin stock.

Fishing pressure strongly affected the shark and mid-trophic level fish groups, both increasing under static fishing pressure and decreasing in the 0.5F scenarios. This increase in biomass of mid-trophic level fish is in agreement with reported and hypothesized changes from higher fishing pressure (Kitchell et al. 2002; Polovina et al. 2009). However, the decrease in the biomass of sharks under a reduced fishing scenario does not concur with previously reported ecosystem responses for this region. For example, in their model baseline scenario of the CNP ecosystem, Kitchell et al. (2002) report that a doubling of fishing effort results in a 50 % reduction of shark biomass in 10–15 years. However, banning shark finning in the baseline scenario resulted in a strong positive shark biomass response. While these increases did not completely counter the biomass loss due to increased fishing, it implies that there are compounding fishing pressures on the shark groups in this ecosystem. Currently, there is a prohibition of finning by all persons under U.S. jurisdiction. Recent reports, including the latest stock assessment, indicate that blue shark biomass has been increasing due to a possible recovery of the species from previously high fishing mortality (Sibert et al. 2006; Kleiber et al. 2009). However, the latest assessment also states that there is a large degree of uncertainty associated with the findings based on poor reporting of the catch, and some probability in the assessment that overfishing may be occurring. Based on data limitations through the time series, shark finning was not included in the HLFG1 model. Although this omission results in some uncertainty around the shark biomass estimates used, the assessment findings support the increasing trend in shark biomass during the 1991–2010 period used to fit the model.

The observed trend in shark biomass may also be linked to the proportion of mid-trophic level fish in the diet of the shark groups. While initially the mid-trophic level group only accounted for a small percentage of the sharks' diet (5 %), this grew to 15 % by simulations' end, tracking the increase in mid-trophic level fish biomass. Tuna, not sharks, had the greatest impact on mid-trophic level fish through competition and predation. Detailed

studies on sharks' diet may help refine future predictions of the impacts of changes in climate and fishing pressure on these species.

4.2 Fishing and climate change impacts on HLFG fishing yield

Modeled declines in target species catch by the Hawaii longline, especially bigeye tuna, are not unexpected. A recent stock assessment of the species reports that achievement of a sustainable fishing mortality would require up to a 39 % reduction from 2006 to 2009 levels (Davies et al. 2011). The assessment also concludes that greater overall yields could be obtained by reducing the mortality on small bigeye individuals taken as bycatch in the purse seine fleets targeting primarily skipjack and yellowfin tuna (Davies et al. 2011). The purse seine fleet is effectively removing potential adult bigeye from the ecosystem before they reach maturity and lowering the species' maximum sustainable yield (MSY). Less adult bigeye in the ecosystem could cause longline fleets in the CNP region to catch younger, smaller bigeye tuna, further decreasing bigeye MSY.

In the WCPO region, the Western and Central Pacific Fisheries Commission (WCPFC) adopted Conservation and Management Measure (CMM) 2008-001 for both bigeye and yellowfin tuna to reduce fishing mortality to levels that could sustain these stocks through time (WCPFC 2008). CMM 2010–01 was also adopted to attempt to reduce total catches of North Pacific striped marlin in response to concerns that the species is subject to unsustainable fishing mortality (WCPFC 2010). These management measures were based on singles species assessments and represent a balance struck by managers to sustain fish stocks and fisheries in the region, including both longline and purse seine. CMM 2008-001 was put into full effect by the end of 2010, the year used for the "business as usual" fishing scenarios, and the F scenarios represent the fishery under current management. However, the F scenarios showed overall declines in target species biomass of around 60 % by the end of the 21st century, with increases of ~45-74 % in non-target species. Even a 50 % reduction in fishing effort led to a $\sim 10-35$ % decline in target species, with a corresponding decline in non-target species. The HLFG1 model results indicate that a further reduction in fishing mortality may be necessary, especially under a climate change regime, which alone may lead to a 25–29 % decline in longline target species' yield. This decline in longline target species has been predicted in another ecosystem study investigating possible climate impacts. Using the GFDL phytoplankton data combined with a size-based ecosystem modeling approach, Woodworth-Jefcoats et al. (In review) reported a 19 % decrease in the yield of large fish by 2100 in the North Pacific Subtropical Gyre.

Compounding these catch trends is the possible shift in fish habitat as a result of climate change. The modeled 300–400 km shift in the 17 °C northern boundary of the study area would force fishers to travel farther either to target swordfish at more distant frontal zones or to track bigeye tuna that are less densely populated in an expanded habitat. These modeled catch losses would have a large impact on supply and income generated from fish caught in the HLFG region and exported worldwide. This includes bigeye tuna, the highest priced tropical Pacific tuna on the sashimi market. For example, in 2009, the domestic Hawaii pelagic fisheries landed 12.3 thousand tonnes of pelagic fish, valued at \$67 million, largely from the Hawaii longline fishery (WPRFMC 2010). If the simple assumption is made that target fish supply were to decrease, but demand to stay constant, economic theory states that this would most likely lead to higher prices and lower quantity. One alternative could be to supplant higher trophic level catch with the faster turnover mid-trophic level fish. While certain species, including skipjack tuna, mahi mahi, wahoo, and opah are commercially viable, others, such as lancetfish and snake mackerel, are smaller, less palatable, and less

robust to capture and storage. Some current fisheries (purse seine) do exploit more midtrophic species. For longline fishery, the current market demand and ecological implications of such a scenario make this a more problematic outcome. Current levels of fishing mortality still appear high based on the results of this study, especially when climate impacts are considered. Based on modeling results, a further reduction in fishing mortality may be necessary to mitigate climate impacts, and to help sustain longline yields of commercially preferred fish species. While there is uncertainty in the magnitude of the long-term impacts of climate change on fisheries, future fisheries will certainly depend on progress made in the next few years in reducing current levels of fishing mortality and mitigating climate impacts (Brander 2010). This will necessitate continued diligence in management of commercial fish stocks and continued monitoring of fisheries and ecosystems. Increased information in these areas would allow refinement of ecosystem models such as the one developed in this study, which could be used to better inform fishery managers of possible climate effects on the ecosystem.

4.3 Model caveats, uncertainty, and future directions

The coupling of a multi-species model such as EwE with output from a climate model is appealing, and has been used in several studies (Watters et al. 2003; Brown et al. 2010; Ainsworth et al. 2011). However, there are important caveats and sources of uncertainty, including uncertainty in the coupled climate-biogeochemical TOPAZ model output, a lack of feedback between the TOPAZ and ecosystem models, and a lack of spatial structure in the ecosystem model warrant discussion. The TOPAZ model captures the magnitude of the north–south phytoplankton gradient in the North Pacific fairly well, but tends to shift the subtropical gyre boundary to the south in the western and central basins (Rykaczewski and Dunne 2010). We have attempted to address this by setting a dynamic northern boundary to the model, yet there still may be an overestimation of phytoplankton groups, especially large phytoplankton, in the northern region of the model. Additionally, we have only used the output from one climate model. Future work may hopefully take advantage of advances in climate modeling and use a suite of climate-driven phytoplankton estimates to decrease uncertainty in time series of primary production.

While integration of climate data into the model was straightforward in this application, paying attention to specific modeling aspects may improve the methodology in the future. While monthly phytoplankton information was available from TOPAZ, we used an annual time step in the EwE scenarios. This was done based on high intra-annual variability in lower trophic level groups in initial Ecosim simulations. The use of an annual time series removed this variability while maintaining long-term trends in the results. An annual time step was sufficient for this study, but model applications covering a shorter time domain may benefit from the ability to use a monthly time increment. Additionally, while the climate data could be used to replace the EwE biomass in the scenarios, there is no feedback from EwE back to the climate data. Future studies may benefit from bidirectional feedback between the models.

A final caveat is the lack of spatial structure within the EwE model framework. Habitat range movements (i.e. "range shifts"), either horizontally towards the poles and/or vertically by depth have been documented across numerous wildlife and fish species (Parmesan and Yohe 2003; Perry et al. 2005). Range shifts have also been identified as an important aspect of climate change in a similar analysis for the Northeast Pacific (Ainsworth et al. 2011). The use of a shifting northern boundary within the model attempts to address such movements by moving the northern limit of fisheries through time, yet future work could expand on the

current model by including an internal spatial component. A future study could investigate the importance of range shifts under climatic change by expanding the model to include the Ecospace model framework (Christensen and Walters 2004).

While there are associated caveats and uncertainty with models such as those discussed here, their results are intended to complement, and not replace traditional methods (e.g., stock assessment) to assist in policy decision making through an increased understanding of ecosystem structure and functioning (Pláganyi and Butterworth 2004). It is the combination of traditional methods and ecosystem modeling, along with efficient and regular ecosystem monitoring that will provide effective near- and long-term understanding and forecasts of ecosystem changes.

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