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Can marine fisheries and aquaculture meet fish demand from a growing human population in a changing climate?

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ABSTRACT

Expansion in the world's human population and economic development will increase future demand for fish products. As global fisheries yield is constrained by ecosystems productivity and management effectiveness, *per capita* fish consumption can only be maintained or increased if aquaculture makes an increasing contribution to the volume and stability of global fish supplies. Here, we use predictions of changes in global and regional climate (according to IPCC emissions scenario A1B), marine ecosystem and fisheries production estimates from high resolution regional models, human population size estimates from United Nations prospects, fishmeal and oil price estimations, and projections of the technological development in aquaculture feed technology, to investigate the feasibility of sustaining current and increased *per capita* fish consumption rates in 2050. We conclude that meeting current and larger consumption rates is feasible, despite a growing population and the impacts of climate change on potential fisheries production, but only if fish resources are managed sustainably and the animal feeds industry reduces its reliance on wild fish. Ineffective fisheries management and rising fishmeal prices driven by greater demand could, however, compromise future aquaculture production and the availability of fish products.

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1. Introduction

The world's population is projected to reach 9.3B in 2050 according to the medium variant of UN projections (UN, 2010). Fish is a key source of protein, essential amino-acids and minerals, especially in low-income, food-deficit countries (Easterling, 2007; FAO, 2009, 2010; Rice and Garcia, 2011). The extent to which marine fisheries and aquaculture will be able to provide fish for the population in the future will depend, in part, on climate-driven changes in ecosystems productivity (Brander, 2007; Cheung et al., 2009a,b), the performance of fisheries management (Rice and Garcia, 2011) and on the capacity to expand aquaculture while reducing its environmental impact (Naylor et al., 2009).

The maximum potential fish production from current marine fisheries is estimated to be around 80 Mt per year (FAO, 2010). Around two-thirds of global fisheries production is consumed directly by humans and a third is processed to produce fishmeal and fish oils as feed for aquaculture and livestock industries (Naylor et al., 2000, 2009; Smith et al., 2011). Climate change is expected to change future fisheries production patterns, either by shifting production as species move to new habitats (Cheung et al., 2009a,b) or as a result of changes in the net marine primary production (Brander, 2007; Cheung et al., 2009b). In the first part of this study we investigate the differences in catch potential by 2050, as driven by climate (A1B SRES scenario, Nakicenovic and Swart (2000)), biochemical and ecological models in 69 marine Exclusive Economic Zones (EEZ). These EEZ cover 30 Large Marine Ecosystems (LME, www.seaaroundus.org), and currently account for over 60% of the world's marine fisheries catch. Specifically, we will estimate catch potential for large fish (direct consumption)

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and for small low trophic level fish, which are generally used to produce fishmeal and fish oil (Smith et al., 2011).

Aquaculture growth has averaged 8% per year since the late 1970s (faster than human population growth), bringing fish production to a total of 142 Mt in 2008 (FAO, 2010; Hall et al., 2010). About 115Mt are currently directed to human use, providing an estimated *per capita* supply of about 17 kg person^{-1} yr^{-1}, an all time high (FAO, 2010). However, aquaculture growth has relied heavily on fishmeal and fish oil. Fishmeal is an internationally traded, high protein powder, which results from the industrial processing of small pelagic fish (e.g. anchovy, sardine, capelin, herring). It is a key component of the aquafeed of salmon, trout, shrimp and other farmed marine species (Naylor et al., 2009), supplying essential amino acids, fatty acids and other micronutrients (Tacon and Metian, 2008). At lower inclusion rates, it is also used as feed to culture freshwater, non-carnivorous species, such as carps and tilapias (Tacon and Metian, 2008). Given the limited supply of fishmeal and oil from wild catches, the efficient use and sharing of these products is a major issue for the aquaculture industry (Kaushik and Troell, 2010; Tacon and Metian, 2009). The Fish In-Fish Out ratio (FIFO) is the efficiency at which aquaculture converts a weight-equivalent unit of wild fish into a unit of cultured fish. Currently, aquaculture converts 65% of the wild fish reduced into fishmeal at a FIFO ratio of between 0.66 (Jackson, 2009; Kaushik and Troell, 2010) and 0.7 (Tacon and Metian, 2008). The share of global fishmeal production used in aquaculture is increasing as other livestock industries (currently consuming 35% of fishmeal) have replaced fishmeal from their feeds (Jackson, 2009). Aquaculture expansion and market volatility have driven a consistent rise of fishmeal and fish oil price in international markets (Merino et al., 2010b), and combined with legislation and environmental fluctuations (Torrisen et al., 2011) have contributed to reduce aquaculture's FIFO rates (Jackson, 2010; Kristofersson and Anderson, 2006; Naylor et al., 2009; Tacon and Metian, 2008). Based on these facts, it is expected that future demand for marine feeds to support aquaculture will be driven by human capacity to reduce even further the dependency of aquaculture on raw material of marine origin (Delgado et al., 2003).

In the second part of this study we investigate how the demand stress that results from the use of fishmeal in aquaculture can eventually jeopardize the sustainable exploitation of the fisheries used to produce it, as most of them are sub-optimally managed (Asche and Tveterås, 2004). To do that, we use a published bioeconomic model of the global production/consumption of fishmeal (Mullon et al., 2009) to investigate how a set of well known aquaculture development scenarios (Delgado et al., 2003) impact the sustainability of the main fisheries used to produce fishmeal. Additionally, we investigate how fishmeal production is responding to the expansion of aquaculture and whether current trends follow any of the proposed future scenario pathways.

Finally, we assess whether global *per capita* fish consumption rates can be maintained or even increased in 2050, taking into account projections of human population growth, a set of fish consumption targets, our own estimates of future marine fisheries potential and projections of current trends in the technological efficiency of aquaculture. In addition, we investigate how global consumption rates translate to national scales, by exploring production and consumption trends in three countries which differ in terms of economic development, population growth, expected climate change impacts and dominant forms of aquaculture.

2. Materials and methods

The impacts of climate change and demand drivers on marine fish and fisheries production were investigated using several numerical models. Production changes in the fishable fraction of the ecosystem were estimated using a validated, coupled physical-ecosystem model (POLCOMS-ERSEM, Blackford et al., 2004; Holt and James, 2006), and a size-based ecosystem model that used the outputs of the previous models (Blanchard et al., 2009, 2011). An existing global bioeconomic model comprising the top fishmeal producing and consuming countries (Mullon et al., 2009) was set up to examine the alternative aquaculture development scenarios proposed by Delgado et al. (2003), and the projected changes in fishmeal production. Details of these models are provided below.

2.1. The coupled physical-ecosystem model

The downscaling simulations of the physical-ecosystem model for the 30 LMEs considered coastal oceans were performed using the POLCOMS hydrodynamic model (Holt and James, 2006), coupled to the ERSEM ecosystem model (Blackford et al., 2004), as part of the Global Ocean Modelling Systems framework, GCOMS (Holt et al., 2009). POLCOMS-ERSEM is a mature modelling system that has been extensively evaluated in the Northwest European Shelf (e.g. Allen et al., 2007; Holt et al., 2005). In this study, the models were employed to set up and run 12 regional models at 1/10° horizontal resolution and 42 vertical layers, with bathymetry derived from the GEBCO 1-arcminute dataset (IOC et al., 2003). These 12 domains cover the 30 LMEs of concern, capturing the main processes driving these coastal and shelf seas. Two time slices were considered using boundary conditions obtained from the Institut Pierre Simon Laplace Climate Model (IPSL-CM4, Marti et al., 2006), run for the 4th IPCC Assessment Report on Climate Change (Solomon et al., 2007): Present day (ca. 2000), and near-future (ca. 2050). The near-future time slice reflected the A1B "business as usual" emissions scenario. The boundary data consisted of wind stress, cloud cover, mean sea level pressure, air temperature, downwelling shortwave, long-wave radiation and freshwater fluxes from the atmospheric component of the IPSL model and temperature, salinity, sea surface elevation and zonal and meridional velocities from the ocean component. For each time slice we run a total of 13 years of simulations, with the final 10 used to capture both the signal as well as natural variability.

2.2. Predicting fisheries production

To predict aggregate fish catches of 69 EEZs, a published size-based marine ecosystem model (Blanchard et al., 2009, 2011) was forced with the output from the POLCOMS-ERSEM simulations (daily mean temperature and daily mean phytoplankton, micro-zooplankton and detritus biomass density). The size-based model can be used to investigate the dynamics of the coupled pelagic-benthic communities under changing levels of productivity and fishing mortality. The dynamical model is comprised of two partial differential equations that predict changes in community abundance at mass through time. These are driven by changes in growth rates (from feeding) and death rates from predation, intrinsic and senescence mortality and fishing mortality (see Appendix B.1). In the "pelagic predator" community, predators feed on prey smaller than themselves and in the "benthic detritivore" community, animals feed on a shared unstructured detritus source (they are not size-selective feeders). The model has also been modified to incorporate temperature effects on the feeding and intrinsic mortality rates of organisms (Jennings et al., 2008; Maury et al., 2007). Overall the model captures the transfer of energy from primary producers and detritus to larger benthic and pelagic consumers and outputs predictions of size-based abundance density, biomass density, production rates and catch rates (when

fishing mortality is included). For this study, only the predicted outputs from the "pelagic predator" community are used, spanning size-ranges that are typically dominated by fish (see below).

The size based model is forced with outputs from the POLCOMS-ERSEM runs at every time step. The plankton size-spectrum was described as $\log N(m) = a + b\log(m)$ where N is abundance density per unit volume at mass, and mass is m (in grams). We estimated a from the total biomass density of phytoplankton and microzooplankton groups from ERSEM output and convert this to numerical density across a realistic size range (10^{-14} to 10^{-4} g) assuming a fixed slope b of -1, in keeping with global empirical studies of phytoplankton size spectra (Barnes et al., 2011). Near sea floor detritus biomass density estimates from ERSEM were used to force the detritus dynamics as opposed to explicitly modelling the flux and recycling of detritus within the communities that arise from egestion (Blanchard et al., 2009, 2011). Therefore, fluxes from egestion to detritus were not included. Temperature output from POLCOMS was used as input to modify the feeding and intrinsic mortality rates. The temperature effect was a multiplier of these rates and was calculated as $\tau = e^{c1-E/(kT)}$, where $c1$ is a constant (25.55 °C), E is the activation energy of metabolism (0.63 eV), T is temperature and k is the Boltzman constant (8.62×10^{-5}). This is similar to the approach used in Jennings et al. (2008).

A range of fishing mortalities from 0 to 1 were tested and it was observed that an $F = 0.8$ resulted in maximum equilibrium catches. Therefore, we used an $F = 0.8$ for all ecosystems, equally distributed across all size-classes. For simplicity, we examined changes in catches from two size classes: (i) 'small' (1.25 g = 5 cm to 80 g = 20 cm) and (ii) 'large' (80 g = 20 cm to 100 kg = 215 cm). Outputs for "small" class were used as a proxy for future small pelagic fisheries potential production and thus fishmeal availability for the top twelve fishmeal producing nations from Merino et al. (2010b). Catches from the "large" size class provided an estimate of fish availability for direct human consumption.

Our approach was cross-validated by comparing estimated small pelagic fisheries catch potential using 1992–2001 climate conditions and the Sea Around Us catch data (www.seaaroundus.org). Results demonstrate that the size based model produces realistic catch estimates (see Appendix A, Figs. A1 and A2).

Further details of the equations driving the dynamical fish model are available in Appendix B.

2.3. The bioeconomic model

A global bioeconomic network model developed by Mullon et al. (2009) was used to investigate how aquaculture development could affect small pelagic fisheries (Merino et al., 2010a,b; Mullon et al., 2009). The model considers the twelve most important fishmeal-producing nations (accounting for more than 80% of the world's production) and the fifteen largest fishmeal and six fish oil consumers. For each producer, the dynamics of its fish stocks, fishing fleets and processing industries are modelled, and a set of export pathways to consumers estimated from trade records. The fishmeal consumers considered (China, Japan, Taiwan, Chile, Peru, UK, Norway, USA, Denmark, Indonesia, South Africa, Canada, Iceland, Morocco and Vietnam), are described by a commodity price function based on demand and supply. The relationship between producer and consumer is thus purely economic. The producer satisfies the demand and obtains an income. This income is then used to change fishing strategies by investing/disinvesting in fishing capacity.

In the biological component of the model, catch depends on the size of the fishing industry and the biological parameters of each of the stocks (intrinsic growth rate r and carrying capacity K) (Schaefer, 1954). Initially, all fish stocks are assumed to be fished at *Maximum Sustainable Yield* (*MSY*) conditions. However, a 20% deviation is included, which allows the fishing industry to increase its yearly catch beyond MSY if there is an economic incentive to do so. The 20% deviation is arbitrary but mimics what Asche and Tveterås (2004) describe as "sub-optimal management". A selection of the key equations driving fish stock dynamics is shown and explained in Appendix B. A sensitivity analysis and broader description of the model can be found in Mullon et al. (2009).

The parameterization of the fishing fleets and markets was based on a previous set up that corresponds to present day conditions (Merino et al., 2010b), which was used to investigate whether aquaculture expansion could, in synergy with environmental variability, jeopardise fisheries sustainability. In this study, the fish stocks population parameters (r and K) and demand parameters were modified. Demand parameters were set according to published scenarios for aquaculture development (Delgado et al., 2003). Biological parameters of the stocks were linked to the size-based model (Section 2.2) as follows: the size-based model provided estimates of maximum sustainable yield (MSY) of the "small" fraction of the fish community under future and present scenarios for each of the top-twelve fishmeal producers (Fig. 1D). We calculated the ratio of future MSY to present MSY. We then used this ratio as a scalar to multiply K in the bioeconomic model. We kept r fixed at a value of 1. The bioeconomic model sets simulated quotas = rK/4, therefore quotas and catch in the bioeconomic model are directly informed by K from the size-based model. It must be noted that our intention was not to obtain accurate numerical outcomes of a single production system, but to compute global differences of alternative market development scenarios.

Predicted trends in human populations were based on UN projections (UN, 2010). These implied that the human population by 2050 would be 6% larger than that assumed in the storyline associated with the A1B emission scenario, where the global population was expected to reach 8.7B by 2050. A preliminary analysis showed that this discrepancy had no qualitative effect on our results.

3. Results

3.1. Capture fisheries production under climate change

Our coupled physical–biological models estimate that climate change will result in a small (6%) global increase in the potential catches of "large" fish from the systems considered by 2050. This estimate corresponds to the fraction for direct human consumption and is based on predicted responses of fish communities to changes in temperature and primary production (Fig. 1A–C). Using the production in the "small" size range for the top twelve fishmeal-producing countries as a proxy for global fishmeal production we predict a potential growth of ca. 3.6% of fishmeal by 2050 (Fig. 1D). It is important to recognise that this global figure masks important regional differences, with high latitude countries predicted to benefit from increases in production (e.g. Norway, Iceland), while low latitude and tropical regions are expected to suffer production decreases (e.g. Peru).

3.2. Consequences of alternative future scenarios for fishmeal and aquaculture

To examine the combined impacts of changes in fishmeal production and use, we considered five scenarios for aquaculture development: "Replacement efficiency", "Slow aquaculture", "Baseline", "Fast aquaculture" and "Ecological collapse"

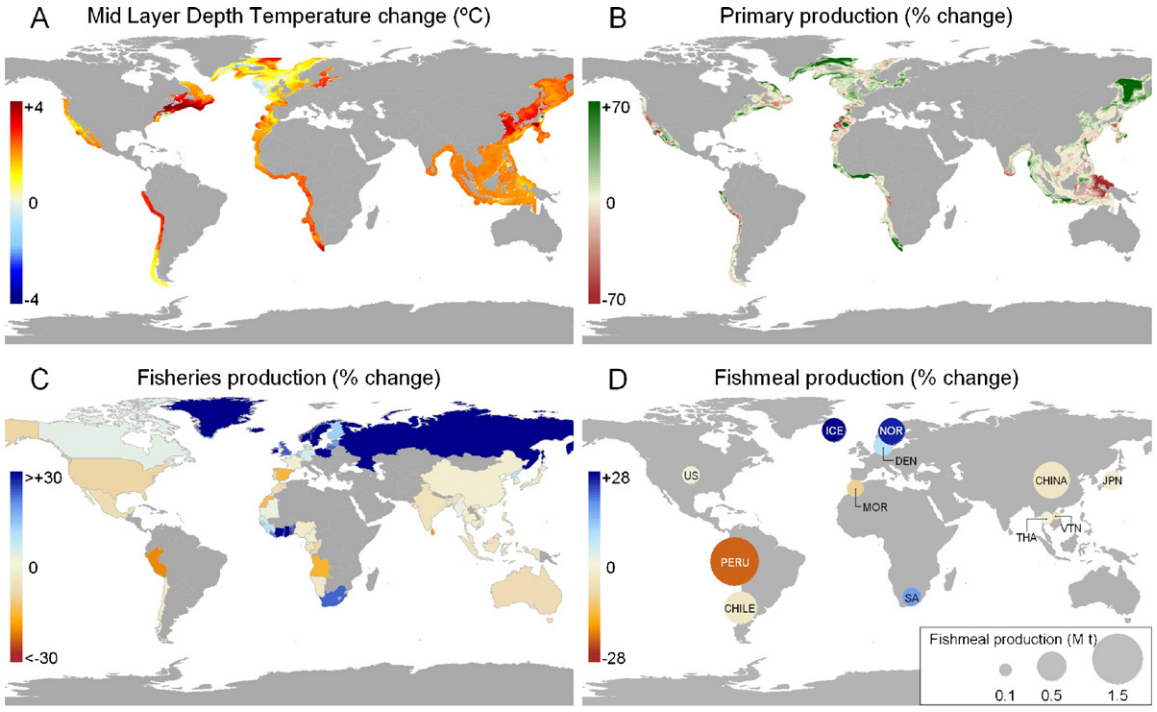

Fig. 1. Climate change impacts on regional ecosystems and relevant national fisheries by 2050. Data shown are absolute and relative differences between future A1B "business as usual" and Present Day Control scenarios for (A) mid-layer depth temperature (°C); (B) primary production (%); (C) National marine fisheries production (%) and, (D) fishmeal supply by the 12 top producers (VTN = Vietnam, US = United States, THA = Thailand, SA = South Africa, NOR = Norway, MOR = Morocco, JPN = Japan, ICE = Iceland, DEN = Denmark, Peru, Chile and China). For the latter, circle size is estimated absolute fishmeal production (Mt).

(Fig. 2). These scenarios describe different patterns of fish consumption and demand, and have been used to assess the prospects and constraints for aquaculture and to predict associated fishmeal and oil prices (Delgado et al., 2003). Our simulations indicate that the fishmeal production-consumption system is relatively stable with price increases ranging from −16 to 42% for fishmeal and from −5 to 50% for fish oil. However, very high price increases (the "Ecological collapse" scenario, Fig. 2E) could trigger a sequential collapse of geographically distant small pelagic fisheries. In this case, the short-term economic incentive to exceed maximum sustainable yield is high, potentially leading to increases in fishing capacity and rapid depletion of resources. When the real evolution of fishmeal price in the recent past years is compared with our scenarios, fishmeal price appears to follow a path consistent with the "Ecological collapse" storyline (Fig. 2F). Short-term fluctuations driven by environmental events such as the El Niño can be observed, as well as a consistent increase in price that parallels the percentage of fishmeal used in aquaculture (Merino et al., 2010b).

3.3. Human population growth: can aquaculture provide enough fish?

This section uses three pieces of information: (i) our estimates of capture fisheries production under climate change, for both "large" (for direct consumption) and "small" fish (to produce fishmeal); (ii) per capita fish consumption estimates from Delgado et al. (2003); and (iii) extrapolations of recent and expected future FIFO ratios in aquaculture from Tacon and Metian (2008) and Jackson (2010). Using these figures we estimate how much aquaculture will have to reduce its FIFO rates in order to maintain or grow current fish per capita intake rates with simple algebraic models. We used UN projections for human population size (UN, 2010) to investigate if a set of assumptions about future fish per capita consumption rates was feasible (Fig. 3). Accounting for the 6% overall predicted increase in marine fisheries production of "large" fish (direct consumption) (Fig. 1C) and assuming that *per capita* annual fish consumption remains between 15 and 20 kg, aquaculture will need to produce between 71 and 117 Mt of fish, with an average global fishmeal supply of 5.3 Mt. To achieve this figure would require reduced FIFO ratios and/or an increased share of the global fishmeal supply by aquaculture. Considering the short-term variability of fishmeal producing, small pelagic fisheries (Barange et al., 2009), a log-normal stochastic term with a coefficient of variation of 20% was applied to fishmeal supply predictions. The same approach was adopted to project global human population growth, so that low, medium and high variants could be considered with a 90% confidence interval. If aquaculture uses 80% of the traded fishmeal (compared to current 65%), fish production will only be sufficient to sustain a *per capita* intake of 17 kg/year in 2050 ('likely', probabilistically speaking, as defined by IPCC, 2005) if the global FIFO ratio falls below 0.25 (Fig. 3B). If all fishmeal was dedicated to aquaculture, the same objective would be met with a lower average technological adaptation (FIFO) of 0.28. If the aim was to increase per-capita consumption, larger technological adaptation would be needed. For instance, a more challenging food production objective of 20 kg per person and year may only be achieved with an overall FIFO of 0.16 and 80% of fishmeal utilization in aquaculture. A projection of FIFO trends suggests that overall FIFO could be reduced to 0.1 by 2030 (Fig. 3F), and therefore achieving values below 0.16 by 2050 appears possible.

The above computations use global averages, which do not necessarily translate into similar conclusions at national level. To appreciate the differential impact at smaller geographical units, we repeated this analysis using information from three national case studies.

3.3.1. Case study 1: China

China's population is expected to fall to 1.29B by 2050 (a decrease of 0.9%, Fig. 3A) and its current *per capita* fish consumption of 26.5 kg/cap is estimated to increase (Delgado

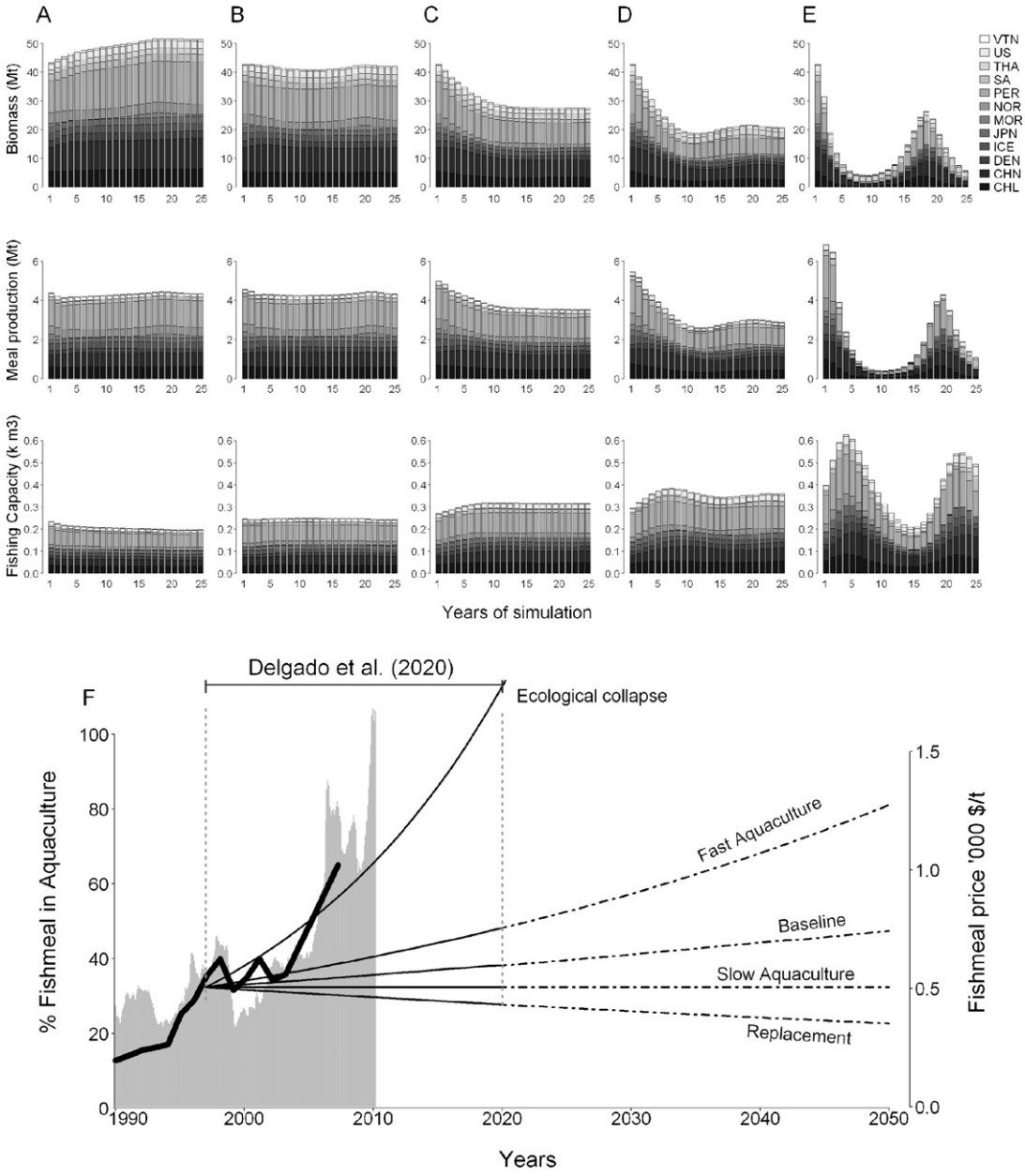

Fig. 2. (A–E) Exploratory 25 years simulations of the synergic impact of climate change (A1B) and socio-economic factors on fish stock biomass, estimated national fishmeal production and industries' fishing capacity for five aquaculture development scenarios (Delgado et al., 2003): (A) "Replacement efficiency" (fishmeal price (−16%), fish oil price (−5%)), (B) "Slow aquaculture" (fishmeal price (0%), fish oil price (−4%)), (C) "Baseline" (fishmeal price (+18%), fish oil price (+18%)), (D) "Fast Aquaculture" (fishmeal price (+42%), fish oil price (+50%)), and (E) "Ecological Collapse" (fishmeal price (+134%), fish oil price (+128%)). The twelve most important fishmeal producers are included: VTN = Vietnam, US = United States, THA = Thailand, SA = South Africa, PER = Peru, NOR = Norway, MOR = Morocco, JPN = Japan, ICE = Iceland, DEN = Denmark, CHN = China and CHL = Chile. (F). Observed fishmeal price (k $/t) from World Bank commodity database from 1990 to 2010 (shaded area), % of global fishmeal supplied utilization by aquaculture from 1990 to 2007 from Jackson (2009) (thick line) and fishmeal price (k $/t) scenarios by Delgado et al. (2003): scenarios to 2020 (thin line) and projections to 2050 (dashed lines).

et al., 2003). According to our models, climate change is expected to decrease marine capture fisheries production in China by approximately 3%, with resulting fishmeal production estimated to be 0.7 Mt by 2050 (Fig. 1C and D). The Chinese aquaculture industry will therefore need to produce an additional 27–50 Mt of fish to meet a fish consumption of 26.5–44 kg per capita (Delgado et al., 2003). China's current overall 0.37 FIFO will need to be reduced by over 70% to 0.1 to meet a 30 kg cap^{-1} yr^{-1} objective using 80% of its national fishmeal production (Fig. 3C). However, China is the world's largest market, with total fishmeal imports of 1 Mt in 2005. If these imports were maintained, a 44 kg *per capita* production objective could be met if FIFO rates decrease to just ca. 0.15.

3.3.2. Case study 2: Bangladesh

Listed as a low human development index (HDI) country, Bangladesh's population is expected to grow to 194.3 M by 2050 (Fig. 3A). The direct impacts of climate change on Bangladeshi marine fisheries predicted with our modelling framework are not significant (Fig. 1C). Fish is a key component of the Bangladeshi diet with a consumption rate of 14 kg *per capita* and year, making up 50–60% of total animal protein intake (FAO, 2007). Bangladeshi aquaculture produces carp at a current FIFO of 0.2, which contributes 40% of the national fish intake. Another 40% is obtained from inland fisheries (FAO, 2007). Our models project that marine fish production (currently 20% of national fish supply by volume) may be reduced by 5%, leaving aquaculture to produce

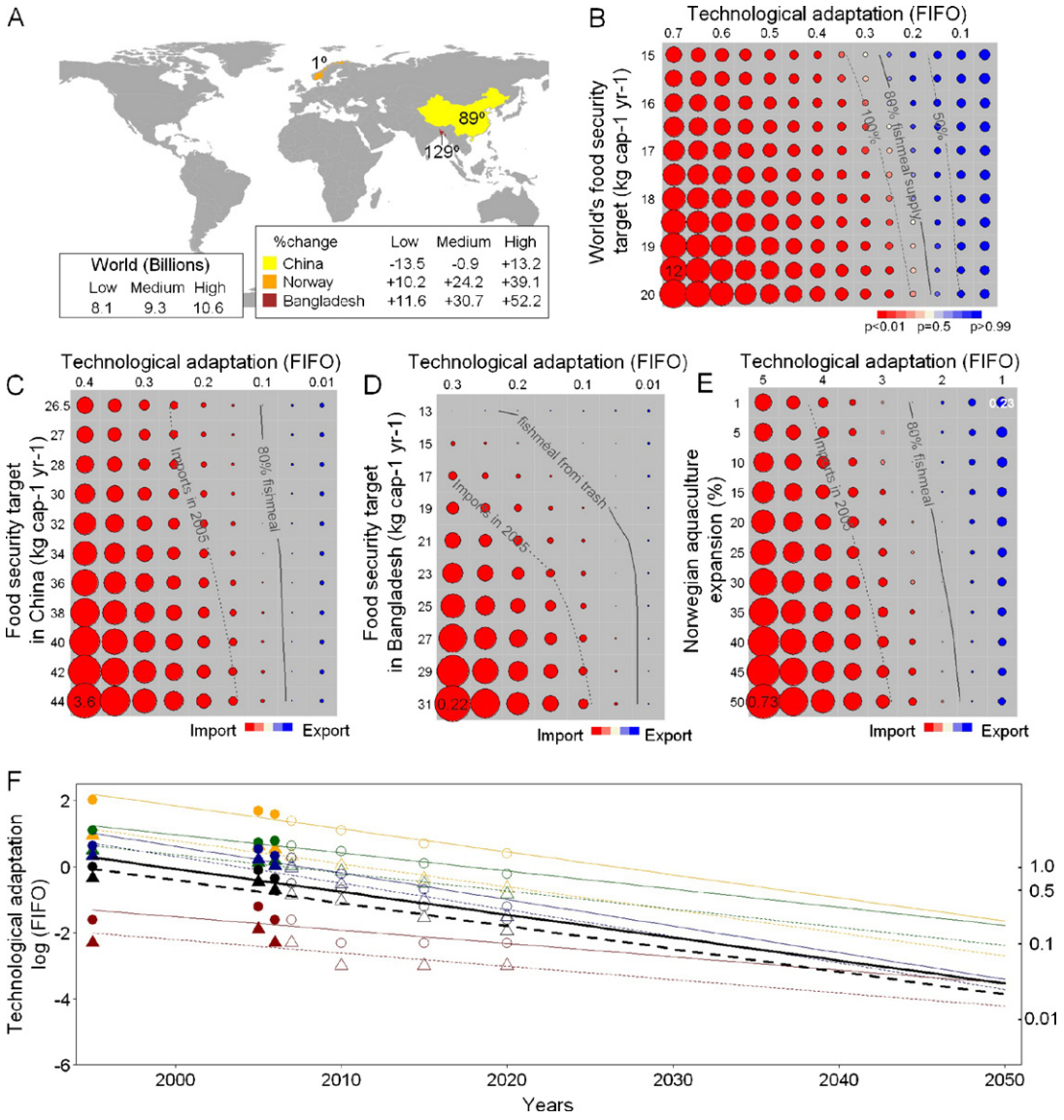

Fig. 3. (A) Population estimates for 2050, absolute values for the world and relative changes for the case studies according to the low, medium and high range projections (UN, 2010) and Human Development Index (HDI) for Norway, China and Bangladesh. (B–E) Technological adaptation required from the aquaculture industry (FIFO ratios) to likely meet alternative fish production/consumption targets. (B) World, (C) China), (D) Bangladesh and (E) Norway. Probability ranges between exceptionally unlikely ($p < 0.01$) to virtually certain ($p > 0.99$) (IPCC, 2005). Sizes of the circles represent the volume of fishmeal required to likely ($p > 0.667$) achieve a given target (if red) or how much excess fishmeal is available for other uses (if blue). In (B), a sequence of estimations was performed for a variable rate of fishmeal utilization by aquaculture, from 50 to 100%. Lines represent fish consumption objectives achieved with $p = 0.667$ for each FIFO. In (C, D and E), solid lines represent fish consumption objectives achieved with $p = 0.667$ for each FIFO without imports and 2005 fishmeal imports are also indicated (dashed lines). In (B–E), numbers in bottom left (and bottom right for Norway) circles show the scale of deficit (red) or excess (blue) of fishmeal (Mt) to likely achieve fish consumption targets. (F) Linear regression and projection of log(FIFO) of the major cultured species according to Tacon and Metian (2008) (circles, solid lines) and Jackson (2010) (triangles, dashed lines). Solid symbols indicate observed rates and empty symbols reflect predictions up to 2020. Values are averages of the most important cultured categories: average of all categories (black), salmon (orange), shrimp (blue), marine species (green), and carp type species (red).

between 0.3 and 3.8 Mt of fish to achieve national fish consumption targets of 13–31 kg fish/cap. Our calculations assume that 83% of the marine fisheries production is used for direct human consumption and that the remainder (dubbed trash fish) is reduced to fishmeal (FAO, 2007). If consumption was increased to 21 kg cap^{-1} yr^{-1}, the FIFO ratio would need to be reduced to 0.025 (Fig. 3D), almost 90% lower than current rates. Recent projections of FIFO estimates for carps (Jackson, 2009; Tacon and Metian, 2008) suggest that this value could be reached before 2030 for carp aquaculture (Fig 3F).

3.3.3. Case study 3: Norway

Potential fishmeal production in Norway is predicted to increase by up to 27% as a result of the impacts of climate change on small pelagic fisheries (Fig. 1D). Maintaining current fishmeal imports, salmon FIFO would need to be reduced to below 3 to support a 50% increase in salmon production (Fig. 3E). If salmon FIFO fell below 1, Norway would be able to export 0.23 Mt of fishmeal per annum while still sustaining current levels of production.

4. Discussion

We conclude that marine ecosystems may be able to sustain current and increased per capita consumption rates through 2050, provided that effective fisheries management measures are implemented and that significant technological adaptations are developed. If fisheries management remain suboptimal and

fishmeal prices rose as a consequence of greater demand, these conclusions would not hold. Our analysis was predicated on assumptions about how changes in climate affect marine fisheries, the effectiveness of fisheries management, trends in human population size and the capacity to reduce FIFO in aquaculture.

We predicted an overall 6% increase on marine fisheries potential for "large" fish across the studied areas and a 3.6% increase on "small" fish in the top-twelve fishmeal producing nations. Our estimates are based on climate change driven future net primary production and assumptions about how it passes through the food web from prey to predator (Brander, 2007), but do not make assumptions on the set of species that will use available production, as opposed to other studies that use specific bio-climate relationships (e.g. Cheung et al., 2009b). Our model predicts qualitatively similar results to predictions based on bio-climate envelopes (Cheung et al., 2009b) but with some specific differences. For example, with our physical-ecosystem model we predict significantly lower potential production in the small size fraction (5–20 cm) in Japan and Peru and higher production for Icelandic and South African fisheries than Cheung et al. (2009b). We favour our approach because it is recognized that the relationship between primary production and the abundance of individual populations of small species is weaker than the relationship with total fish abundance (Iverson, 1990). However, it is feasible that variable proportions of the fish comprising a "small" size class would be suitable for fishmeal production and we encourage efforts to improve methods for predicting long-term species-specific biomass trajectories for small pelagic fishes.

Furthermore, it must be noted that our estimates focus on the direct effects of climate change on ecosystem production, and do not take into account other compounding factors, such as habitat degradation. It is known that such impacts, for example coral reef bleaching, are negatively affecting fish production (Graham et al., 2007; Pratchett et al., 2008).

It is also worth noting that the estimated changes in potential fisheries production as a result of climate change are smaller than the production fluctuations caused by climate variability (Barange et al., 2009; Baumgartner et al., 1992).

The global physical-ecosystem modelling framework used to estimate primary production captures the regional detail in a consistent and high resolution manner, thus allowing regional comparisons. Previously, coupled physical-ecosystem POLCOMS-ERSEM models have focused on a single region when considering future climate forcing (Holt et al., 2011; Neumann, 2010). Our approach allows the sensitivity of the system to be explored based on relative changes for the desired variables under different climate scenarios, and has been validated against present day data, providing additional confidence to the predicted yield of small pelagic fisheries (see Appendix A). However, in choosing only one coupled physical-biogeochemical model we introduce a degree of structural and parameter uncertainty. In addition, by employing only one forcing scenario (A1B) from one global climate model (IPSL-CM4), we are unable to quantify the spread in the forcing uncertainty. Thus our results should be treated heuristically and used to formulate a robust methodology for future use.

Sustainable yields from capture fisheries are needed to support direct consumption and aquaculture production. On the other hand, economic globalization can ensure that raw materials are funnelled to areas with lower fish production and higher demand to be consumed directly or to produce farmed fish. However, economic globalization has also provided short-term economic incentives for the unsustainable use of marine resources (O'Brien and Leichenko, 2000). The "Ecological collapse" storyline considered in Fig. 2 reflects that if producers and consumers do not modify their behaviour, then this could cause projected global fish production to decline more than half between 1997 and 2020 (Delgado et al., 2003). Our simulations indicate that the production decline could be abrupt rather than the smooth pattern assumed by Delgado et al. (2003), if management compliance is less than 80%. The price increase associated with the "Ecological collapse" and "Fast aquaculture" scenarios would result in consumers with less economic power to substitute fish for cheaper sources of animal protein in their diets, an option not always available in poor countries such as Bangladesh.

It is worth noting that current trends in fishmeal price indicate that conditions tend to favour the realization of what Delgado et al. (2003) dubbed the "Ecological Collapse" scenario. This does not mean that we are or will be experiencing a sequential collapse of stocks, but rather that there is a growing demand for marine products, resulting in a high fishmeal price and imposing additional pressures to secure the sustainability of marine resources (Berkes et al., 2006). An example of this is the predicted future state of exploitation of bluefin tuna, a highly priced fish, if market considerations shape environmental policy (Pauly et al., 2003). In our model, the increase in the price of the marine commodity encourages exploiters to maximize their short-term economic profits and exceed the yearly quota limitations. The latter implies eroding the capital of the fish stocks and reduces the long term benefit of mantaing stocks at MSY levels. The consequence of this is that strict fisheries management and market stabilization measures will be crucial to ensure the sustainability of fisheries dedicated to fishmeal and oil production. Thus management systems need to be sufficiently robust to control fishing mortality despite increasing demand (Berkes et al., 2006; Merino et al., 2011; O'Brien and Leichenko, 2000). While some recent management efforts have led to improved controls of fishing mortality, along with stock stabilization and recovery in some places (Branch et al., 2011; Worm et al., 2009), some small pelagic fisheries continue to be sub-optimally managed and sensitive to demand changes (Asche and Tveterås, 2004). Encouragingly, however, the management of the large Peruvian anchoveta fishery, the largest producer of fishmeal, has proven to be increasingly robust to environmental fluctuations and high demand (Arias-Schreiber et al., 2011).

Globally, an effective management of small pelagic fisheries would support a stable and high supply of fishmeal and oil. By effective management we imply a management that maximises fishmeal supply, even though some authors have suggested that small pelagic fish stocks should be exploited at levels below MSY to protect the marine food webs that depend on them (Smith et al., 2011).

There are other potential developments in fisheries and aquaculture that are not considered here but would have a large impact on the fish protein supply. The use of low trophic level fish for direct consumption instead of for fishmeal/oil production (Sánchez and Gallo, 2009), the use of bycatches and byproducts from consumption fisheries to produce fishmeal (FAO, 2007), the development of Antarctic krill fisheries (Hill et al., 2009), the proliferation of previously unfished species that can be used to produce fishmeal (White et al., 2011) and the use of microalgae to produce aquafeed (Becker, 2007), would all influence realized outcomes. From the above, it is expected that developments of alternatives to feeds produced from wild fish will reduce price and the pressure on marine stocks ("Replacement efficiency", "Slow aquaculture") and those that will reduce supplies will increase price and pressure on wild stocks as in the "Ecological collapse" scenario.

The above raise only a few of the uncertainties associated with our analysis. There is also considerable uncertainty associated with the coupled bioeconomic model. To start with, the model is initialized under a bioeconomic equilibrium condition, even though no fishery is currently under equilibrium, and many stocks

are below their corresponding biomass at MSY (Smith et al., 2011; Barange et al., 2009). However, the initial equilibrium conditions are considered adequate to show how alternative economic pressures could potentially distabilize global stocks. In addition, the biological and economic parameters used were imposed to fit with the bioeconomic equilibrium. Thus, our results are not comparable with the parameters associated with single stock assessments for each of the production systems considered in the model.

We predict a slight 6% increase in the potential yields of "large" fish production by 2050, significantly less than the expected growth of human population. In the future, increasing the price of the marine commodities will encourage seeking for substitutes and reducing the potential of price increases (Sumaila et al., 2011). If aquaculture is to grow to feed a 9.3B population in a sustainable manner, technological adaptation will be needed to produce more fish with less environmental impact. Replacement of fishmeal in aquafeed is achieved by using alternative protein sources such as soya (Drakeford and Pascoe, 2007). In some developing countries, fish food has been produced using manure and animal carcasses from livestock farming (Delgado et al., 2008). We estimate that the fish use in aquaculture feed to produce one unit of output would have to be reduced by at least 50% from current levels to secure sustainability. Projecting recent observations and predictions (Fig. 3F) suggests that such a scenario is theoretically feasible. The FIFO scenarios and projections implicitly assume that the proportion of major cultivated species will remain the same in the future. At present, those cultured species that require less than a unit of wild fish to yield a unit of cultured product include most cyprinids (Tacon and Metian, 2008; Torrisen et al., 2011), but not salmonids. To maximize food production, therefore, small pelagic production would best be used for direct human consumption or directed to the culture species with lower FIFO rate. Other changes in aquaculture will need to accompany reductions in FIFO, including reduced spatial occupation, pollution and other environmental impacts per unit of cultured fish (Naylor et al., 2000, 2009). We acknowledge that while our projections are based on published calculations and projections to 2020 (Tacon and Metian, 2008; Jackson, 2010), extrapolating these into 2050 involves a degree of uncertainty. However, these projections are used to develop future scenarios for aquaculture technological adaptation, and not as absolute predictions.

The technological adaptation scenarios described in this study imply that some of the environmental impacts of aquaculture would be transferred from marine to terrestrial ecosystems. Producing plant or other materials for aquaculture has an environmental impact that affects the supply of these materials, or the supply of materials that could be produced on the same land, for other purposes (Torrisen et al., 2011). For example, if aquafeed is produced from soya, aquaculture may possibly compete with biofuel and agricultural production for food (Bostock et al., 2010; Koning and van Ittersum, 2009). Further analysis of the impact of fishmeal replacement with terrestrial sources will be necessary.

We have shown that global fish production has the potential to support both direct human consumption and a growing aquaculture industry at the global scale. The FIFO rates used in this analysis reflect mean global figures, computed on the basis of a very diverse portfolio of aquaculture species in relation to their fishmeal dietary needs. The national case studies help us to assess the consequences of variations at national scale given the different national developmental pathways and fish production/consumption patterns.

China produces over 2/3rds of global aquaculture production, a proportion that is expected to grow in coming decades (FAO, 2008). Fish consumption in China already exceeds basic recommended nutritional requirements (Brugère and Ridler, 2004; Delgado et al., 2003), owing to the culture of freshwater fish. In the last 20 years China has created and developed a shrimp farming industry that is highly dependent on fishmeal and is now the largest global producer (Deutsch et al., 2007; FAO, 2011). Whether Chinese aquaculture moves towards species with high fishmeal inclusion rates or continues with current species composition will be a critical driver for the future of fishmeal markets. If current species are cultivated in the future, the Chinese aquaculture industry can potentially keep increasing fish supplies to meet their current and larger per capita demands.

Although the direct impacts of climate change on Bangladeshi fish production do not seem significant (as opposed to the impacts of sea level rise (Karim and Mimura, 2008) or flooding (Adger et al., 2005), which were not accounted for in this analysis), the country is considered highly vulnerable to climate change (Allison et al., 2009). Fish represents a major source of animal protein in Bangladesh and *per capita* availability would need to remain above the global average to meet nutritional needs. If the Bangladeshi aquaculture industry is not flexible enough to reduce its dependency on fishmeal below FIFO = 0.025, then the country will require fishmeal imports to increase fish production. To achieve this, Bangladesh, which is not currently one of the top fishmeal importers, will have to enter the globalized fishmeal network. This would pose a significant challenge for Bangladesh as a relatively small economy with limited buying power (its marine export products were 10 times larger than imports in 2008 (FAO, 2011)).

Norway is at the top of the human development index rankings and is the world's main Atlantic salmon producer with 0.862 Mt in 2009 (FAO, 2011), equivalent to 89% of its total aquaculture production. Salmon aquaculture has the highest FIFO ratios (currently 4–5) and salmon production is mainly exported, generating 2.75B US$ in revenues (Brugère and Ridler, 2004; Failler, 2007). Farming species with a lower FIFO would further increase expansion opportunities, as conversion ratios below 1 are projected for some marine species in the near future. In terms of fish protein production, cultivating salmon is not an effective way of transforming fish of marine origin into farmed fish, but the investments made by the aquaculture industry are strongly influenced by consumers' preferences and profitability (Deutsch et al., 2007; Torrisen et al., 2011). Aquaculture growth in Norway is expected to be boosted by the favourable consequences of climate change and reduced dependence on fishmeal imports. However, there are concerns that the demand for fish oil and not fishmeal will limit aquaculture's growth (Naylor et al., 2009). Salmon production will require additional technological advances to replace fish oil (Ganuza et al., 2008; Miller et al., 2007) as well as fishmeal. Until such technological efficiencies are in place, it could be argued that salmon aquaculture represents an inefficient use of capture fish production that could otherwise be used directly to meet human food needs, although salmon aquaculture is not driven by food demands but by its economic benefits (Torrisen et al., 2011).

This modelling study suggests that realistic scenarios for technological change in aquaculture and institutional development in capture fisheries can combine to ensure that both current per capita consumption levels and reasonable projected increases in per capita consumption levels can be sustained with the right investments in the fish production sector. Climate change impacts on production may not be the major factor in achieving the required levels of fish production to feed a growing, wealthier global population with a higher fish protein intake. This should not be interpreted as suggesting that climate change will not affect food systems sustainability or the costs of producing food. Food systems are impacted through multiple pathways, from the health and safety of food producers to the costs of transport and storage

(Parry et al., 2004). Our conclusion is that in the case of capture fisheries, climate change impacts on production may not be the most significant factor in securing fish availability in the near future (to 2050). Ensuring that fisheries are efficiently governed and that aquaculture continues to grow in a sustainable manner will be the main constraints to the sustainability of global fish production. Policies encouraging improved environmental standards in aquaculture production and greater commitment to address governance weaknesses in capture fisheries will both be required. Recent reviews of successful governance reform in fisheries (Costello et al., 2008; Gutierrez et al., 2011) and of improving environmental standards in aquaculture (Hall et al., 2010) give reasons for hope.

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Appendix A

A.1. Predicted small pelagic fish catch and observations

In order to validate our predictions of fisheries production, we forced the size-based models for the period 1992–2001 with Ocean and Atmospheric reanalysis data sets used to provide the boundary conditions in the physical-ecosystem model. Fish production estimates at $F = 0.8$ were compared with catch data for small pelagic fishes over the same period, as allocated to EEZ by the Sea Around Us project (www.seaaroundus.org). Model predictions mostly fall within the range of the observations (Figs. A1 and A2), and exhibit similar

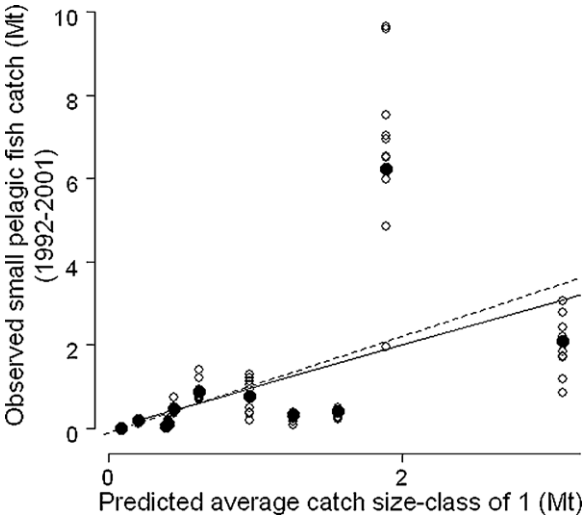

Fig. A1. Predicted average catch of size class 1 against observations of small pelagic fisheries landings. Filled circles are observation averages. Linear regression is dashed line and solid line is the perfect fit line. Summary of the linear regression excluding Peru: Multiple R-squared: 0.7412, Adjusted R-squared: 0.7089, F-statistic: 22.91 on 1 and 8 DF, p-value: 0.001379. Summary of the linear regression considering all values: Multiple R-squared: 0.3323, Adjusted R-squared: 0.2581, F-statistic: 4.48 on 1 and 9 DF, p-value: 0.0634.

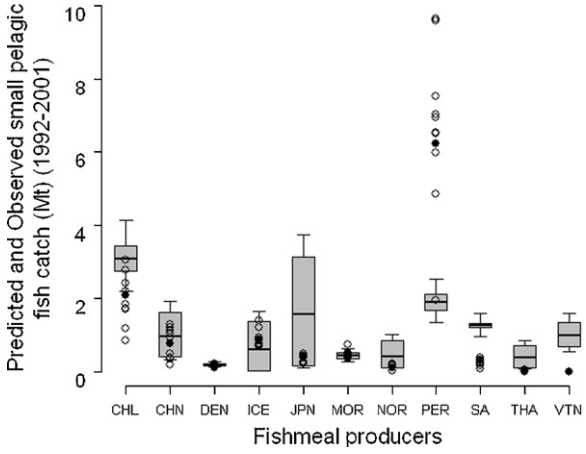

Fig. A2. Variability on model predictions and observations. Boxes represent 90 of the variability in EEZ level size class 1 predicted catches at $F = 0.8$ for the largest fishmeal producers. Error bars indicate the total variability considered for the future scenarios. Average catch of small pelagic fish is shown with filled circles. Empty circles are yearly observations.

variability. Predictions are among the closest to data for China and Norway (two of the three case studies analyzed in our work) while predictions for Peru are not. Ratios of fish production to primary production in the Humboldt current are known to be higher than elsewhere and catches of small pelagics from the Humboldt current can average around 30 g m^{-2} yr^{-1} (depending on the measurement of productive area) (Carr, 2002; Carr and Kearns, 2003) implying a very high transfer efficiency that was not captured by our generalised model. Excluding this system, R^2 would be 0.7, comparable to that reported in another study (Ware and Thomson, 2005) for relationships between observed primary production and fish yields. More detailed cross validations are ongoing (Blanchard et al., 2010a,b; Holmes et al., 2010) and will be updated with appropriate references. For the estimation of future fisheries production we did not use the absolute estimates of fisheries yield but weighted the production estimates in the bioeconomic network model by the relative change in production through time. Thus the discrepancy in absolute value for the Peruvian EEZ would not affect this process, only any difference in the ratio of primary production and potential fish production through time.

Appendix B

B.1. Fish model

The fish model used in our calculations is a coupled community size spectra where coupling consists of predation and production linkages between two size-structured communities: "pelagic predators" and "benthic detritivors". Although the model is not taxonomically structured, fish typically dominate the size range captured by the "pelagic predators" and it is this community from which model outputs are used to estimate future potential sustainable yields of small pelagic fish (to produce fishmeal) and "large" fish (for direct human consumption).

The dynamical model is comprised of two partial differentials equations of the form $\partial N_i/\partial t = -(\partial/\partial m)(G_i N_i) - D_i N_i$ that predict changes in abundance at mass through time. N is the numerical density, t is time, m is body mass, G is the growth rates at (m,t) from feeding and D is the death rate at (m,t), from predation, intrinsic and

senescence mortality and fishing mortality. There are two dynamical community size spectra, $i \in$ {pelagic predators, benthic detritivores}, that have different ecological interactions. In the "pelagic predator" community, predators feed on preys that are smaller than themselves. They have equal access to prey from both communities according to prey availability and suitable size. In the "benthic detritivore" community, animals feed on a shared unstructured resource (they are not size selective). Model background and details are given in Blanchard et al. (2009, 2011). In the current implementation of the model, the dynamics of the detritus pool were not included and were replaced by time-varying detritus biomass input from the ERSEM model.

B.2. The bioeconomic model

(i) *Biological component:* In the biological component, the dynamics of the twelve production systems fish populations depend on their intrinsic growth rate (r), carrying capacity (K) and yield (Y) (Schaefer, 1954) (Eq. (1)). Yield is estimated using a set of rules considering fleets technological limitations, management and fleets compliance to management. First, production systems are limited by their technical capacity. Countries catchability coefficient (q) and fleet dynamics, based on fishing investment (Effort = E) will be used to estimate the exploitation of producers if no regulation was implemented (Y^{tech} in Eq. (2)). Quotas are set to be at maximum sustainable yield levels (Eq. (3)). Additionally, a compliance parameter will allow modeling fleets deviations from regulation and effective yield (Eq. (4)). A free-access fishery would mean zero compliance ($comp = 0$) fishery. We used a suboptimal fishery value of $comp = 0.8$, while a fishing industry perfectly compliant with the management scheme is obtained with $comp = 1$ (Eq. (4)). Note that if regulation is less restrictive than technological limitation, Y^{tech} will be the real effective yield for any compliance level. Compliance will play a role only when exploiters are economically incentivized to exploit at higher rates than those set by quotas.

$$X_{ps}(t+1) = X_{ps}(t) + r_{ps}X_{ps}(t)\cdot\left(\frac{1-X_{ps}(t)}{K_{ps}}\right) - Y_{ps}(t) \tag{1}$$

$$Y^{tech}_{ps}(t) = q_{ps}\cdot E_{ps}(t)\cdot X_{ps}(t) \tag{2}$$

$$\text{Quota}_{ps} = MSY_{ps} = \frac{r_{ps}K_{ps}}{4} \tag{3}$$

$$Y_{ps}(t) = \text{Min}(Y^{tech}_{ps}(t), \text{Quota}_{ps}(t)) + (1 - \text{comp})\text{Quota}_{ps}(t) \text{if Quota} < Y^{tech} \tag{4}$$

(ii) *Economic component:* International markets for a commodity i (1 = meal, 2 = oil), are supplied by regional production systems. The total commodity quantity placed in an international market ($Q_{i,m}$) is the sum of the reduced product (following a proportionality index yield/commodity λ_i), traded from geographically distant fish stocks (Eq. (5)). Φ identifies the paths from producers to consumers; if the path from a production system ps to a market m exists, then $\Phi = 1$, if not, $\Phi = 0$. The price of the commodity is estimated following a linear function: α is the asymptotic price of the product and β is the price elasticity to supply changes (Eq. (6)):

$$Q_{i,m}(t) = \sum_{i-1}^{2}\sum_{ps=1}^{PS}\Phi\cdot\lambda_{i,ps}Y_{ps}(t) \tag{5}$$

$$p_{i,m}(t) = \alpha_{i,m} - \beta_{i,m}\cdot Q_{i,m}(t) \tag{6}$$

A strategic interaction arises because the price each producer gets for its commodity production results from its own and others' production, the so called *market externality* (Oakerson, 1992), and, furthermore, its profits depend not only on its own production but on the other producers' production too. The economic balance (I) between the income from selling the regional production into the global markets is shown in Eq. (7) (cf are the costs of using a fishing unit, cr the costs of reducing fish into meal and oil and cs the average costs of shipping into international markets):

$$I_{ps}(t) = \lambda\cdot p_i\cdot Y_{ps}(t) - cf_{ps}E_{ps}(t) - cr_{ps}Y_{ps}(t) - cs_{ps}Q_{ps}(t) \tag{7}$$

(iii) *Activity component:* Production systems modulate their fishing strategies based on previous years net profits (estimated in the economic component) and a set of economic parameters: The fishing capacity in a production system is the result of previous $E(t)$ and the investment (i) in new fishing units with a price of (ν) each, including capital (KC) and amortisement costs of the current fishing units at a rate j.

$$E_{ps}(t+1) = E_{ps}(t) + i_{ps}\cdot\left(\frac{I_{ps}(t) - KC_{ps}(t)}{\nu_{ps} - j_{ps}E_{ps}(t)}\right) \tag{8}$$

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