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IOCCG Report Number 8, 2009

Remote Sensing in Fisheries and Aquaculture: The Societal Benefits

Edited by:
Trevor Platt, Marie-Helene Forget and Venetia Stuart

Report of a SAFARI workshop on the use of remote sensing in fisheries and aquacultures chaired by Trevor Platt, and based on contributions from (in alphabetical order):

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Nicholas Hardman-Mountford, Alida Bundy, Nicholas K. Dulvy, Trevor Platt

Chapter 2

Climate Change, Ecosystem Variability and Fisheries Productivity

Nicholas K. Dulvy, Emmanuel Chassot, Johanna Jacomina Heymans, Kimberly Hyde, Daniel Pauly, Trevor Platt, Kenneth Sherman

Climate-driven variation on the timing and location of phytoplankton blooms has profound effects on the number of larval fish and invertebrates surviving and recruiting each year and ultimately on the structure and dynamics of marine ecosystems. The spring phytoplankton bloom is the only source of food for many fish and invertebrate larvae. The degree of spatial and temporal overlap of the spring phytoplankton bloom with the timing and spatial distribution of the spawning of eggs into the surface waters has a strong influence on larval fish survival (Hjort, 1914; Cushing, 1990; Mertz and Myers, 1994; Platt *et al.*, 2003). Eggs and larvae develop in the planktonic zone of the water column for 1-2 months before descending to the seabed habitat. Fish and invertebrate larvae have sufficient yolk stores to survive for only a small fraction of the total time spent developing in the surface waters. Larvae starve and die unless they are spawned into, or transported into, a patch of phyto- and zooplankton that is sufficiently large and productive enough to sustain their development. The variable pattern of fish and invertebrate recruitment to juvenile stages is modulated by physical forcing of phytoplankton and ultimately, this environmental variability has a measurable effect on recruitment of new individuals to exploited stocks and the productivity and biomass of higher trophic levels. Remote sensing of ocean colour has finally provided data at the resolution in time and space necessary to elucidate the linkages between climate-driven changes in the marine environment and the dynamics of fish and ecosystem productivity. Here in this chapter we focus on large-scale year-by-year variability in the physical environment and consider how this influences fish and invertebrate production. In particular we consider the likely effect of climate change on ocean temperature and productivity and highlight emerging approaches toward understanding the consequences for global fisheries yields.

2.1 Climate change, ocean temperature and productivity

2.1.1 Sea surface temperature

The global temperature has risen by 0.6 °C in the past 100 years (IPCC, 2007). Over the last 25 years most of the 64 Large Marine Ecosystems have warmed. Only two have cooled, the Pacific upwelling regions of the California and Humboldt Current LMEs (Sherman *et al.*, 2007; Belkin, in review). The warming trends span from 0.08-1.35 °C for the Patagonia Shelf and the Baltic Sea LMEs respectively. The rapid warming of the Baltic and North Sea has been verified with daily temperature records from light ships and annual fisheries research vessel records showing that the Baltic and adjacent parts of the North Sea have increased by at least a degree with greatest increase in summer temperatures of ∼1.6 °C in the past 25 years (MacKenzie and Schiedek, 2007; Dulvy *et al.*, 2008). Mid to high-latitude LMEs are experiencing the fastest warming (>0.6 °C over 25 years), with greatest warming occurring in the North Atlantic (e.g. Figure 2.1). This is consistent with the observation of rapid climate change in the Arctic resulting in rapid heat penetration into Atlantic waters through the deep convention patterns characteristic of this ocean (Barnett *et al.*, 2005).

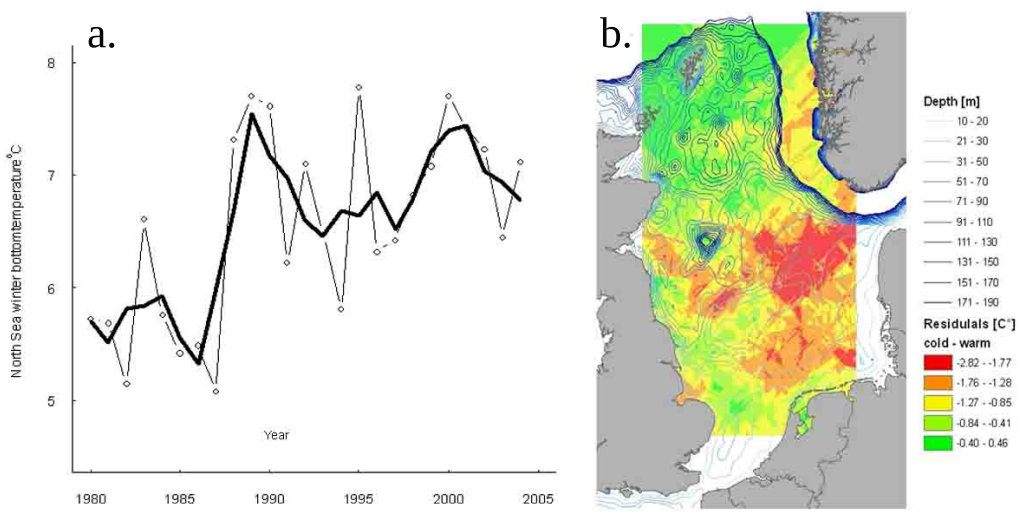

Figure 2.1 (a) The change in average North Sea winter bottom temperature over time, with a centred three-year running average (redrawn from Dulvy *et al.* 2008). (b) the spatial variation in the warming of North Sea summer bottom temperature. The warming was calculated as the temperature difference between a cold period (1983-1987) and a warm period (1990-2003) (Dulvy and Stelzenmüller, unpublished data).

2.1.2 Ocean productivity

The relationship between climate change and future ocean primary production is likely to be a key determinant of fish and fisheries production (Cushing, 1982). Metabolic scaling theory suggests that the balance between primary production and respiration will be profoundly affected by rising temperatures, with respiration rates increasing more than production rates (López-Urrutia *et al.*, 2006). Consequently metabolic models predict that the epipelagic ocean biota will capture 4 gigatonnes of Carbon per year less by 2100, representing 21% less CO_2 being captured (López-Urrutia *et al.*, 2006). At present there is considerable uncertainty in empirical measures of the effects of climate change on global primary production and the regional variation of these effects. The declines in production predicted by metabolic theory are consistent with coupled ocean biogeochemical and GCM models. These models predict climate change will lead to more nutrient-depleted conditions in the ocean surface which will favour small phytoplankton at the expense of larger diatoms (Bopp *et al.*, 2005).

Global ocean chlorophyll concentration has varied considerably over the past 25 years, declining since the 1980s, followed by an increase between 1998 and 2000 and a subsequent decline in response to climatic forcing. Recent comparisons of two datasets - Coastal Zone Color Scanner (CZCS, 1979-1986) and Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean color observations (1998-2002) - suggest the world ocean average chlorophyll concentration has declined by 6% since the 1980s (Gregg et al., 2003). Nearly 70% of the global decadal decline occurred in northern high latitudes corresponding with increases in sea surface temperature and decreases in atmospheric iron deposition to the oceans (Gregg and Conkright, 2002; Gregg *et al.*, 2003). Mid-ocean gyres exhibited limited changes (Gregg and Conkright, 2002) or declining concentrations (Antoine *et al.*, 2005). There is further heterogeneity among regions. Sea surface warming in the Northeast Atlantic is accompanied by increasing phytoplankton abundance in cooler regions and decreasing phytoplankton abundance in warmer regions (Richardson and Schoeman, 2004). Sea temperature increases have led to an 80% decrease in macrozooplankton biomass since 1951 in waters off southern California (Roemmich and McGowan, 1995). More recently, since 1998 global chlorophyll concentration increased following a strong El Niño year in 1998, the increase persisted until a La Niña in 2000 whereupon global chlorophyll concentration decreased. These changes are largely attributed to changes in surface temperatures and stratification associated with the ENSO cycle and the multivariate ENSO index (Behrenfeld *et al.*, 2006).

Insight into the future is provided by an analysis of six coupled Atmosphere-Ocean Global Circulation Models (AOGCMs) indicates that primary production may increase very little, 0.7 - 8.1% by 2050 relative to a pre-industrial state (Sarmiento *et al.*, 2004). However, the level of confidence in this prediction is low, mainly due to large increases in the intertropical areas (Antoine *et al.*, 2005). However this slight

increase at the global scale belies marked differences in the responses of regions and biomes. The AOGCMs predict reduction in the area of permanently stratified low productivity waters in the subtropical gyres (Sarmiento *et al.*, 2004).This pattern has already been observed in ocean color estimates, which suggest during this time there was a 15% increase in the size of the ocean's most oligotrophic waters with lowest chlorophyll concentrations <0.07 mg chl m^{-3} (Polovina *et al.*, 2008). The Atlantic Ocean has exhibited the greatest increase in the size of its oligotrophic gyre which is expanding by 4.3% yr^{-1}. This is consistent with predictions of increased heat content and vertical stratification in mid-latitudes due to global warming.

2.2 Fisheries oceanography: linking physical oceanography, phytoplankton and fish

The recent advent of global, systematic, daily, fine-scale estimates of primary production from satellites has created unprecedented opportunities to predict abundance, biomass and production of fish and other higher trophic level crustaceans, molluscs, reptiles, birds and mammals. Integrating data across ecological scales and from low to high trophic levels remains challenging and requires the combination of a range of field observations and the development of new collaborations between theoreticians, field scientists and model developers (Platt *et al.*, 2007; Cury *et al.*, 2008). There are four broad approaches available to estimate the production and biomass of fish and other high trophic level organisms from primary production: statistical models, size spectra models, energy mass-balance models and 'end-to-end' or 'physics-to-fish' ecosystem models. The statistical approach relies on relationships derived from analyses of ecosystem properties at large spatial scales. The other three approaches are mechanistic founded in physical, chemical and ecological laws and principles.

2.2.1 Statistical links from plankton to fish

Detailed links have been uncovered between environmental variability and the population dynamics and catches of exploited species of octopus, shrimp, pelagic fish, eels and Pacific salmon. These studies provide greater insight into the mechanisms linking physical oceanography to phytoplankton production and on to the production of higher trophic levels. Here we focus on the invertebrate examples but point the reader toward some other examples (Cole, 1999; 2000; Hardman-Mountford *et al.*, 2003; Mueter *et al.*, 2005; Bonhommeau *et al.*, 2008). In the North-West Gulf of St. Lawrence the sea surface temperature and sea-surface chlorophyll a concentrations, estimated through remote sensing at the time of larval emergence of the northern shrimp (*Pandalus borealis*), were correlated with larval survival and the subsequent cohort abundance (Ouellet *et al.*, 2007). Chlorophyll concentrations were positively related to larval survival and absolute temperature negatively correlated to larval

survival. However greatest larval survival was correlated with the greatest rate of warming. The subsequent carapace length of young northern shrimp is heavily influenced by the initiation, timing and intensity of the spring bloom (Fuentes-Yaco *et al.*, 2007). Catches of octopus (*Octopus vulgaris*) in the coastal water of North-West Spain exhibited strong relationships with wind structure and upwelling. The percentage of days of upwelling (offshore Ekman transport >500 m^3 s^{-1} km^{-1}) in spring and summer (April-September) two years prior were positively related to octopus catches (Otero *et al.*, 2008). The strength of upwelling was positively correlated with remotely-sensed estimates of primary production. Octopus larvae hatch at the end of summer through early autumn during the end of the upwelling and peak of primary productivity. Strongest upwelling, leading to enhanced primary productivity, during this period had greatest positive effects on the catches of octopus two years later.

A prevailing view in ecology is that bottom-up processes control the abundance and biomass of high trophic level organisms, notably through the level and variability of primary production at the base of the food web. Primary production, combined with assumptions on the number of trophic levels in food chains and the loss of energy from one trophic level to the next (transfer efficiency), has long been viewed as good indicator of the global production of capture fisheries (Ryther, 1969). At large spatial scales primary production has been shown to be broadly correlated with fish yields (Iverson, 1990). Positive relationships between primary production (or annual mean chlorophyll a concentration used as a proxy for primary production) and long-term average fishery catches have been described for 9 fisheries areas in the mid-latitude region of North-West Atlantic (Frank *et al.*, 2006), 11 fisheries areas in the North-West Pacific (Figure 2.2) (Ware and Thomson, 2005), 14 European ecoregions (Chassot *et al.*, 2007) and 1000 exploited fish and invertebrates (Cheung *et al.*, 2008a).

In the North-West Atlantic, higher production in the south was associated with higher fisheries yields. Such correlations might overlook the long history of exploitation on these ecosystems, which combined with the large spatial scale of the analysis may obscure any top-down predatory control of fish and other secondary production (Frank *et al.*, 2006). Less productive northerly systems with lower fisheries yields exhibited collapses of predator populations in response to fishing. This is largely due to the lower intrinsic rates of population increase of larger-bodied predator populations at lower temperatures (Myers *et al.*, 1997). In less productive areas, declining predator numbers could result in increased primary production. This would be mediated by reduced predation on mesopredatory fishes which would in turn increase predation on and reduce zooplankton abundance (Frank *et al.*, 2006). Untangling the effects of fishing and climate on plankton variability remains a challenging task as both forcing factors can act simultaneously upon ecosystem structure (Greene and Pershing, 2007). While less productive systems are more vulnerable to fisheries mediated top-down control, ultimately primary production

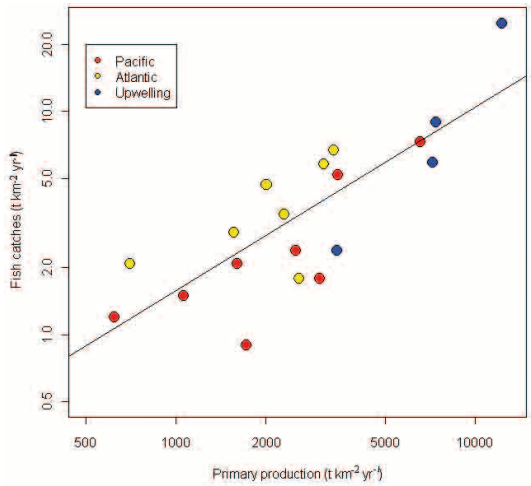

Figure 2.2 The relationship between fishery landings (catches) and primary production in a range of large marine ecosystems (Redrawn from Ware 2000). Approximately 1 mt km^2 yr^{-1} of fish catch is derived from 1000 mt km^2 yr^{-1} of primary production.

sets a top limit to the long-term average of higher trophic level production or food web carrying capacity (Frank *et al.*, 2006; Chassot *et al.*, 2007). These limits can be used to understand the primary production required to support fisheries and the sustainability or the ecological footprint of fisheries.

2.2.1.1 Measuring the footprint of fisheries based on remote sensing

Ecological footprints represent the effective ecosystem area appropriated by fishers and others in the form of ecosystem products and services. Ecological footprints are measured as the ratio between the ecological productivity of the ecosystem and human consumption (Wackernagel and Rees, 1996). The advent of satellite remote sensing has enabled fisheries scientists to calculate the primary production required to support fisheries based on phytoplankton-based ecosystems and the footprint of coral-reef fisheries.

The footprint of plankton-based fisheries, which make up the bulk of the world fish catch, has yet to be estimated. However the primary production required (PPR) to sustain the food pyramid upon which the animals feed which are caught by global fisheries in different ecosystem types (coastal, shelf, upwelling, oceanic) has been calculated for the early 1990s (Pauly and Christensen, 1995). The PPR of fisheries depends on their trophic level of the constituents of the catch: far more primary production is required to produce one metric tonne of a high-level trophic fish (e.g., tuna), than of a low level-trophic fish (e.g., sardine) because the transfer efficiency from one trophic level to the next is typically 10% in the ocean (Pauly and Christensen, 1995; Ware, 2000). Thus, to calculate the primary productivity of

a given tonnage of fish catch, we need the average trophic level (TL) of the fish, an assumption about trophic efficiency (TE), the number of catch and this equation from Pauly and Christensen (1995):

$$PPR = catch \cdot (1/TE)^{TL-1}, \tag{2.1}$$

or assuming a TE of 10%:

$$PPR = catch \cdot 10^{TL-1}. \tag{2.2}$$

To refine the broad ecosystem types used by Pauly and Christensen (1995), the catch data used were from the Sea Around Us Project, which has spatialised the statistics submitted to the Food and Agriculture Organization of the United Nations (FAO) into ½ degree cells and regrouped them by Exclusive Economic Zones (EEZ) and Large Marine Ecosystems (LME) (Watson *et al.*, 2004). To date these 'nominal' landings exclude discarded by-catch, illegal and other unreported catches, as these have been estimated for only a few countries (Zeller *et al.*, 2007; Zeller and Pauly, 2007). Trophic levels for the fish and invertebrate taxa in the FAO statistics were derived from time- and location-specific diet composition studies (www.fisheries.org and www.sealifebase.org). Global estimates of primary production were derived from remotely sensed SeaWiFS data (Satellite-derived chlorophyll estimates from the Sea-viewing Wide Field-of-view Sensor), under the responsibility of Nicolas Hoepffner, and made available on a monthly basis in form of an annual cycle (October 1997 to September 1998), with a spatial resolution of 9 km. These data, thus, represent only approximately the primary production of specific years and the average primary production over the period from which catch data are available (1950 to 2004) (for more details see www.seaaroundus.org). In order to facilitate comparisons between EEZs and LMEs, the maximum PPR was calculated from the mean of the 5 years with the highest values.

The primary production required to support the fisheries within EEZs ranges between 1-2% for the Australian EEZ up to 60-80% for the Icelandic EEZ. The EEZ of Mauritania is fished by distant water fleets from European and Asian countries, along with the relatively small Mauritanian fisheries. Together these fleets appropriate between 15 and 20% of the observed primary production (Figure 2.3).

The maximum primary production required to support the fisheries of most of the Large Marine Ecosystems is below 20%, with 30 LMEs having PPR below 10% (Figure 2.4). Of these, 16 are Arctic, Antarctic and Australian LMEs. On the other hand, a few LMEs have unrealistically high PPR values (> 50%). These high values may be due to: (1) the assumptions and data used for implementing the method itself (e.g. the use of a year's worth of SeaWIFs global remote sensing data to derive annual PP taken as representative for all years since 1950); (2) over-reported landings, i.e., catches that were not made anywhere, or which are reported from an area, but caught elsewhere (Watson and Pauly, 2001); and (3) massive range

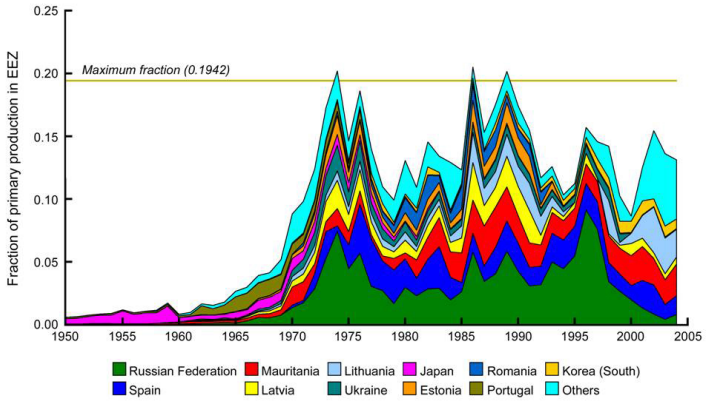

Figure 2.3 The Primary Production Required by the fisheries operating in the Exclusive Economic Zone of Mauritania, Northwest Africa. In this ecosystem, it is distant-water fleets from Europe and East Asia which appropriate most of the primary production, leaving little for Mauritanians; a maximum PPR of nearly 20% was taken in the early 1970s and late 1980s.

extension in periods of peak abundance, or migration of targeted species, especially feeding migrations, extending beyond the limits of an LME. This occurs in the Kuroshio LME where sardine, for a few years, greatly expanded their range; and some of the smaller LMEs of the North Atlantic where cod and other groundfish may be fished in a LME, but feed in another. Problems in the estimation of primary production will occur throughout the world, however, and it is likely to be small and hence not the cause of the pattern in Figure 2.4. While this approach can provide insight into the amount of primary production required to support fisheries, further work is required to determine what proportion of primary production can be sustainably removed each year without compromising ecosystem resilience and integrity, i.e. the ecological footprint or 'fishprint' of plankton-based fisheries.

The global extent of coral reefs has recently been measured accurately for the first time, by combining aerial photography and satellite sensors, enabling the calculation of the first estimates of the footprint of coral reef fisheries (Spalding and Grenfell, 1997; Spalding *et al.*, 2001). The ecological footprints of the coral reef fisheries of 49 island nations were calculated; this represents 41% of the world's coral reefs. The human consumption of coral reef fishes, molluscs and crustaceans was estimated from the nominal fisheries landings reported to the UN FAO and sustainable fisheries production was assumed to be 5 metric tonnes km^{-2} $year^{-1}$. It was estimated that total landings of coral reef fisheries are currently 64% higher than can be sustained. Consequently, the area of coral reef appropriated by fisheries exceeds the available effective area by 75,000 km^2, or 3.7 times the area of Australia's Great Barrier Reef (Newton *et al.*, 2007). The size of the footprint was greater in nations with higher human population densities per unit area of coral reef (Figure 2.5).

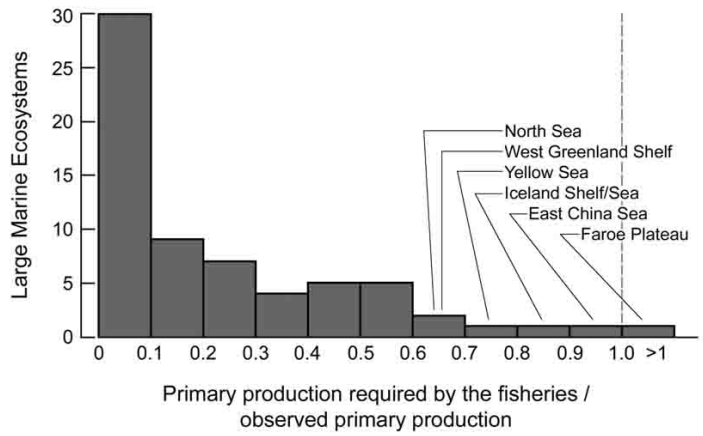

Figure 2.4 The distribution of the maximum Primary Production Required to support fisheries in the World's 66 Large Marine Ecosystems. The majority of LMEs have maximum PPR <20%; some LMEs have unrealistically high values (>60%), due to catch over-reporting, and/or boundaries that fail to encompass the entire distribution range of important species.

As human populations grow so will their footprint increase from 1.64 to 2.7 by 2050 and the area appropriated exceeds the available area by 196,000 km^2 (Figure 2.6). There are key assumptions which will require further work to refine the footprint estimate (Newton *et al.*, 2007), including: revised coral reef habitat area definitions and estimates (Andréfouët *et al.*, 2006), better estimates of coral reef fisheries landings (Zeller *et al.*, 2006; Zeller *et al.*, 2007) and a better understanding of sustainable yields of coral reefs (Halls *et al.*, 2006; McClanahan *et al.*, 2008). However, it is becoming increasingly clear that this first estimate of the footprint of coral reef fisheries may be underestimated. Adding more coral reef habitat to the world's oceans is not a feasible management option. However these footprints, for the first time, provide an indication of the scale of the challenge facing tropical island nations - which is to sustain the livelihoods of an increasing number of people while ensuring the continued resilience and productivity of coral reefs.

2.2.1.2 Observed primary production and the changing fisheries catches of Large Marine Ecosystems

A key question is how the predicted and observed changes on ocean productivity have affected fisheries catches? To answer this question researchers are examining changes in primary production and fish catches at the scale of Large Marine Ecosystems (LME) (Sherman *et al.*, 2007; Sherman *et al.*, in review). Over the last ten years there was no consistent trend in primary productivity, and of the 63 LMEs examined; only the annual primary production trends of four LMEs were significant. Primary productivity declined in one LME (Bay of Bengal), and increased in three others

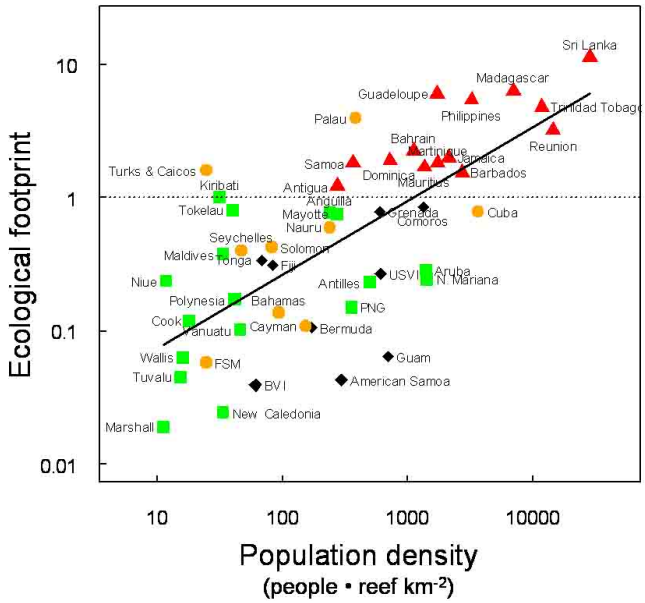

Figure 2.5 Densely populated islands have unsustainable coral reef fisheries footprints. There is a positive relationship between human population density per unit area of island coral reef ecological footprints. Island reef fisheries status is represented by four colours: green squares – underexploited, orange circles – fully exploited, red triangles– overexploited, black diamonds – collapsed. The line represents the least squares regression model $\log_{10}Y$ = -1.59 + 0.53($\log_{10}$ persons per km^2 coral reef). The partial dashed line represents an ecological footprint = 1 for an MSY of 5 tonnes km^{-2} yr^{-1} (redrawn from Newton *et al.*, 2007).

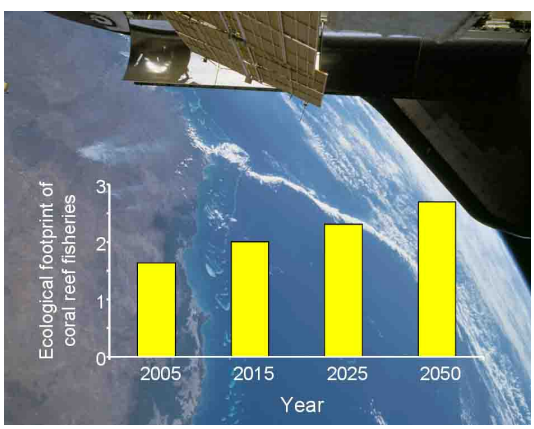

Figure 2.6 The increase in the ecological footprint of coral reef fisheries of 49 island nations as human population size grows. In 2005 the area of coral reef appropriated by fisheries exceeded the available effective area by 75,000 km^2, or 3.7 times the area of Australia's Great Barrier Reef. The background is the Great Barrier Reef, Queensland, Australia as seen from the space shuttle Atlantis (Photo courtesy of NASA).

(Hudson Bay, Humboldt Current and Red Sea) (Sherman *et al.*, 2007). Monthly and annual means of primary production estimates were derived from satellite-borne data of NOAA's Northeast Fisheries Science Center, Narragansett Laboratory calculated from modeled chlorophyll and light attenuation profiles derived from satellite chlorophyll and photosynthetically active radiation (PAR) measurements using the Ocean Productivity from Absorption of Light (OPAL) model.

The effects of warming on global biomass yields were non-uniform in relation to any persistent global pattern of increasing or decreasing yields. The response of global fisheries yields to warming trends varies by LME clusters. Both increasing and decreasing fishery trends were observed in fast-warming, moderate-warming and slow-warming LMEs. The results, however, are complicated by increased fishing effort that has led to exploited and overexploited fish stocks, driven by the fish protein and food security needs of many developing countries. Increasing fisheries biomass yields were observed in half (31) of LMEs while decreasing trends were detected in the remaining 32 LMEs (Sherman *et al.*, in review). A clear example of increasing fisheries yields in response to warming climate is in the Norwegian Sea, Faroe Plateau and Iceland Shelf LMEs. These three LMEs account for 5% of the world marine fisheries yield and are influenced by bottom-up forcing of increasing zooplankton abundance and warming hydrographic conditions in the northern areas of the North Atlantic. Here stocks of herring, blue whiting and capelin are benefiting from an expanding prey field of zooplankton (Beaugrand *et al.*, 2002; Skjoldal and Saetre, 2004; Hjermann *et al.*, 2007). The productivity and fisheries of these LMEs are benefiting from the increasing strength of the sub-Polar gyre bringing warmed waters to the northeast Atlantic. In contrast, the warmer water from the sub-Polar gyre is contributing to decreasing production and fisheries yields in the relatively warmer southern LMEs of the northeast Atlantic (the North Sea, Celtic Biscay, and Iberian Coastal LMEs). In these southern Europe fast-warming LMEs, the mean annual marine fisheries biomass yields have decreased due to over exploitation but may also be suffering from declining abundance levels of warm water zooplankton (Valdés *et al.*, 2007) and northward and deepening distribution of fishes (Perry *et al.*, 2005; Dulvy *et al.*, 2008).

2.2.1.3 Future climate change impacts on fish and fisheries distributions

If distributions of fishes change how will the distributions of fisheries catches change? Using a bioclimatic envelope modeling approach and assuming a 2.5 °C temperature rise, the geographic distribution of the yellow croaker (*Larimichthys polyactis*) was predicted to move northwards, with the area of occupancy increasing, expanding out from the China Sea and invading Japanese waters (Cheung *et al.*, 2008b). The fisheries productivity remains unchanged (assuming the distribution and quantity of primary production are unchanged), however the geographic distribution of potential catches changes markedly (Figure 2.7). Currently, most of the catch is taken by

China and South Korea, but under the climate-shifted scenario catch potential would increase, particularly in Japan and North Korea (Cheung *et al.*, 2008a).

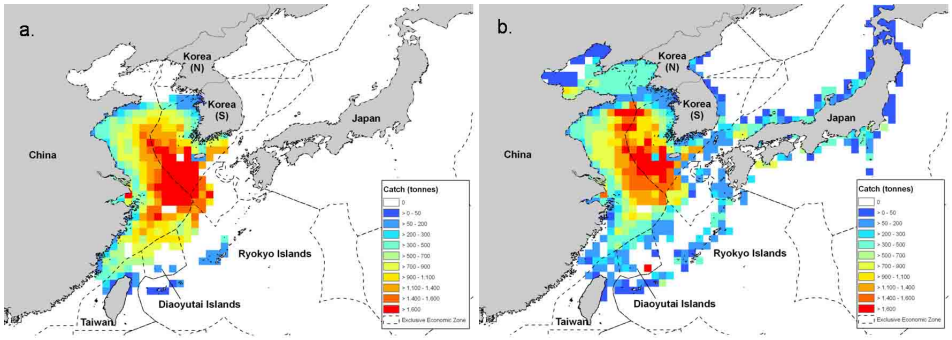

Figure 2.7 (a) Current (early 2000s) and (b) climate-shifted distributions of the small yellow croaker (*Larimichthys polyactis*: Sciaenidae). The current distribution was generated from the method described by Close et al. (2006). The climate-shifted distribution was predicted by a dynamic bioclimate envelope model described by Cheung et al. (2008), under a hypothetical increase in average global ocean temperature of 2.5°C (redrawn from Cheung *et al.*, 2008a).

2.2.2 Size spectra

Static size spectra models can be used to predict equilibrium abundance and biomass of animals in the sea from three variables and two parameters: (i) primary production, (ii) phytoplankton size distribution, (iii) sea surface temperature, (iv) predator-prey mass ratio, and (v) transfer efficiency (Figure 2.8). The advent of satellite remote sensing allows time-integrated measures of primary production and sea surface temperatures across the globe on small spatial scales. Most oceanic primary production (∼90%) is accounted for by remote-sensing estimates; except seasonally-icebound high latitude areas and areas dominated by non-planktonic production such as coral reef, kelp forest, seagrasses and microphytobenthos (Duarte and Cebrián, 1996). The size distribution of phytoplankton cells depends upon local productivity. The most productive areas occur in shallow well-mixed inshore shelf systems and coastal upwelling zones. These support very large phytoplankton cells (>100 μm in diameter) that can often form large gelatinous colonies that can be directly grazed by herbivorous fishes. Offshore oceanic oligotrophic zones are mainly dominated by nano- and picoplankton (5-25 μm and <5 μm in diameter) (Agawin *et al.*, 2000; Marañón *et al.*, 2001; 2007). Biological rates increase with temperature in a manner described by the Boltzmann factor or Van't Hoff-Arrhenius equation $e^{-E/kT}$, where E is the activation energy of metabolism (0.63 eV), k is Boltzmann's constant (8.62 x 10^{-5} eV K^{-1}), and T is temperature in Kelvin (°C + 273) (Brown *et al.*, 2004). In the sea, predators are typically between 300 and 1000 times heavier than their prey (Cushing, 1975; Jennings, 2005; Brose *et al.*, 2006). The relatively limited predator-prey mass ratio arises from allometry; the size of mouth parts of fishes and

many other marine predators increase in a fixed proportion to total body size. A fundamental consequence is that only larger organisms can catch and consume larger prey. This limits the number of trophic levels that can be supported: the larger the phytoplankton cells at the base of the food chain, the shorter the food chain (Ryther, 1969; Jennings and Warr, 2003). Longer food chains are less efficient and less productive than shorter food chains because energy is lost at each trophic level due to low transfer efficiency. Between 5 and 15% of energy in each trophic level is lost due to respiration and excretion or transport out of the ecosystem (Pauly and Christensen, 1995; Ware, 2000).

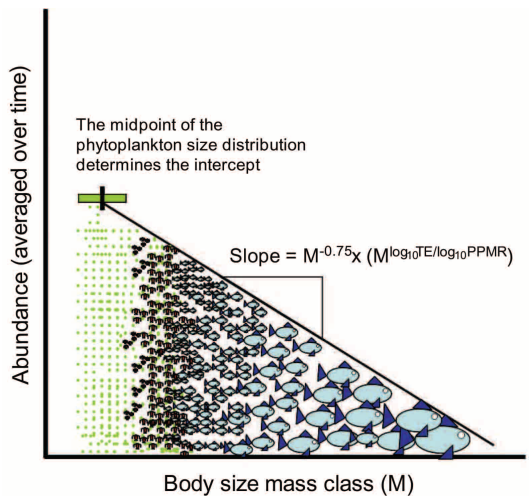

Figure 2.8 The pelagic size spectrum of time averaged abundance in each body mass class. The slope of the body mass (M) size spectrum is a function of transfer efficiency (TE) and predator-prey mass ratio (PPMR). The height of the intercept or start of the spectrum depends on primary production which also determines the phytoplankton size distribution at the start of the size spectrum. This pelagic spectrum consists of phytoplankton, zooplankton and fishes. In reality benthic and pelagic invertebrates (jellyfish, squid, crabs, worms) occupy intermediate size classes and mammals and sea birds occur in the largest size classes.

A static or equilibrium size spectra approach has been used to estimate global fish production and biomass, in the absence of fishing, using remotely-sensed estimates of primary production on a 36 km^2 scale. Based on an estimate of total primary production of 4.1 x 10^{11} mt yr^{-1}, the global biomass of marine animals ($> 10^{-5}$ g wet weight) is 2.6 x 10^9 t and annual production is 1 x 10^8 mt (Jennings *et al.*, 2008). Globally the areas of highest fish biomass and production were found in upwelling areas and mid-latitude shelf seas and the total biomass of fish > 10 g was 5.3 x 10^8 mt and production of 1.1 x 10^8 mt (Figure 2.9).

While this approach is simple to implement and requires few parameters, it is sensitive to the expected range of transfer efficiencies and predator-prey mass ratios. Further refinement requires fundamentally new research into trade-offs between transfer efficiencies and predator-prey mass ratio and how these parameters vary

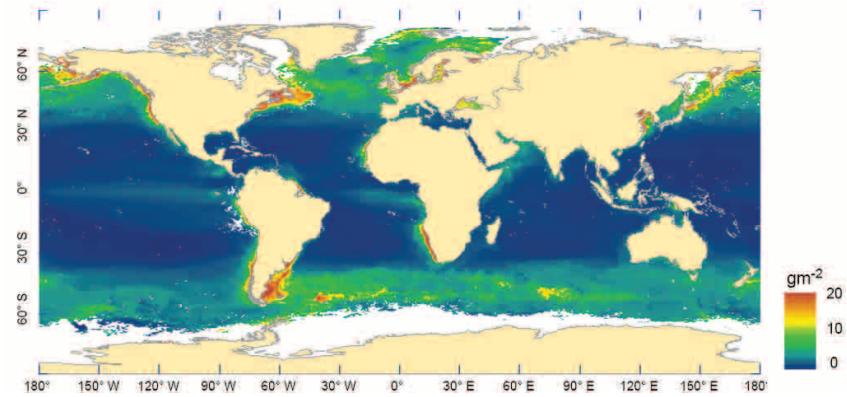

Figure 2.9 The global distribution of marine teleost fish biomass. The overlays show the FAO fishing areas and their corresponding codes. Primary production estimates were not available for the areas shown in white (redrawn from Jennings *et al.* 2008)

across environments. At present the approach can only provide size-based outputs for large functional groupings, (e.g. bony fishes and elasmobranch), further fundamental work on the partitioning of the energy niche and the optimal distribution of life histories by size and energy availability is required to predict species abundances from size spectra (Jennings *et al.*, 2008). Currently, dynamic size spectra models are being developed to utilize new measurements of the size distribution of primary production (Hirata *et al.*, in press) and provide predatory feedback to phytoplankton production to derive more realistic estimates of local fish biomass and production. (Blanchard *et al.*, In Press)

2.2.3 Energetic mass-balance models

The flow of energy through ecosystems can be described by various food web models, such as Ecopath with Ecosim and ecological network analysis. Ecopath with Ecosim models rely on balancing the production and biomass of functional groups of organisms based on their feeding relationships and the efficiency of energy transfer between trophic levels (Figure 2.10)(Polovina, 1984; Pauly *et al.*, 2000).

Ecological network analysis incorporates analytical techniques for studying the indirect trophic effects and the structure of recycling pathways (Ulanowicz, 1986). Specifically, the indirect trophic effects and energy and/or nutrient recycling due to changes in primary production can be described with ecological network analysis in the dynamic simulation of the Ecopath with Ecosim suite (Christensen *et al.*, 2005). Ecopath models have been used for a range of issues including calculating the primary production required to support global fisheries catches (Pauly and Christensen, 1995) and to evaluate the relative importance of climate change and fishing in determining the dynamics of high trophic level species (Guénette *et al.*, 2006). The effect of environmental variation on an ecosystem is readily seen in

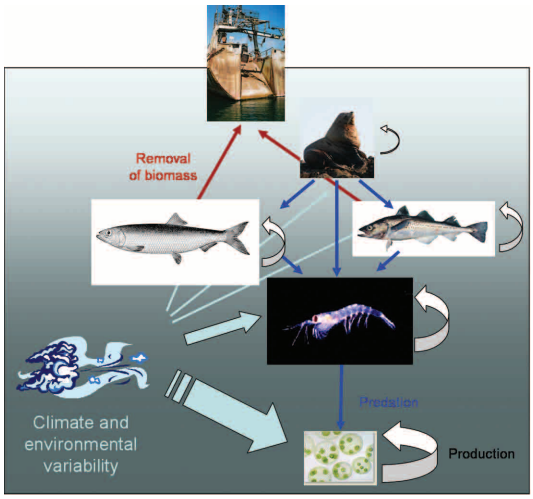

Figure 2.10 An Ecopath mass balance 'box' model of a marine ecosystem. Standing biomass is represented by the size of each picture; production is represented by the size of the curved arrow. Energy transfer up through the food web through predation is shown by blue arrows and energy removal by exploitation shown in red arrows. The whole ecosystem is embedded within the effects of climate change and environmental variability, with greatest, most direct effects at lowest trophic levels, largely mediated through the effect of environmental variability on phytoplankton production.

the changes in the total systems throughput of that system. The total ecosystem throughput is the total amount of energy flowing through the ecosystem, from low to high trophic levels via predation and decomposition pathways and is therefore affected by environmental variability (Ulanowicz, 1986).

For example, in the Gulf of Alaska, the total ecosystem throughput (Figure 2.11a,b) is driven by the changes affected on the primary production of the ecosystems by the Aleutian Low Pressure system and the sea surface temperatures as described by the Pacific Decadal Oscillation (Heymans *et al.*, 2005). The Pacific Decadal Oscillation positively influences ecosystem throughput in Southeast Alaska and has a negative influence in the western and central Aleutian Islands. However, when the direct effects of the environmental drivers are removed, the effects of the changes in flow structure can be observed. Specifically, the average mutual information (AMI) is a network analysis index which measures the degree of organization of the fluxes of energy and matter among ecosystem compartments of functionally-similar species (Ulanowicz and Abarca-Arenas, 1997).

We can see that in two different ecosystems in the Gulf of Alaska (the western and central Aleutian Islands and Southeast Alaska) the average mutual information was very different and did not directly relate to the environmental driver (Figure 2.11c). The reduction in large predators (Steller's sea lions) in the Aleutian Islands simplified the pathways for energy and matter flow in the ecosystem after the regime shift in the late 1970s, while no such simplification was experienced in Southeast

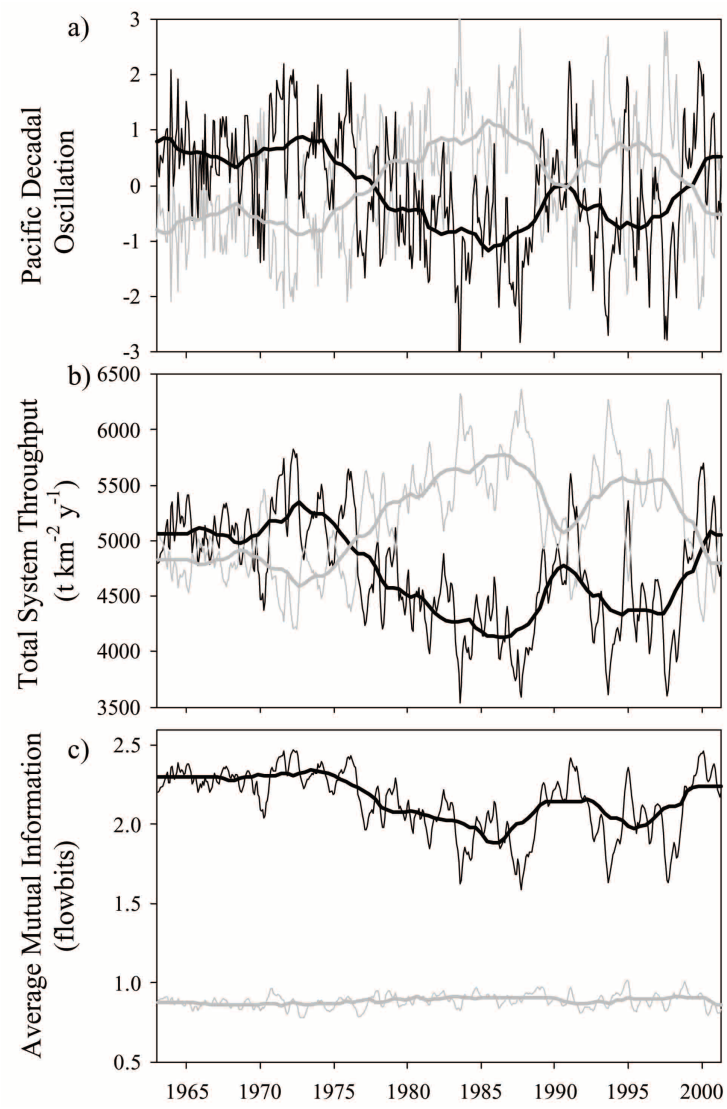

Figure 2.11 (a) Pacific Decadal Oscillation (PDO) the Aleutian islands (black) and Southeast Alaska (grey) and changes in (b) total ecosystem throughput and (c) average mutual information (redrawn from Heymans *et al.*, 2005)

Alaska, where most species increased over the study period.

2.2.4 End-to-end models

End-to-end models aim to (i) represent all ecosystem components, from the abiotic components and the biological food web, (ii) integrate physical and biological processes at different scales, (iii) using two-way interactions and feedback, and (iv) account for the dynamic forcing of climate variability and other human impacts acting through multiple pathways and trophic levels (Travers *et al.*, 2007; Cury *et al.*, 2008). The models are founded on first principles and aim to represent accurately the dynamic physical forces affecting oceans (wind, tides, currents, and light penetration) and their effects on primary and secondary production. These models usually consist of linked or coupled models that use some form of hydrodynamic model to drive a biogeochemical model to provide primary production and zooplankton production to higher trophic levels (Lehodey *et al.*, 1997; Megrey *et al.*, 2007).

The simplest biogeochemical models focus on the pelagic environment and include some plankton functional groups (e.g. Nutrient-Phytoplankton-Zooplankton dynamics models, such as ROMS-NPZD [Regional Ocean Model System-NPZD], NEMURO [North Pacific Ecosystem Model for Understanding Regional Oceanography] POLGCOMS [Proudman Oceanographic Laboratory-Global Coastal Ocean Modeling System], DGOM [Dynamic Green Ocean model]) (Le Quéré *et al.*, 2005; Kishi *et al.*, 2007). The more complex models include coupled benthic - pelagic habitats and include benthic functional groups and sediment chemistry (ERSEM [European Regional Seas Ecosystem Model]) (Allen *et al.*, 2001; Siddorn *et al.*, 2007). The key challenge is to convert the output of the biogeochemical or low trophic level (LTL) models into fish and higher trophic levels, and eventually to feed predation from higher trophic levels back into low trophic level models (Travers *et al.*, 2007).

At present there is no generic model for converting dynamics at low trophic levels to dynamics at higher trophic levels relevant to fisheries. There are some important case-studies of location-specific population dynamic models that provide the proof of principle. They focus on the dynamics of low-trophic level pelagic fishes, such as Pacific herring (*Clupea harengus pallasi*) and Pacific saury (*Cololabis saira*) (Ito *et al.*, 2004; Megrey *et al.*, 2007). There are still difficult theoretical and practical challenges associated with end-to-end models including data availability, the coupling of submodels based on different formalism and discretization methods, the representation of major ecological processes such as excretion and egestion that can generate feedbacks between components, and the integration of different trophic level components characterized by distinct spatio-temporal scales and functional complexity (deYoung *et al.*, 2004). The development of such integrative models is a key challenge for assessing the combined impacts of fishing and climate changes on marine ecosystem structure and functioning (deYoung *et al.*, 2004; Cury *et al.*, 2008). The synoptic character of satellite data makes them particularly suitable

inputs for end-to-end models and for model evaluation through data assimilation techniques, for instance (Kuroda and Kishi, 2004).

While the approaches to end-to-end modeling of population dynamics are tailor-made and context-specific they have the advantage that they explicitly capture the role of biodiversity in the emergence of alternative trophic pathways, which may emerge such as climate-forced shift between sardine and anchovy dominated states (Cury *et al.*, 2008). One pragmatic way of extending the approach to and end-to-end model of higher trophic level ecosystem dynamics might be to link a low trophic level hydrodynamic-biogeochemical model to either size spectra models or Ecopath with Ecosim models (Figure 2.12).

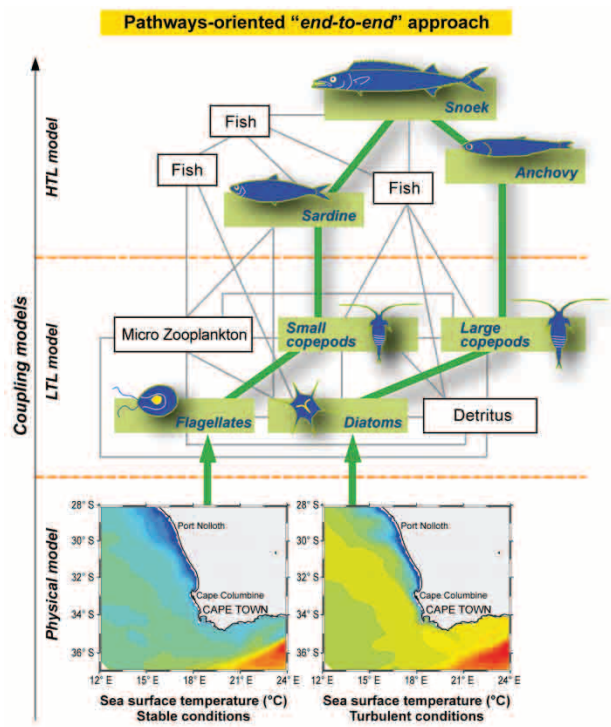

Figure 2.12 End-to-end models can be built by coupling physical atmospherically forced hydrodynamic models to models of lower trophic levels (pelagic and benthic) to high trophic level fish production models (Cury *et al.*, 2008). The boxes represent key species or groups of species, the lines represent the trophic interactions (pathways) and the arrows represent the forcing of hydrodynamic models on the lower trophic level model (reprinted with permission from Trends in Ecology and Evolution).

2.3 Concluding remarks

After a century, fisheries oceanography is coming of age. The combination of rapid theoretical development, collaborative and integrative modeling efforts, and

in particular, the accumulation of a sufficiently long global time-series of remotely-sensed ocean colour and sea surface temperatures allow hypothesis testing at large spatial scales and rapid model development and validation. The development of cross-trophic level models linking phytoplankton to fish production is timely given the urgent need to understand and predict the effects of global climate change on marine ecosystems.