

Accelerated Warming and Emergent Trends in Fisheries Biomass Yields of the World's Large Marine Ecosystems

Information on the effects of global climate change on trends in global fisheries biomass yields has been limited in spatial and temporal scale. Results are presented of a global study of the impact of sea surface temperature (SST) changes over the last 25 years on the fisheries yields of 63 large marine ecosystems (LMEs) that annually produce 80% of the world's marine fisheries catches. Warming trends were observed in 61 LMEs around the globe. In 18 of the LMEs, rates of SST warming were two to four times faster during the past 25 years than the globally averaged rates of SST warming reported by the Intergovernmental Panel on Climate Change in 2007. Effects of warming on fisheries biomass yields were greatest in the fast-warming northern Northeast Atlantic LMEs, where increasing trends in fisheries biomass yields were related to zooplankton biomass increases. In contrast, fisheries biomass yields of LMEs in the fast-warming, more southerly reaches of the Northeast Atlantic were declining in response to decreases in zooplankton abundance. The LMEs around the margins of the Indian Ocean, where SSTs were among the world's slowest warming, revealed a consistent pattern of fisheries biomass increases during the past 25 years, driven principally by human need for food security from fisheries resources. As a precautionary approach toward more sustainable fisheries utilization, management measures to limit the total allowable catch through a cap-and-sustain approach are suggested for the developing nations recently fishing heavily on resources of the Agulhas Current, Somali Current, Arabian Sea, and Bay of Bengal LMEs.

INTRODUCTION

The heavily exploited state of the world's marine fisheries has been well documented (1–3). Little, however, is known of the effects of climate change on the trends in global fisheries biomass yields. The Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) stated with “high confidence” that changes in marine biological systems are associated with rising water temperatures affecting shifts in pelagic algae and other plankton and fish abundance in high latitudes (4). The report also indicated that adaptation to the impacts of increasing temperatures in coastal systems will be more challenging in developing countries than in developed countries because of constraints in adaptive capacity. From a marine resources management perspective, the eight regions of the globe examined by the IPCC (i.e., North America, Latin America, Europe, Africa, Asia, the Australia and New Zealand region, and the two Polar regions), are important fisheries areas but at a scale too large for the determination of temperature trends relative to the assessment and management of the world's marine fisheries biomass yields produced principally in 64 large marine ecosystems (LMEs) (Fig. 1). These LMEs, in coastal

waters around the globe, annually produce 80% of the world's marine fisheries biomass (Fig. 2).

LMEs are areas of an ecologically based nested hierarchy of global ocean biomes and ecosystems (5). Since 1995, LMEs have been designated by a growing number of coastal countries in Africa, Asia, Latin America, and eastern Europe as place-based assessment and management areas for introducing an ecosystems approach to recover, develop, and sustain marine resources (6). The LME approach to the assessment and management of marine resources is based on the operationalization of five modules, with suites of indicators for monitoring and assessing changing conditions in ecosystems: *i*) productivity, *ii*) fish and fisheries, *iii*) pollution and ecosystem health, *iv*) socioeconomic, and *v*) governance (7). The approach is part of an emerging effort to relate the scale of place-based ecosystem research and assessment to improved ecosystem-based management of ocean resources within the natural boundaries of LMEs (8, 9). In recognition of the observational evidence of global warming from the Fourth Assessment Report of the IPCC (4) and the lack of information on trends in global warming at the LME scale, where most of the world's marine fisheries biomass yields are produced, we undertook a study of the physical extent and rates of sea surface temperature (SST) trends in relation to fisheries biomass yields and satellite-derived primary productivity of the world's LMEs.

METHODS

Fisheries biomass yields are not presented here as representative of individual fish stock abundances; they are representative of fisheries catches and are used here to compare the effects of global warming on the fisheries biomass yields of the world's LMEs. The comparative analysis of global temperature trends, fisheries biomass yields, and primary productivity was based on available time-series data at the LME scale on SSTs, marine fisheries biomass yields, and Sea-viewing Wide Field-of-view Sensor (SeaWiFS)-derived primary productivity values. The SST of LMEs is a thermal parameter routinely measured worldwide. Subsurface temperature data, albeit important, are limited in the spatial and temporal density required for the reliable assessment of thermal conditions at the LME scale worldwide. The UK Meteorological Office Hadley Center SST climatology was used in this analysis (10) as the Hadley data set has a resolution of 1 degree latitude by 1 degree longitude globally. A detailed description of this data set has been published by Rayner et al. (11). Mean annual SST values were calculated for each 1° x 1° cell and then were area-averaged within each LME (10).

LME primary productivity estimates were derived from satellite-borne data of the National Oceanic and Atmospheric Administration's Northeast Fisheries Science Center, Narragansett Laboratory. These estimates originated from SeaWiFS (satellite-derived chlorophyll estimates), Coastal Zone Color Scanner (CZCS), a large archive of *in situ* near-surface chlorophyll data, and satellite SST measurements to quantify the spatial and seasonal variability of near-surface chlorophyll

Large Marine Ecosystems of the World and Linked Watersheds

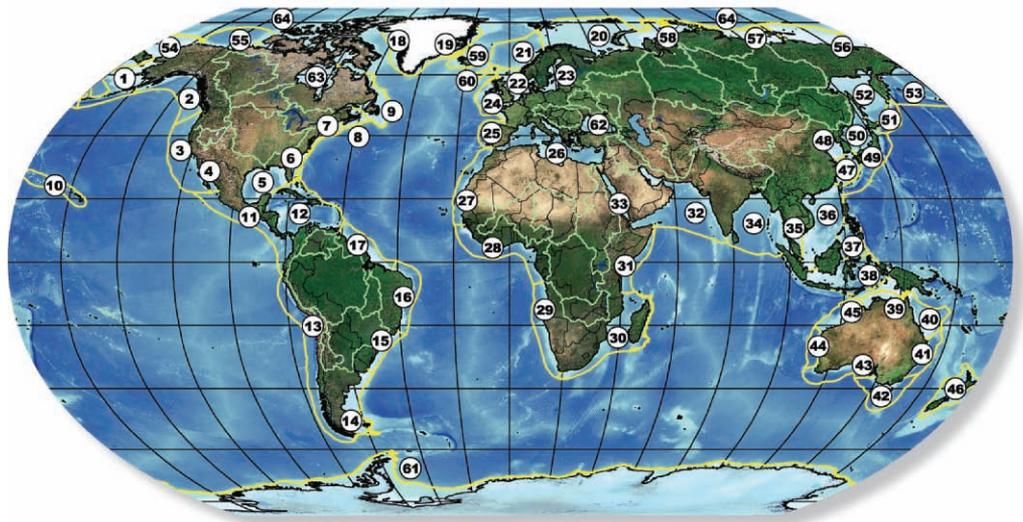


Figure 1. Large marine ecosystems of the world.

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|-------------------------------------|-------------------------|---------------------------|--|----------------------|------------------|
| 1 East Bering Sea | 13 Humboldt Current | 25 Iberian Coastal | 37 Sulu-Celebes Sea | 48 Yellow Sea | 60 Faroe Plateau |
| 2 Gulf of Alaska | 14 Patagonian Shelf | 26 Mediterranean Sea | 38 Indonesian Sea | 49 Kuroshio Current | 61 Antarctic |
| 3 California Current | 15 South Brazil Shelf | 27 Canary Current | 39 North Australian Shelf | 50 Sea of Japan | 62 Black Sea |
| 4 Gulf of California | 16 East Brazil Shelf | 28 Guinea Current | 40 Northeast Australian Shelf-Great Barrier Reef | 51 Oyashio Current | 63 Hudson Bay |
| 5 Gulf of Mexico | 17 North Brazil Shelf | 29 Benguela Current | 41 East-Central Australian Shelf | 52 Okhotsk Sea | 64 Arctic Ocean |
| 6 Southeast U.S. Continental Shelf | 18 West Greenland Shelf | 30 Agulhas Current | 42 Southeast Australian Shelf | 53 West Bering Sea | |
| 7 Northeast U.S. Continental Shelf | 19 East Greenland Shelf | 31 Somali Coastal Current | 43 Southwest Australian Shelf | 54 Chukchi Sea | |
| 8 Scotian Shelf | 20 Barents Sea | 32 Arabian Sea | 44 West-Central Australian Shelf | 55 Beaufort Sea | |
| 9 Newfoundland-Labrador Shelf | 21 Norwegian Shelf | 33 Red Sea | 45 Northwest Australian Shelf | 56 East Siberian Sea | |
| 10 Insular Pacific-Hawaiian | 22 North Sea | 34 Bay of Bengal | 35 Gulf of Thailand | 57 Laptev Sea | |
| 11 Pacific Central-American Coastal | 23 Baltic Sea | 35 Gulf of Thailand | 46 New Zealand Shelf | 58 Kara Sea | |
| 12 Caribbean Sea | 24 Celtic-Biscay Shelf | 36 South China Sea | 47 East China Sea | 59 Iceland Shelf | |

and SST in the LMEs of the world. Daily estimates of global primary productivity ($\text{g carbon m}^{-2} \text{d}^{-1}$) were calculated using the Ocean Productivity from Absorption and Light model, a derivative of the model first formulated in Marra et al. (12).

Prior to the Sea Around Us Project (SAUP), projections of marine fisheries yields at the LME scale were largely defined by the range of vessels exploiting a given resource (13). The need for countries to manage fisheries within Exclusive Economic

Zones under United Nations Convention on the Law of the Sea initiated efforts to derive fisheries yields at the national level (14) and is consistent with the emergence of ecosystem-based management at the LME scale (15, 16). The time series of fisheries biomass yields (1950–2004) used in this study was based on the time series data provided at the LME scale by the SAUP at the University of British Columbia (5, 16, 17).

RESULTS

Comparative SST Clusters

The 1957–2006 time series revealed a global pattern of long-term warming; however, the long-term SST variability since 1957 was not linear over the period. Specifically, most LMEs underwent a cooling between the 1950s and the 1970s, replaced by a rapid warming from the 1980s until the present. Therefore, we recalculated linear SST trends using only the last 25 years of data (18). Net SST change in each LME between 1982 and 2006 based on linear SST trends is summarized in Table 1.

The most striking result was the consistent global-scale warming of LMEs, with the notable exceptions of two—the California Current and Humboldt Current. These LMEs experienced cooling over the last 25 years. Both are in large and persistent upwelling areas of nutrient-rich cool water in the eastern Pacific. The Arctic Ocean LME was not included because of perennial ice cover. The SST values were partitioned into 0.3°C intervals to allow for comparison among LME warming rates. The warming trend observed in 61 LMEs ranged from a low of 0.08°C for the Patagonian Shelf LME to a high of 1.35°C in the Baltic Sea LME (Table 1). The relatively rapid warming exceeding 0.6°C over 25 years was observed almost exclusively in moderate- and high-latitude LMEs. This pattern is generally consistent with the model-predicted polar-and-subpolar amplification of global warming (4). The warming in low-latitude LMEs was several times slower than the warming in high-latitude LMEs (Table 1). The most rapid warming

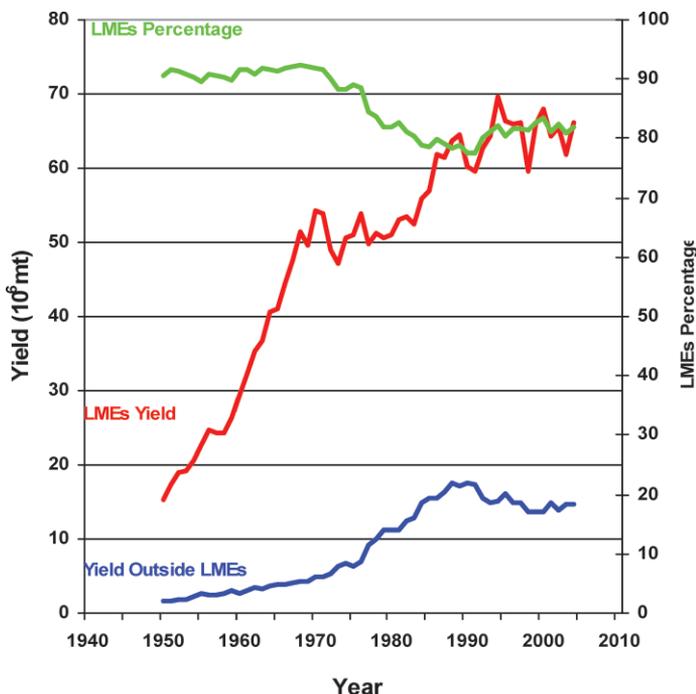


Figure 2. Annual global marine fisheries biomass yields (in tonnes) of the world's LMEs. From the University of British Columbia's SAUP.

Table 1. SST change, slope of linear regression, and standard error of slope for 63 LMEs.

LME # and name	SST net change (°C) 1982–2006	SST warming rate (°C decade ⁻¹) 1982–2006	Slope of linear regression (°C y ⁻¹)	Standard error of slope (°C y ⁻¹)
LME23 = Baltic Sea	1.35	0.5625	0.0563	0.0151
LME22 = North Sea	1.31	0.5458	0.0544	0.0099
LME47 = East China Sea	1.22	0.5083	0.0509	0.0077
LME50 = Sea of Japan/East Sea	1.09	0.4542	0.0453	0.0098
LME9 = Newfoundland-Labrador Shelf	1.04	0.4333	0.0435	0.0108
LME62 = Black Sea	0.96	0.4000	0.0401	0.0124
LME8 = Scotian Shelf	0.89	0.3708	0.0370	0.0105
LME59 = Iceland Shelf	0.86	0.3583	0.0360	0.0091
LME21 = Norwegian Sea	0.85	0.3542	0.0356	0.0072
LME49 = Kuroshio Current	0.75	0.3125	0.0312	0.0062
LME60 = Faroe Plateau	0.75	0.3125	0.0311	0.0078
LME33 = Red Sea	0.74	0.3083	0.0309	0.0048
LME18 = West Greenland Shelf	0.73	0.3042	0.0304	0.0064
LME24 = Celtic-Biscay Shelf	0.72	0.3000	0.0301	0.0076
LME26 = Mediterranean Sea	0.71	0.2958	0.0294	0.0055
LME54 = Chukchi Sea	0.70	0.2917	0.0290	0.0087
LME25 = Iberian Coastal	0.68	0.2833	0.0283	0.0072
LME48 = Yellow Sea	0.67	0.2792	0.0279	0.0097
LME17 = North Brazil Shelf	0.60	0.2500	0.0252	0.0049
LME51 = Oyashio Current	0.60	0.2500	0.0250	0.0086
LME15 = South Brazil Shelf	0.53	0.2208	0.0221	0.0068
LME27 = Canary Current	0.52	0.2167	0.0217	0.0082
LME12 = Caribbean Sea	0.50	0.2083	0.0208	0.0050
LME19 = East Greenland Shelf	0.47	0.1958	0.0197	0.0074
LME28 = Guinea Current	0.46	0.1917	0.0194	0.0063
LME10 = Insular Pacific Hawaiian	0.45	0.1875	0.0187	0.0056
LME36 = South China Sea	0.44	0.1833	0.0182	0.0063
LME53 = West Bering Sea	0.39	0.1625	0.0162	0.0064
LME2 = Gulf of Alaska	0.37	0.1542	0.0154	0.0081
LME40 = NE Australian Shelf-Great Barrier Reef	0.37	0.1542	0.0153	0.0101
LME56 = East Siberian Shelf	0.36	0.1500	0.0149	0.0092
LME41 = East-Central Australian Shelf	0.35	0.1458	0.0145	0.0056
LME55 = Beaufort Sea	0.34	0.1417	0.0140	0.0066
LME46 = New Zealand Shelf	0.32	0.1333	0.0135	0.0105
LME4 = Gulf of California	0.31	0.1292	0.0130	0.0069
LME5 = Gulf of Mexico	0.31	0.1292	0.0130	0.0161
LME52 = Sea of Okhotsk	0.31	0.1292	0.0129	0.0053
LME16 = East Brazil Shelf	0.30	0.1250	0.0126	0.0062
LME63 = Hudson Bay	0.28	0.1167	0.0117	0.0076
LME1 = East Bering Sea	0.27	0.1125	0.0113	0.0070
LME32 = Arabian Sea	0.26	0.1083	0.0110	0.0048
LME29 = Benguela Current	0.24	0.1000	0.0100	0.0072
LME34 = Bay of Bengal	0.24	0.1000	0.0098	0.0061
LME38 = Indonesian Sea	0.24	0.1000	0.0098	0.0067
LME45 = Northwest Australian Shelf	0.24	0.1000	0.0098	0.0049
LME7 = Northeast US Continental Shelf	0.23	0.0958	0.0096	0.0043
LME37 = Sulu-Celebes Sea	0.23	0.0958	0.0096	0.0125
LME30 = Agulhas Current	0.20	0.0833	0.0085	0.0079
LME42 = Southeast Australian Shelf	0.20	0.0833	0.0084	0.0042
LME31 = Somali Coastal Current	0.18	0.0750	0.0074	0.0059
LME39 = North Australian Shelf	0.17	0.0708	0.0070	0.0068
LME6 = Southeast US Continental Shelf	0.16	0.0667	0.0067	0.0061
LME35 = Gulf of Thailand	0.16	0.0667	0.0067	0.0064
LME58 = Kara Sea	0.16	0.0667	0.0066	0.0065
LME11 = Pacific Central-American Coastal	0.14	0.0583	0.0059	0.0101
LME20 = Barents Sea	0.12	0.0500	0.0051	0.0092
LME57 = Laptev Sea	0.12	0.0500	0.0048	0.0088
LME43 = Southwest Australian Shelf	0.09	0.0375	0.0039	0.0057
LME44 = West-Central Australian Shelf	0.09	0.0375	0.0038	0.0093
LME14 = Patagonian Shelf	0.08	0.0333	0.0034	0.0059
LME61 = Antarctic	0.001	0.0004	0.00004	0.0011
LME3 = California Current	-0.07	-0.0292	-0.0030	0.0119
LME13 = Humboldt Current	-0.10	-0.0417	-0.0042	0.0112

exceeding 0.9°C over 25 years was observed in the Baltic Sea, North Sea, East China Sea, Sea of Japan/East Sea, Newfoundland-Labrador Shelf, and Black Sea LMEs. The 18 fast- and super-fast-warming LMEs (net change over 0.6°C between 1982 and 2006) were warming at rates approximately two to four times higher than the IPCC 2007 global average SST warming rate of $0.133 \pm 0.047^\circ\text{C decade}^{-1}$ (4) (Fig. 3).

Primary Productivity

The importance of primary productivity in supporting the bottom-up trophic links to fisheries productivity is well known

(20–22). No large-scale, consistent pattern of either an increase or a decrease in primary productivity was observed (23). Of the 64 LMEs examined, only four of the productivity trends were significant ($P < 0.05$). Primary productivity declined in the Bay of Bengal, and increased in the Hudson Bay, Humboldt Current, and Red Sea LMEs. The general declining trend in primary productivity with ocean warming reported by Behrenfeld et al. (24) was limited to the Bay of Bengal LME. No consistent, statistically significant trend among the LMEs was observed (Table 2). However, as previously reported (25–27), fisheries biomass yields did increase with increasing levels of primary productivity ($P < 0.001$) in all 63 LMEs (Fig. 4).

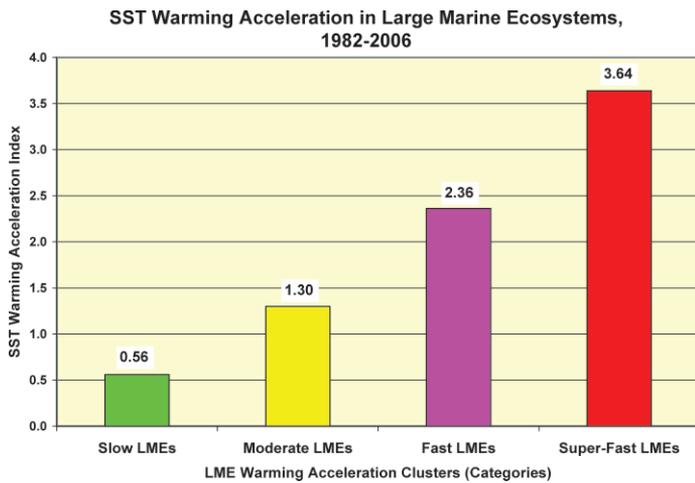


Figure 3. Accelerated warming of SST in LMEs, 1982–2006. Shown is the warming acceleration index (WAI) for four clusters of LMEs, grouped according to their net SST change between 1982 and 2006, categorized as slow (0.0–0.3°C, net SST change), moderate (0.3–0.6°C), fast (0.6–0.9°C), and super-fast (>0.9°C) (Table 1). The WAI (shown at the top of each bar) is calculated as the ratio of the cluster's average SST warming rate (10) to the IPCC 2007 global average SST warming rate of $0.133 \pm 0.047^\circ\text{C decade}^{-1}$ (19).

Fisheries Biomass Yield Trends

The effects of warming on global fisheries biomass yields were nonuniform in relation to any persistent global pattern of increasing or decreasing yields (28). The relationship between the change in LME yield and SST change was not significant; the slight suggestion of a trend in the regression was influenced by the data for the Humbolt LME (Fig. 5). Partitioning of the results into LMEs with increasing trends in fisheries biomass yields and those with declining trends divided the trends into two groups. Increasing yields were observed in 31 (49.2%) and decreasing trends in 32 (50.8%) LMEs. Differences were similar in fast-warming (8 increasing, 10 decreasing) and in moderately warming LMEs (10 increasing, 8 decreasing). In the slower-warming LMEs, most, 14, were undergoing increasing biomass yields, and 6 were in a decreasing condition (Table 3). Linear warming trends from 1982 to 2006 for each LME were distributed in distinct global clusters: *i*) the fast-warming LME clusters were in the Northeast Atlantic, African, and Southeast Asian waters; *ii*) the moderately warming LMEs were clustered in the Atlantic and North Pacific waters; and *iii*) the slow-warming LME clusters were located principally in the Indian Ocean and in locations around the margins of the Atlantic and Pacific Oceans (Fig. 6). Comparisons of fisheries biomass yield trends for 11 LME warming clusters were examined.

Comparative Fisheries Biomass Yields (in Tonnes) in Fast-warming European LMEs

In the Norwegian Sea, Faroe Plateau, and Iceland Shelf, the fisheries biomass yield was increasing. These three LMEs

LME	PP
Bay of Bengal	– *
Hudson Bay	+ *
Humboldt Current	+ *
Red Sea	+ *

* P < 0.05

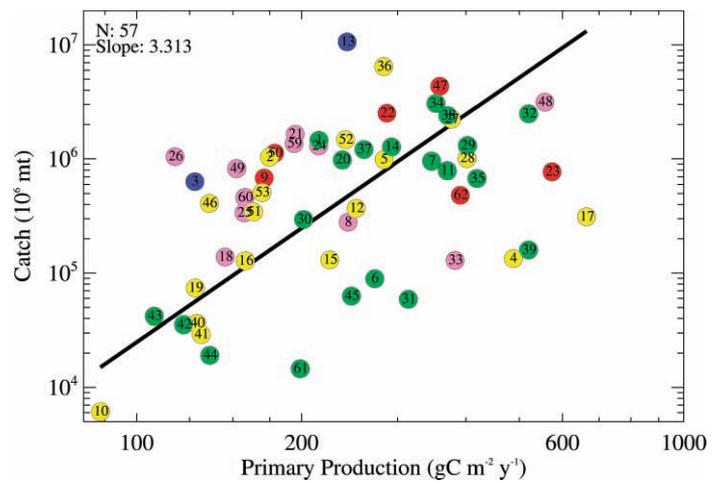


Figure 4. Positive correlation of 5-y mean annual fisheries biomass yield with 9-y mean annual primary production in fast-warming (red), moderately warming (yellow), and slower-warming (green) LMEs. The two blue circles represent cooling LMEs. $P < 0.001$.

accounted for 3.4 million tonnes, or 5%, of the world biomass catch. This cluster of LMEs was influenced by bottom-up forcing of increasing zooplankton abundance and warming hydrographic conditions in the northern areas of the North Atlantic, where stocks of herring, blue whiting, and capelin were benefiting from an expanding prey field of zooplankton (29, 30), supporting growth and recruitment of these three species. The warming trend in the Norwegian Sea driving the increase in the biomass of herring, capelin, and blue whiting yields has been reported by Skjoldal and Saetre (31). On the Faroe Plateau LME, Gaard et al. (32) indicated that the increasing shelf production of plankton is linked to the increased production of fish and fisheries in the ecosystem. Astthorsson and Vilhjálmsson (33) have shown that variations of zooplankton in Icelandic waters are greatly influenced by large-scale climatic factors and that warm Atlantic water inflows favor zooplankton, which supports larger populations of capelin that serve as an important prey of cod. The productivity and fisheries of all three LMEs were benefiting from the increasing strength of the sub-Polar gyre bringing warmed waters to the LMEs of the region generally in the northern Northeast Atlantic and contributing to

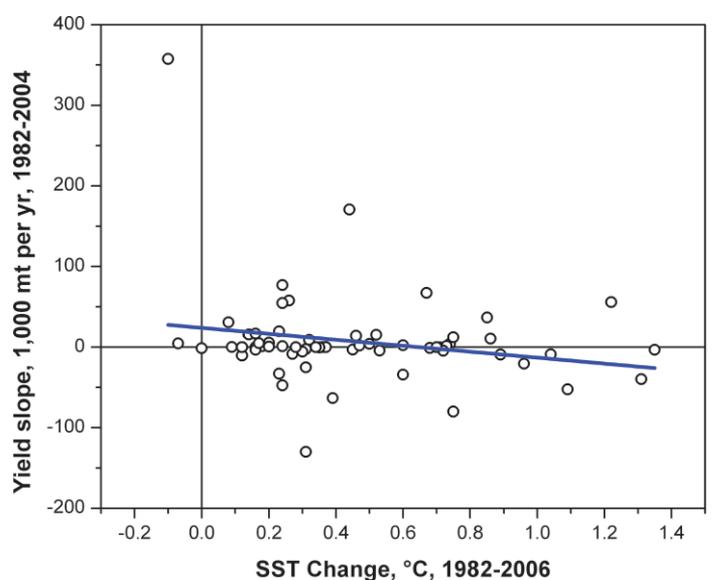


Figure 5. Relationship (shown with blue trend line) between LME yield trend slope and net SST change. The yield trend data span the period 1982 to 2004, whereas the net SST change data span the period 1982 to 2006.

Table 3. Fisheries biomass trends in LMEs adjacent to developed and developing countries, where the gross domestic product in one or more countries bordering the LME is classified by the World Bank as in an economically developing condition.

Fisheries biomass trend	Status of adjacent countries	Fisheries biomass in millions of tonnes	Percentage of total
Increasing fisheries (20 LMEs)	Developing countries	32.0	49%
Decreasing fisheries (9 LMEs)	Developing countries	6.2	9%
Increasing fisheries (11 LMEs)	Developed countries	4.4	6%
Decreasing fisheries (15 LMEs)	Developed countries	11.0	17%
California Current, Humboldt Current, and 7 Arctic LMEs (9 LMEs)		11.4	19%
Total fisheries biomass	All categories	65.0	100%

decreasing production and fisheries yields in the relatively warmer southern waters of the Northeast Atlantic (34).

In southern Europe, three LMEs in fast-warming clusters, the North Sea, Celtic Biscay, and Iberian Coastal LMEs, were experiencing declines in biomass trends representing 4.1 million tonnes (6.4%) of the mean annual global biomass yield. It has been reported that zooplankton abundance levels in the three LMEs are in decline, reducing the prey field for zooplanktivores (30, 35, 36). Although we did not detect any significant decline in primary productivity in the three LMEs, the declining phytoplankton level in the region (34) was consistent with the declines in primary productivity in warming ocean waters reported by Behrenfeld et al. (24) and the subsequent expected reduction in fisheries productivity (37). The fisheries biomass yields of 80% of the targeted species were in an overexploited or fully exploited condition (Table 4), suggesting that the observed decline in biomass yield of pelagic species was related to both heavy exploitation and warming.

The three semi-enclosed European LMEs—the Mediterranean, the Black Sea, and the Baltic Sea—and the adjacent area of the Red Sea are surrounded by terrestrial areas and are fast warming, with heavy fishing as a dominant feature. The four LMEs contributed 2.4 million tonnes (3.7%) of the mean annual global biomass yield. In three European LMEs, the fisheries biomass trend was decreasing, while in the Red Sea it was increasing. In the case of the Black Sea, the fisheries biomass was severely depleted, with 85% of fisheries stocks overexploited

due to heavy fishing and a trophic cascade (38). In the Baltic Sea, Red Sea, and Mediterranean Sea LMEs, 78% of the stocks were in a fully exploited condition. Mixed species dominated in the Red Sea, where 88% of the species fished were fully exploited and 10% were overexploited (Table 4). It appears that heavy exploitation was the dominant driver of the biomass trends observed in all four LMEs.

Comparative Fisheries Biomass Yields (in Tonnes) in Other Fast-warming Clusters

The three LMEs in the Northwest Atlantic region contributed 1.1 million tonnes (1.7%) to the global biomass yield. In two LMEs of the Northwest Atlantic, the downward trends in fisheries yield have been attributed to the cod collapse in the Newfoundland-Labrador Shelf (39) and to the cod collapse and the collapse of other demersal fisheries in the Scotian Shelf LME from excessive fishing mortality (40, 41). In the West Greenland Shelf LME, where the cod stock has collapsed from excessive fishing mortality, there has been a recent increase in the landings of shrimp and other species (42).

Biomass Yields of the Fast-warming LMEs of East Asian Seas

The 7.5-million-tonne biomass yields of the Yellow Sea and East China Sea LMEs constitute 11% of the global yield. In

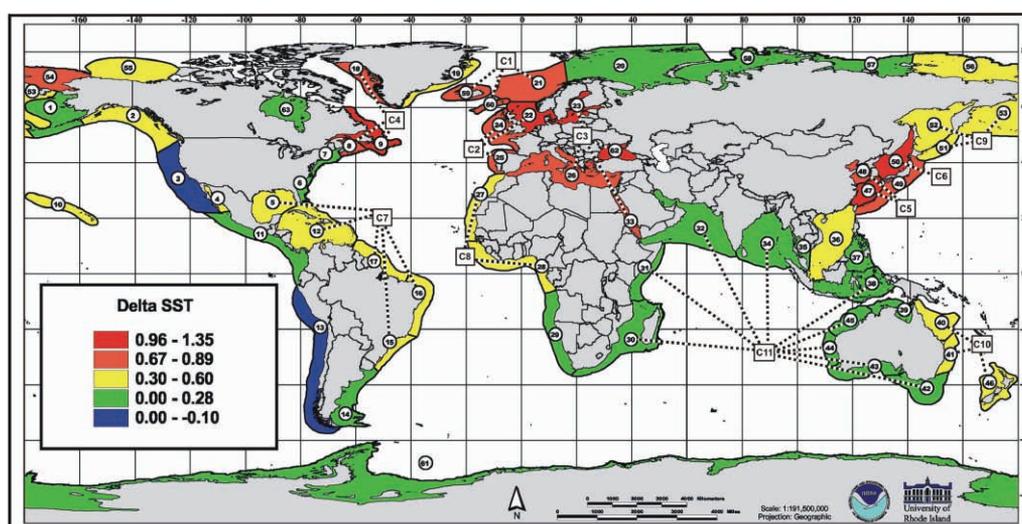


Figure 6. Warming clusters of LMEs in relation to SSTs, 1987–2006.

Warming Clusters of LMEs in Relation to SSTs, 1982–2006:

FAST WARMING:

C1 Northern European Cluster; C2 Southern European; C3 Semi-Enclosed European Seas; C4 of the NW Atlantic; C5 Fast Warming East Asian LMEs; C6 Kuroshio Current and Sea of Japan/East Sea LMEs.

MODERATE WARMING:

C7 Western Atlantic LMEs; C8 Eastern Atlantic LMEs; C9 NW Pacific LMEs; C10 SW Pacific LMEs. Several Non-Clustered, Moderate Warming LMEs: NE Australia, Insular Pacific Hawaiian, Gulf of Alaska, Gulf of California; South China Sea, East Greenland Shelf;

SLOW WARMING:

C11 Indian Ocean and Adjacent Waters.

Non-clustered, Slow Warming LMEs include the U.S. Northeast Shelf, the U.S. Southeast Shelf, the Barents Sea, East Bering Sea; Patagonian Shelf, Benguela Current and Pacific Central American Coastal LMEs.

Table 4. LMEs, rates of warming, 5-y mean fisheries biomass yields adjacent to developing or developed countries, and the status of stock exploitation.

LME category	Adjacent countries' development	Fisheries biomass trend	5-y mean fisheries biomass in tonnes*	Fisheries biomass yield status from SAUP: fully exploited, overexploited
Fast-warming LMEs				
East China Sea	developing	increasing	4 339 890	77% fully exploited, 21% overexploited
Red Sea	developing	increasing	129 206	88% fully exploited, 10% overexploited
Yellow Sea	developing	increasing	3 147 211	70% fully exploited, 18% overexploited
Fast-warming LMEs				
Mediterranean Sea	developing	decreasing	1 045 214	78% fully exploited, 22% overexploited
Baltic Sea	developing	decreasing	771 911	88% fully exploited, 12% overexploited
Black Sea	developing	decreasing	481 699	0% fully exploited, 85% overexploited
Moderately warming LMEs				
North Brazil Shelf	developing	increasing	311 848	70% fully exploited, 29% overexploited
Canary Current	developing	increasing	2 229 215	72% fully exploited, 6% overexploited
Caribbean Sea	developing	increasing	370 231	40% fully exploited, 58% overexploited
Guinea Current	developing	increasing	1 010 453	71% fully exploited, 24% overexploited
East Brazil Shelf	developing	increasing	127 969	40% fully exploited, 48% overexploited
South Brazil Shelf	developing	increasing	130 669	20% fully exploited, 40% overexploited
Sea of Okhotsk	developing	increasing	1 472 394	10% fully exploited, 78% overexploited
South China Sea	developing	increasing	6 454 043	83% fully exploited, 13% overexploited
Moderately warming LMEs				
Gulf of Mexico	developing	decreasing	987 865	36% fully exploited, 60% overexploited
West Bering Sea	developing	decreasing	508 804	1% fully exploited, 79% overexploited
Gulf of California	developing	decreasing	134 297	45% fully exploited, 48% overexploited
Slower-warming LMEs				
Arabian Sea	developing	increasing	2 486 227	84% fully exploited, 11% overexploited
Bay of Bengal	developing	increasing	3 062 147	83% fully exploited, 15% overexploited
Indonesian Sea	developing	increasing	2 392 818	88% fully exploited, 12% overexploited
Gulf of Thailand	developing	increasing	676 304	37% fully exploited, 50% overexploited
Sulu Celebes	developing	increasing	1 207 946	82% fully exploited, 17% overexploited
Agulhas Current	developing	increasing	295 364	30% fully exploited, 32% overexploited
Somali Current	developing	increasing	58 961	45% fully exploited, 50% overexploited
Pacific Central American	developing	increasing	788 191	42% fully exploited, 18% overexploited
Patagonian Shelf	developing	increasing	1 269 644	30% fully exploited, 69% overexploited
Slower-warming LMEs				
Antarctic	developing	decreasing	14 553	0% fully exploited, 0% overexploited
Barents Sea	developing	decreasing	980 781	0% fully exploited, 60% over exploited
Benguela Current	developing	decreasing	1 307 649	50% fully exploited, 8% overexploited
Fast-warming LMEs				
Norwegian Sea	developed	increasing	1 643 808	2% fully exploited, 23% overexploited
Iceland Shelf	developed	increasing	1 359 767	0% fully exploited, 80% overexploited
Faroe Plateau	developed	increasing	460 686	83% fully exploited, 10% overexploited
West Greenland Shelf	developed	increasing	138 369	90% fully exploited, 0% overexploited
Fast-warming, declines in fisheries biomass yields				
North Sea	developed	decreasing	2 513 263	19% fully exploited, 63% overexploited
Newfoundland/Labrador Shelf	developed	decreasing	683 480	55% fully exploited, 10% overexploited
Scotian Shelf	developed	decreasing	279 470	29% fully exploited, 55% overexploited
Kuroshio Current	developed	decreasing	823 035	48% fully exploited, 42% overexploited
Sea of Japan/East Sea	developed	decreasing	1 121 826	45% fully exploited, 49% overexploited
Celtic-Biscay Shelf	developed	decreasing	1 296 762	65% fully exploited, 30% overexploited
Iberian Coastal	developed	decreasing	338 049	30% fully exploited, 61% overexploited
Moderately warming LMEs				
New Zealand Shelf	developed	increasing	408 913	77% fully exploited, 21% overexploited
East Greenland Shelf	developed	increasing	73 932	6% fully exploited, 23% overexploited
Moderately warming LMEs				
Oyashio Current	developed	decreasing	343 734	8% fully exploited, 85% overexploited
Insular Pacific Hawaiian	developed	decreasing	6121	1% fully exploited, 54% overexploited
Gulf of Alaska	developed	decreasing	1 035 005	80% fully exploited, 18% overexploited
East Central Australian	developed	decreasing	29 095	18% fully exploited, 64% overexploited
Northeast Australian Shelf/ Great Barrier Reef	developed	decreasing	36 310	46% fully exploited, 30% overexploited
Slower-warming LMEs				
North Australian Shelf	developed	increasing	159 572	78% fully exploited, 18% overexploited
Northwest Australian Shelf	developed	increasing	62 842	59% fully exploited, 18% overexploited
West Central Australian Shelf	developed	increasing	19 079	75% fully exploited, 10% overexploited
Southeast Australian Shelf	developed	increasing	35 339	50% fully exploited, 40% overexploited
Southwest Australia Shelf	developed	increasing	41 844	51% fully exploited, 27% overexploited
Slower-warming LMEs				
East Bering Sea	developed	decreasing	1 454 881	62% fully exploited, 28% overexploited
US Northeast Shelf	developed	decreasing	955 948	33% fully exploited, 45% overexploited
US Southeast Shelf	developed	decreasing	89 216	54% fully exploited, 26% overexploited
Arctic LME yields are too low for trend analysis				
Chukchi			0	
East Siberian			0	
Beaufort Sea			8	
Hudson Bay			50	
Kara Sea			295	
Laptev Sea			0	
Arctic Ocean			242 913	
Two upwelling LMEs, cooling, adjacent to developed countries				
Humboldt Current			10 617 103	
California Current			634 669	

* V. Christensen, SAUP.

both LMEs, yields were increasing. The principal driver of the increase was food security to accommodate the needs of the People's Republic of China and the Republic of Korea (43–46). Biomass yields were dominated by heavily fished “mixed” species. Seventy percent or more of the species constituting the yields were fully exploited or overexploited (Table 4), suggesting that the principal driver of increased biomass yields was full exploitation rather than global warming.

The fast-warming Kuroshio Current and Sea of Japan/East Sea LMEs showed declining fisheries trends. They contributed 1.9 million tonnes (2.9%) to the global marine fisheries yield. For these two LMEs, exploitation levels were high, with 90% of the species in a fully exploited to overexploited condition (Table 4). The fisheries are also subjected to periodic oceanographic regime shifts that affect the abundance of biomass yields (47). Among the fast-warming East Asian Seas LMEs, no analysis was conducted for the ice-covered Chukchi Sea LME, as the data were limited and of questionable value.

Comparative Fisheries Biomass Yields (in Tonnes) in Moderately Warming Atlantic LMEs and Asian Pacific Regions

A large cluster of moderately warming LMEs was found in the Trade Winds region of the Atlantic Ocean. This important cluster of LMEs contributed 5.1 million tonnes (7.9%) to the mean annual global biomass yield. Five LMEs were clustered in the Western Atlantic and two in the Eastern Atlantic. In the Western Atlantic Ocean, the Gulf of Mexico LME fisheries biomass yields were decreasing, while in the Caribbean, North Brazil, East Brazil, and South Brazil Shelf LMEs, fisheries biomass yields were increasing. The fisheries biomass yield trends in the Atlantic Ocean region appeared to be driven principally by heavy exploitation rather than climate warming. The Caribbean, North Brazil, and East Brazil Shelf LMEs were in a fully exploited and overexploited fisheries condition equal to or greater than 88% of the stocks. In the South Brazil Shelf, 60% of fisheries were fully exploited or overexploited (Table 4). The East Brazil Shelf and South Brazil Shelf LMEs were dominated by small pelagics and/or mixed species. The two LMEs of the Eastern Atlantic are important sources of food security to the over 300 million people of West African countries adjacent to the LMEs. The Canary Current and the Guinea Current showed increasing trends in biomass yield with mixed species dominant (48). The fisheries stocks in both LMEs were “at risk.” Oceanographic perturbations are also a source of significant variability in biomass yields in the Guinea Current (49, 50) and in the waters of the Canary Current LME (51, 52).

Three LMEs, the Sea of Okhotsk, the Oyashio Current, and the West Bering Sea, contributed 2.3 million tonnes (3.5%) to the mean annual global biomass yield. They were in a condition where 78% of the fisheries stocks were overexploited (Table 4). The Oyashio Current and the West Bering Sea LMEs showed decreasing trends in fisheries yields. In the Sea of Okhotsk, the biomass yields are dominated by targeted table fish, including pollock and cod. The increasing yield trend in the Sea of Okhotsk LME was related principally to a high level of overexploitation (53).

Comparative Fisheries Biomass Yields in Other Moderately Warming LMEs

The three moderately warming LMEs, two on the east coast of Australia (Northeast and East Central Australia LMEs) and the New Zealand Shelf LME, contributed 0.4 million tonnes (0.7%) to the mean annual global biomass yield. Biomass yields were decreasing in the Australian LMEs, whereas they were

increasing in the New Zealand Shelf LME under a condition of full exploitation (Table 3). Whether their conditions were the result of top-down or bottom-up forcing is not clear. However, individual transferable quota (ITQ) management to promote the recovery and sustainability of high-priority fisheries stocks was in place. Stewardship agencies in Australia and New Zealand have implemented management actions for the recovery and sustainability of the overexploited species. Six moderately warming LMEs occurred in separate locations. Taken together, they contributed 7.7 million tonnes (11.8%) to the mean annual global biomass yields. In the Pacific, landings were too low in the moderately warming Insular Pacific Hawaiian LME to draw any conclusion on biomass yield. In the moderately warming Gulf of Alaska LME, the overall 25-y fisheries biomass trend was decreasing. However, this LME showed evidence of a relatively recent upturn in yield, attributed to increases in the biomass of Alaska pollock and Pacific salmon populations in response to climate warming (54).

The biomass of the moderately warming Gulf of California LME was in a declining trend. The dominant biomass yield in this LME was from small pelagics and mixed species, suggestive of top-down fishing as the principal driver of the decline. The South China Sea fisheries biomass yields were increasing. The dominant biomass yield of the LME was of mixed species, and the level of exploitation was high, with 83% fully exploited and 13% overexploited (Table 4). In this case, high population demand for protein by the adjacent countries contributed to driving the biomass yield upward. The Arctic region's Beaufort Sea LME landings data were unavailable. The moderately warming East Greenland Shelf fisheries biomass yields were increasing, with capelin, redfish, and shrimp dominant, following the earlier collapse of cod and other demersal species. The role of global warming in relation to the cause and effect of increasing yields is not known.

Comparative Fisheries Biomass Yields in Slow-warming Indian Ocean and Adjacent LMEs (C11)

The 10 LMEs of the Indian Ocean, Arabian Sea, Bay of Bengal, Indonesian Sea, Agulhas Current, Somali Current, North Australia, West Central Australia, Northwest Australia, Southeast Australia, and Southwest Australia LMEs were in the slow range of climate warming and their biomass trends were all increasing (Fig. 7). This group of LMEs contributed 8.6 million tonnes, or 13.2%, of the global biomass yield. The slow warming was consistent with the IPCC forecast of slow but steady warming of the Indian Ocean in response to climate change (4). While biomass yields were increasing, the landings adjacent to developing countries were composed primarily of mixed species and small pelagics (48), and the stocks were predominantly fully exploited and/or overexploited (Table 4), suggesting that top-down fishing was the predominant influence on the condition of biomass yield. In the adjacent Southwest Pacific waters, the slow-warming Sulu-Celebes and Gulf of Thailand LMEs contributed 1.8 million tonnes (2.8%) to the mean annual global biomass yield. The consistent pattern of increasing yields of the Indian Ocean LMEs adjacent to developing countries was driven principally by the demand for fish protein and food security (55, 56). In the case of the five LMEs adjacent to Australia, the national and provincial stewardship agencies were promoting stock recovery and sustainable management through ITQs. The fisheries stocks in the LMEs adjacent to developing countries are under national pressure to further continue the expansion of the fisheries to provide food security for the quarter of the world's population that inhabits the region. Given the demands on fisheries for food security for the developing countries bordering the Indian Ocean, there is a

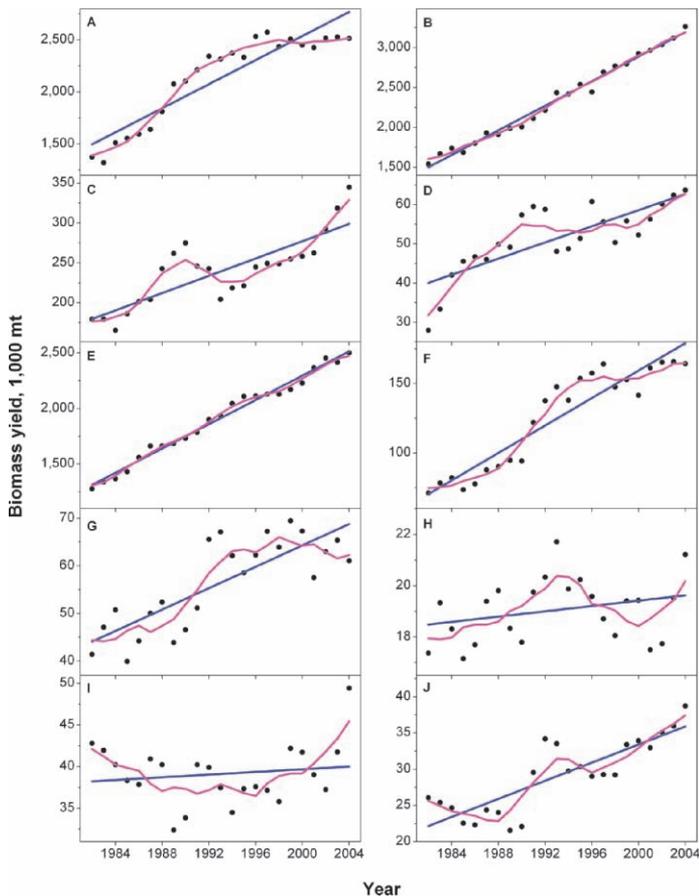


Figure 7. Comparative dynamics of fisheries biomass yield in the slow-warming Indian Ocean and adjacent LMEs (see cluster C11 in Figure 6); Arabian Sea, LME 32 (A); Bay of Bengal, LME 34 (B); Agulhas Current, LME 30 (C); Somali Current, LME 31 (D); Indonesian Sea, LME 38 (E); North Australia, LME 39 (F); Northwest Australia, LME 45 (G); West-Central Australia, LME 44 (H); Southwest Australia, LME 43 (I); and, Southeast Australia, LME 42 (J). The linear regression is shown as a blue trend line, and adjacent averaging smoothing is shown as a magenta trend line.

need to control biomass yields and sustain the fisheries of the bordering African and Asian LMEs.

The Biomass Yields of Other Slow-warming LMEs

There was slow warming taking place in the Northeast US Shelf and in the Southeast US Shelf. The LMEs contributed 1.0 million tonnes (1.6%) to the mean annual global marine biomass yield. For both LMEs, the declines are attributed principally to overfishing (57). For these two LMEs and the Gulf of Mexico, the Gulf of Alaska, the East Bering Sea, Chukchi Sea, Beaufort Sea, Insular Pacific Hawaiian Islands, and the Caribbean, the United States has underway a fisheries stock rebuilding program for increasing the spawning stock biomass of overfished species (58).

Biomass Yields of the Slow-warming LMEs of the Arctic Region

For several of the slow-warming LMEs bordering the Arctic, including the Laptev Sea, Kara Sea, East Siberian Sea, and Hudson Bay, biomass yield data were incomplete and not included in the trend analyses. In the case of the Barents Sea LME, there was a decreasing biomass trend attributed to the overexploited condition of many fish stocks inhabiting the LME (Table 4). During the present warming condition, variability in ice cover has an important influence on biomass yields (59).

Biomass Yields of Other LMEs

Four widely separated LMEs, the East Bering Sea, the Patagonian Shelf, Benguela Current (BCLME), and Pacific Central American LMEs, were located in slow-warming waters. Together, they contributed 3.3 million tonnes (5.1%) to the mean annual global biomass yield. In the North Pacific Ocean, the slow-warming East Bering Sea had an overall decline in fisheries biomass yield. However, in recent years there has been an upturn in yield, attributed to climate warming and increases in the biomass of Alaska pollock and Pacific salmon populations (54). In the Southwest Atlantic Ocean, the increasing biomass yields of the Patagonian Shelf LME were reflective of a very high level of fisheries exploitation, overshadowing any climate change effects: 30% of fisheries were fully exploited, and 69% were overexploited (Table 4). The increasing biomass trends of the Pacific Central American Coastal LME were the result of high levels of exploitation (Table 4), driven principally by the need for fish protein and food security of the adjacent developing countries and secondarily by oceanographic regime shifts (60).

The biomass yields of the BCLME, southwest African coast, were in a declining trend. The living resources of the BCLME have been stressed by both heavy exploitation and environmental perturbations during the past 25 years (61). The trend of a southwestward movement of pelagic fish (sardine and anchovy) populations from the west coast of South Africa around to the southeast coast has been attributed to recent warming. This has also led to a decrease in the availability of the small pelagic fish prey of African penguins in the vicinity of island colonies, resulting in a 40% penguin population decline (62).

DISCUSSION

Emergent Trends

From the analysis, we conclude that in four LME cases, the warming clusters of LMEs are influencing 7.5 million tonnes, or 11.3%, of the world's fisheries biomass yields. The first and clearest case for an emergent effect of global warming on LME fisheries yields is in the increasing biomass yields of the fast-warming temperature clusters affecting 3.4 million tonnes (5.0%) of global yields for the Iceland Shelf, Norwegian Sea, and Faroe Plateau LMEs in the northern Northeast Atlantic. Warming in this region has exceeded levels expected from entering the warm phase of the Atlantic Multidecadal Oscillation (63). The increase in zooplankton has been related to warming waters in the northern areas of the Northeast Atlantic (30) leading to improved feeding conditions for three zooplanktivorous species that are increasing in biomass yields. Herring, blue whiting, and capelin yields are increasing in the Iceland Shelf and Norwegian Sea LMEs, and blue whiting yields are increasing in the Faroe Plateau LME.

The second case is in the contrasting declines in biomass yields of the fast-warming cluster of more southern Northeast Atlantic waters, including the North Sea, the Celtic-Biscay Shelf, and Iberian Coastal LMEs, where declines in warm water plankton (36) and the northward movement of fish (64) are negative influences on 4.1 million tonnes (6.3%) of the mean annual global biomass yields. Recent investigations have found that SST warming in the Northeast Atlantic is accompanied by increasing zooplankton abundance in cooler, more northerly areas and decreasing phytoplankton and zooplankton abundance in the more southerly, warmer regions of the Northeast Atlantic in the vicinity of the North Sea, Celtic-Biscay Shelf, and Iberian Coastal LMEs (34). Due to tight trophic coupling, fisheries are adversely affected by shifts in distribution,

reduction in prey, and reductions in primary productivity generated by strong thermocline stratification inhibiting nutrient mixing (24).

In the third case, recent moderate warming of the Gulf of Alaska and slow warming of the East Bering Sea are supporting increasing levels of zooplankton production and recent increasing biomass yields of Alaska pollock and Pacific salmon (54, 65, 66).

The biomass yields of the fourth case are more problematic. Biomass yields of all 10 LMEs (8.6 million tonnes, or 13.2%) around the western and central margin of the Indian Ocean were increasing (Fig. 7). The increasing yields of the five LMEs adjacent to developing countries, the Agulhas Current, Somali Current, Arabian Sea, Bay of Bengal, and Indonesian Sea LMEs, were dominated by mixed species and small pelagic species, driven by the fish protein and food security needs of nearly one-quarter of the world's population, which inhabits the bordering countries of Africa and Asia (67). The overexploited condition of most species is at present masking any gains in biomass yield that may be attributed to the slow and steady warming of waters predicted for the Indian Ocean by the IPCC (4) and observed during the present study. In contrast, the slowly warming five Australian LMEs on the eastern margin of the Indian Ocean are driven principally by economic considerations and are closely monitored by governmental stewardship agencies that practice an adaptive management system of ITQs (68). Taken together, the 8.6-million-tonne mean annual biomass yield of the Indian Ocean LMEs is critical for the food security of the heavily populated adjacent countries. Recent analyses indicate a growing increase in ecosystem overfishing and loss in fisheries production in the Arabian Sea and the Bay of Bengal LMEs (69). In this region, there is a need to exercise a precautionary approach (70) to recover and sustain the fisheries in the LMEs of eastern Africa and Asia in the slow-warming clusters.

Precautionary Cap-and-Sustain Action

From a global perspective, 38.2 million tonnes, or 58%, of the mean annual 2001–2006 biomass yields are being produced in 29 LMEs adjacent to developing countries (Table 3). This vital global resource is at risk from serious overexploitation (Table 4). Given the importance of sustaining 58% of the world's marine fisheries biomass yield, it would be prudent for the Global Environment Facility supported LME assessment and management projects to immediately cap the total biomass yield at the annual 5-y mean (2000–2004) as a precautionary measure and move toward the adoption of more sustainable fisheries management practices. Application of the capping of fisheries yields as a precautionary action is especially important during a period of climate-induced changes, when nonlinear changes in fish stock abundance are difficult to predict (37). The management strategies for protecting the 26.8 million tonnes, or 42%, of global marine biomass yields in LMEs adjacent to the more developed countries (Table 3) have had variable results ranging from highly successful fisheries biomass yield recovery and sustainability actions for stocks in LMEs adjacent to Australia, New Zealand, the United States, Norway, and Iceland to the less successful efforts of the European Union and LMEs under EU jurisdiction in the Northeast Atlantic (71). An ecosystem-based cap-and-sustain adaptive management strategy for groundfish based on an annual overall total allowable catch (TAC) level and agreed upon TACs for key species is proving successful in the management of the moderately warming waters of the Gulf of Alaska LME and the slow-warming East Bering Sea LME Alaska pollock and Pacific

salmon stocks, providing evidence that cap-and-sustain strategies can serve to protect fisheries biomass yields (72, 73).

In the absence of the capacity for conducting annual assessments of a large number of marine fish species in many developing countries and in recognition of the uncertainties of climate warming effects, in the observed slow warming and increasing fisheries biomass yields of LMEs adjacent to east Africa and south Asia along the margins of the Indian Ocean, it would be prudent for the bordering countries to implement precautionary actions to protect present and future fisheries yields with a cap-and-sustain strategy aimed at supporting long-term food security and economic development needs (37).

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