

Fisheries in a warming ocean: trends in fish catches in the large marine ecosystems of the world

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Received: 1 October 2013 / Accepted: 26 March 2014 / Published online: 8 May 2014
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Abstract Trends in annual catches of fish species in the large marine ecosystems (LMEs) of the world were analysed, relating them with changes in sea surface temperature. LMEs are large coastal areas with broad ecosystem similarities, and the vast majority of them have warmed in the period of 1982–2006. Changes in sea water temperature, induced by climate change, affect the geographic distribution of fish species in marine ecosystems. Shifts in distribution of fish will most likely affect the abundance, distribution and composition of fisheries catches. In the present paper, a decreasing trend in the catches of fish species in warming LMEs was observed. Catches in years of cold and warm winters were compared for each of the eight fish species most caught in the world. Generally, mean catches of polar and temperate species were higher in years of warm winters in the LMEs located in the northern part of the species range and in years of cold winters in LMEs of the southern regions of their ranges. Mean catches of subtropical species were higher in cold years in LMEs of lower latitudes and in warm years in LMEs of higher latitude regions. The results obtained for fish catches agree with a poleward shift of fish species as a response to ocean warming, posing challenges for future fisheries management.

Keywords Climate change · Fish · Fisheries · Large marine ecosystems · Sea surface temperature

Introduction

Global marine fisheries not only face overfishing, pollution and other anthropogenic impacts, but also climate change (Pauly et al. 2002; Halpern et al. 2008). Climate change is the most widespread anthropogenic threat for ocean ecosystems (Halpern et al. 2008), causing sea-level rise, sea temperature change, ocean acidification, changes in precipitation and changes in ocean circulation (Brander 2007). These climate effects on ocean conditions will impact ocean organisms, the composition of marine communities and ecosystem function (Brown et al. 2010), increasing the complexity of the challenges facing current fisheries (Sumaila et al. 2011). Climate change impacts fish stocks either directly or indirectly. Direct impacts affect the physiology and behaviour and alter growth, reproductive capacity, mortality and distribution. Indirect effects change the productivity, structure and composition of the marine ecosystems on which fish depend (Perry et al. 2005; Brander 2010; Hare et al. 2010). Changes in the geographic distribution of fish species in marine ecosystems have already been documented throughout the world (Brander et al. 2003; Perry et al. 2005; Barange and Perry 2009), and several studies have predicted that changes in water temperature, driven by climate change, may lead to local extinctions and also to colonization by species previously absent in those areas (Cheung et al. 2009; Vinagre et al. 2011). These shifts in geographic range will most likely affect the abundance, distribution and composition of fisheries catches, and consequently fishing operations, catch shares and the effectiveness of fisheries management measures (Kim 2010; Sumaila et al. 2011; Gamito et al. 2013). However, these effects might not necessarily be negative, as new fishing opportunities may also arise in some areas of the world. The effects of climate change on fisheries may then be regarded to act on resource availability, fishing operations,

Editor: Wolfgang Cramer.

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fisheries management and conservation measures and profits from fisheries (Cheung et al. 2012).

Both the observation of recent climate change and predictions of climate change in future scenarios show that the effects of climate change will not be homogeneous throughout the world (IPCC 2007). Belkin (2009) has studied changes in sea surface temperature (SST) in large marine ecosystems (LMEs). LMEs are large coastal areas with broad ecosystem similarities, such as bathymetry, hydrography, productivity and trophically dependent populations (Sherman and Duda 1999; Watson et al. 2004). Belkin (2009) has found a coherent global pattern of rapid warming in LMEs, from 1982 to 2006. This rapid warming (net SST change higher than 0.6 °C) was observed for three groups of LMEs: (1) Scotian Shelf, Newfoundland–Labrador Shelf, Canadian Eastern Arctic—West Greenland, Iceland Shelf and Sea, Faroe Plateau and Norwegian Sea; (2) North Sea, Baltic Sea, Black Sea, Mediterranean Sea, Iberian Coastal and Celtic-Biscay Shelf; (3) Yellow Sea, East China Sea, Japan/East Sea and Kuroshio Current. A slow warming was observed in the Indian Ocean LMEs and most LMEs around Australia and between Australia and Indochina. The only cooling LMEs were the California Current and the Humboldt Current, both located in the Eastern Pacific upwelling areas. As the LME spatial system groups together large coastal areas with similar ecosystem characteristics, this methodology has recently been used for several large-scale marine studies (Sherman and Duda 1999; Watson et al. 2004; Pauly et al. 2008; Merino et al. 2012; Pikitch et al. 2014).

From a global perspective, analyses on the LME scale are extremely valuable for marine ecosystem-based management. And, as climate change increases the complexity of fisheries management, it is of the utmost importance that these analyses include the effects of climate change on fisheries. Therefore, the present paper aimed to (1) analyse the trends in annual catches of fish species in LMEs and relate them with changes in SST and (2) compare the mean catches of the most relevant fish species in cold and warm years.

Materials and methods

Large marine ecosystems were classified based on SST change from 1982 to 2006, as described in Belkin (2009). Three categories of LMEs based on SST change were used: rapid warming (0.67–1.35 °C), slow warming (0.00–0.60 °C) and cooling (−0.10 to 0.00 °C) (Belkin 2009) (Fig. 1).

Fish catch data for each LME were collected from the Sea Around Us Project website (www.seaaroundus.org) (Pauly 2007). These time series data were obtained using a method developed by Watson et al. (2004), which maps catches by species for more than 180,000 spatial cells of the

world oceans, each covering 30 min of latitude and longitude. The catches in those spatial cells are then regrouped into the LMEs defined in the world's oceans (Watson et al. 2004; Pauly et al. 2008). All the analyses performed on fisheries catches covered the time series of 1982–2006. Trends in total fish catches for the three categories of LMEs were compared. Catches of the three categories of LMEs were comparatively analysed using a principal components analysis (PCA). The PCA aimed to highlight the similarities among years in terms of catches in these LMEs groups.

SST monthly data were collected from the United States of America National Oceanic and Atmospheric Administration (NOAA) database (http://nomad3.ncep.noaa.gov/ncep_data/), for the period of 1982–2006. As sensitivity to cold has been reported as a very important characteristic in shaping community composition (Henriques et al. 2007; Pörtner and Peck 2010), winter temperatures were used. In each LME, annual winter mean SST was calculated for each considered year and was then averaged for the period of 1982–2006. Winters of SST higher (0.1 °C or more) or lower (0.1 °C or less) than average was considered warm or cold winters, respectively. The catches of the eight most relevant fish species in terms of global catches, excluding the chub mackerel, were analysed. The chub mackerel was excluded, because the database does not provide separate data for the two recognized species (*Scomber colias* Gmelin, 1789, in the Atlantic, and *Scomber japonicus* Houttuyn, 1782, in the Pacific). Therefore, the studied species were: *Engraulis ringens* Jenyns, 1842, *Theragra chalcogramma* (Pallas, 1814), *Sardinops sagax* (Jenyns, 1842), *Clupea harengus* Linnaeus, 1758, *Gadus morhua* Linnaeus, 1758, *Mallotus villosus* (Müller, 1776), *Trichiurus lepturus* Linnaeus, 1758 and *Sardina pilchardus* (Walbaum, 1792). For each species, catches in years of cold and of warm winters were compared through *t*-tests or, whenever the assumptions of normality and homoscedasticity were not met, Mann–Whitney test. A significance level of 0.05 was considered in all test procedures. All the analyses were performed on the environment R (R Core Team 2012), and the R package “lattice” (Deepayan 2008) was used.

Results

Total fish catches in rapidly warming LMEs (0.67–1.35 °C) have decreased in more than 20 % from 1982 to 2006 (Fig. 2). Catches in slowly warming (0.00–0.60 °C) LMEs have had a decrease in 12 % from 1982 (17,092,817 t) to 2006 (14,996,778 t). The total fish catches of the cooling (−0.10 to 0.00 °C) LMEs group increased from 1982 (5,518,121 t) to 1994 (13,100,204 t); from 1995 to 2006, the catch trend oscillated, with a minimum record of 4,073,364 t in 1998.

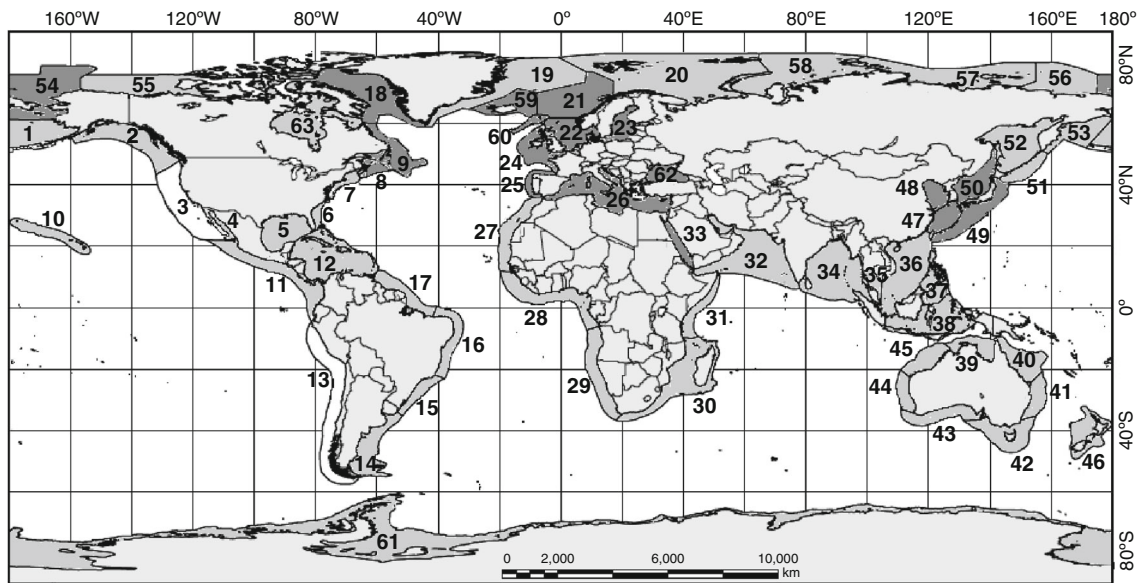
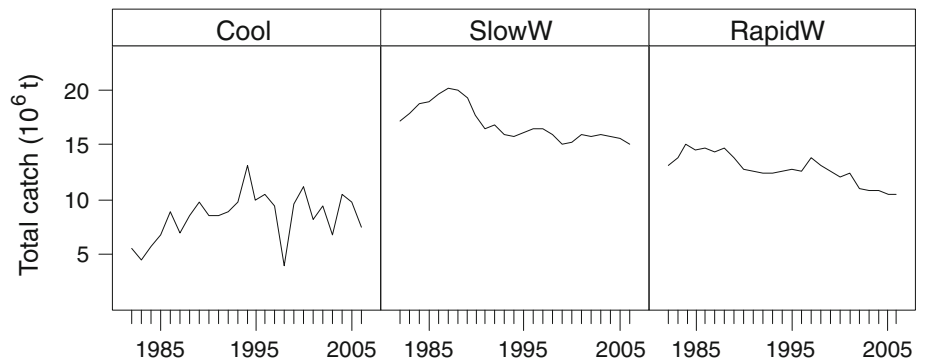


Fig. 1 Sea surface temperature change in LMEs from 1982 to 2006 (Belkin 2009). Cooling (-0.10 to 0.00 °C) LMEs are presented in white, slowly warming (0.00 – 0.60 °C) in light grey and rapidly warming (0.67 – 1.35 °C) in dark grey. 1 East Bering Sea, 2 Gulf of Alaska, 3 California Current, 4 Gulf of California, 5 Gulf of Mexico, 6 Southeast US Continental Shelf, 7 Northeast US Continental Shelf, 8 Scotian Shelf, 9 Newfoundland-Labrador Shelf, 10 Insular Pacific-Hawaiian, 11 Pacific Central-American, 12 Caribbean Sea, 13 Humboldt Current, 14 Patagonian shelf, 15 South Brazil Shelf, 16 East Brazil Shelf, 17 North Brazil Shelf, 18 Canadian Eastern Arctic—West Greenland Shelf, 19 Greenland Sea, 20 Barents Sea, 21 Norwegian Sea, 22 North Sea, 23 Baltic Sea, 24 Celtic-Biscay Shelf, 25 Iberian Coastal, 26 Mediterranean, 27 Canary Current, 28 Guinea

Current, 29 Benguela Current, 30 Agulhas Current, 31 Somali Coastal Current, 32 Arabian Sea, 33 Red Sea, 34 Bay of Bengal, 35 Gulf of Thailand, 36 South China Sea, 37 Sulu-Celebes Sea, 38 Indonesian Sea, 39 North Australian Shelf, 40 Northeast Australian Shelf, 41 East-Central Australian Shelf, 42 Southeast Australian Shelf, 43 Southwest Australian Shelf, 44 West-Central Australian Shelf, 45 Northwest Australian Shelf, 46 New Zealand Shelf, 47 East China Sea, 48 Yellow Sea, 49 Kuroshio Current, 50 Sea of Japan/East Sea, 51 Oyashio Current, 52 Sea of Okhotsk, 53 West Bering Sea, 54 Northern Bering-Chukchi Seas, 55 Beaufort Sea, 56 East Siberian Sea, 57 Laptev Sea, 58 Kara Sea, 59 Iceland Shelf and Sea, 60 Faroe Plateau, 61 Antarctic, 62 Black Sea, 63 Hudson Bay Complex (adapted from the NOAA LME Portal—<http://www.lme.noaa.gov>)

Fig. 2 Total annual fish catch in three different classes of large marine ecosystems, according to changes in sea surface temperature from 1982 to 2006 (Belkin 2009) (Cool: cooling (-0.10 – 0.00 °C); SlowW: slow warming (0.00 – 0.60 °C); RapidW: rapid warming (0.67 – 1.35 °C))



The first two ordination axes of the PCA had a cumulative variance of 95.5 %. The ordination diagram of the first two axes is presented in Fig. 3. The vectors of rapid warming (0.67 – 1.35 °C) and slow warming (0.00 – 0.60 °C) LMEs groups could both be found in the upper left quadrant of the diagram, whereas the cooling (-0.10 to 0.00 °C) LMEs vector was drawn in the upper right section. Years 1984–1990 were strongly associated with warming LMEs, whereas the most recent years could be found in the opposing quadrant.

Mann–Whitney tests and t -tests showed significant differences ($p < 0.05$) in the mean catches of *T. chalcogramma* in the East Bering Sea ($U = 30$; $p < 0.048$), Kuroshio Current ($t = 2.384$; $p < 0.029$) and Sea of Japan/East Sea ($U = 22$; $p < 0.007$); *S. sagax* in the Agulhas Current ($U = 14$; $p < 0.027$), East China Sea ($U = 6$; $p < 0.002$), Yellow Sea ($U = 24$; $p < 0.009$), Kuroshio Current ($U = 24$; $p < 0.016$) and Sea of Japan/East Sea ($U = 27$; $p < 0.018$); *C. harengus* in the Norwegian Sea ($U = 23$; $p < 0.047$); *T. leptocephalus* in the East China Sea

($t = -4.8369$; $p < 0.001$) and Yellow Sea ($t = -2.6535$; $p < 0.016$) and *G. morhua* in the North Sea ($t = 3.8587$; $p < 0.002$).

Mean catches in years of cold and warm years are plotted in Fig. 4 and presented in Table 1. Mean catches of *E. ringens* in years of warm winters were higher in the

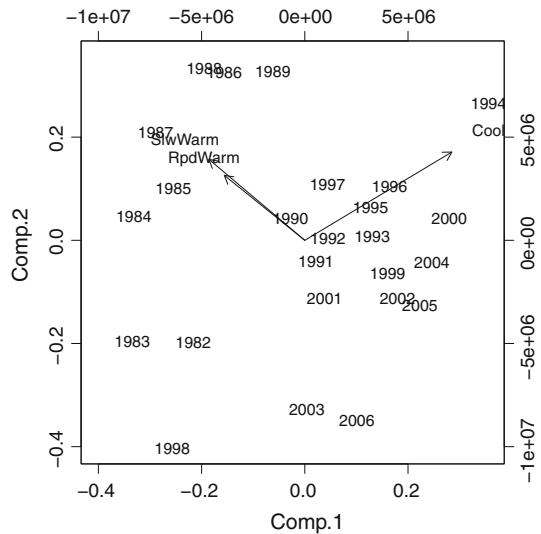


Fig. 3 Ordination plot of principal component analysis for fish catches in LME. Years are indicated. Vectors for different groups of LMEs based on SST change from 1982 to 2006 (Cool: -0.10 to 0.00 °C; SlwWarm: 0.00 – 0.60 °C; RpdWarm: 0.67 – 1.35 °C) are represented

Pacific Central-American LME and lower in the Humboldt Current. *T. chalcogramma* had higher mean catches in years of cold winters in the Yellow Sea, Kuroshio Current, Sea of Japan/East Sea and Oyashio Current and higher mean catches in years of warm winters in the East Bering Sea, Gulf of Alaska, California Current, Sea of Okhotsk and West Bering Sea. Mean catches of *S. sagax* were higher in years of cold winters in most LMEs, except for the Benguela Current, the Agulhas Current, the Oyashio Current and the Sea of Okhotsk, where mean catches were higher in years of warm winters. Mean catches of *C. harengus* were higher in years of warm winters in the West Greenland, Barents Sea, Norwegian Sea, North Sea, Celtic-Biscay Shelf, Iceland Shelf and Sea and Faroe Plateau and lower in the Greenland Sea, Baltic Sea, Northeast US Continental Shelf, Scotian Shelf and Newfoundland–Labrador Shelf. Mean catches of *G. morhua* were always higher in years of cold winters, except for the Northeast US Continental Shelf. Except for the Newfoundland–Labrador Shelf, mean catches of *M. villosus* were higher in years of warm winters. Both *T. lepturus* and *S. pilchardus* had higher mean catches in years of warm winters.

Discussion

The present study has shown a decreasing trend in the catches of fish species in warming LMEs, from 1982 to

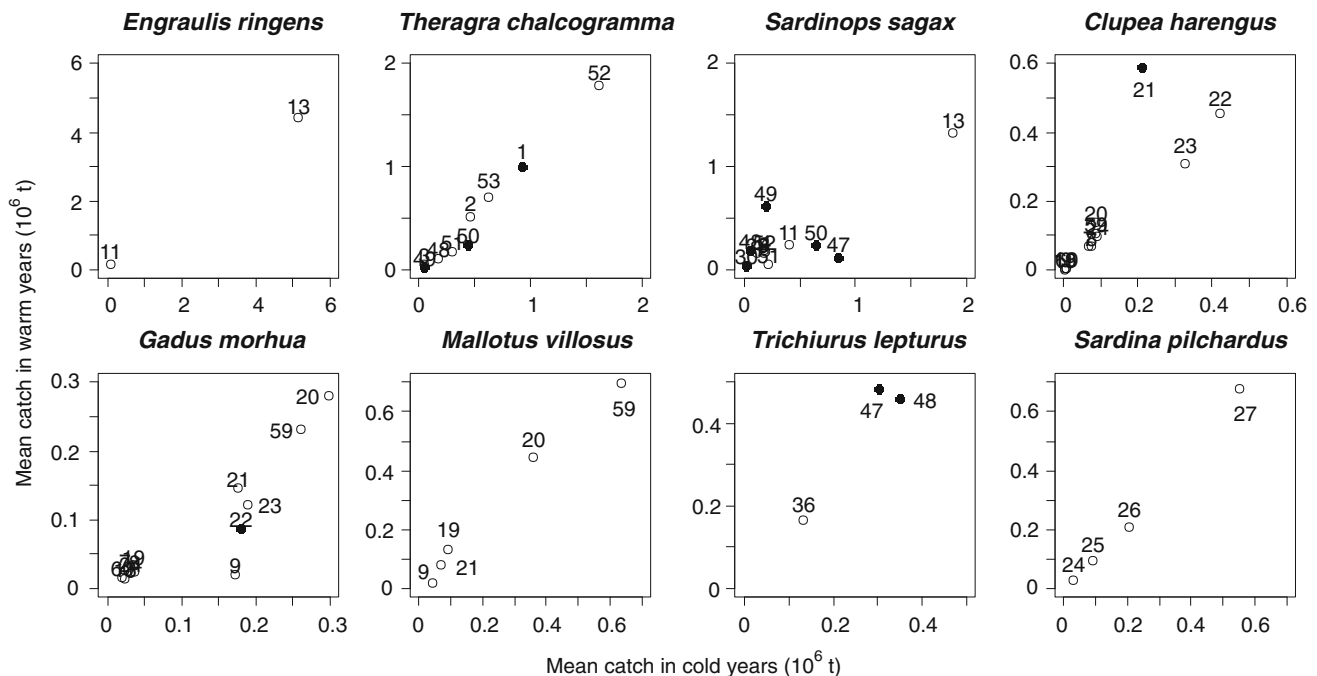


Fig. 4 Mean catches in cold and warm years, for the period of 1982–2006. Black dots represent significant results in t -tests and Mann–Whitney tests. For the codes for the LMEs, see Fig. 1

Table 1 Mean catches (*t*) of the eight most relevant fish species in terms of global catches cold and warm years in each large marine ecosystem, for the period of 1982–2006

LME	<i>Engraulis ringens</i>		<i>Theragra chalcogramma</i>		<i>Sardinops sagax</i>		<i>Clupea harengus</i>		<i>Gadus morhua</i>		<i>Mallotus villosus</i>		<i>Trichiurus lepturus</i>		<i>Sardina pilchardus</i>	
	Cold	Warm	Cold	Warm	Cold	Warm	Cold	Warm	Cold	Warm	Cold	Warm	Cold	Warm	Cold	Warm
1 E Bering Sea			928,428	1,003,091												
2 Gulf Alaska			458,087	519,580												
3 Calif Cur			46,948	51,843	181,141	163,565										
4 Gulf Calif					196,461	173,939	68,354	67,036	23,523	26,938						
7 NE US C S							72,628	67,244	36,490	25,028						
8 Scotian Shelf							6,509	4,830	171,205	19,661	42,006	19,598				
9 Nfld-Lab S																
11 Pac C-Amer	66,144	141,067			400,419	247,988										
13 Humboldt C	5,116,646	4,420,968			1,872,036	13,232,549										
18 W Grnld							2,925	4,441	23,314	14,098						
19 Grnld Sea							2,144	1,544	33,607	33,498	89,393	133,202				
20 Barents Sea							86,484	139,253	298,896	280,200	358,009	445,534				
21 Norwegian							209,001	588,172	176,489	146,716	70,653	80,041				
22 North Sea							419,023	453,400	180,122	87,398						
23 Baltic Sea							325,859	308,145	188,832	122,596						
24 C-Biscay S							90,910	97,608	29,733	22,132					27,221	27,576
25 Iberian C															89,259	95,507
26 Mediterr															205,633	209,303
27 Canary C															554,776	680,215
29 Benguela C					111,399	155,538										
30 Agulhas C					9,377	36,608										
36 S China Sea													131,409	166,983		
47 E China Sea													300,606	484,581		
48 Yellow Sea			172,304	110,507	58,516	190,365							347,892	459,375		
49 Kuroshio C			41,502	25,071	194,633	627,714										
50 S Japan/E S			431,584	241,827	640,373	244,132										
51 Oyashio C			298,670	174,965	210,876	59,094										
52 Sea Okhotsk			1,613,863	1,788,034	176,487	183,130										
53 W Bering S			626,959	707,839			84,955	105,618	259,625	231,416	634,508	696,323				
59 Iceland S S							4,791	5,907	19,369	16,258						
60 Faroe P																

Cold, cold years; Warm, warm years; E Bering Sea, East Bering Sea; Calif Cur, California Current; Gulf Calif, Gulf of California; NE US C S, Northeast US Continental Shelf; Nfld-Lab S, Newfoundland-Labrador Shelf; Pac C-Amer, Pacific Central-American; Humboldt C, Humboldt Current; W Grnld, Canadian Eastern Arctic—West Greenland Shelf; Grnld Sea, Greenland Sea; Norwegian, Norwegian Sea; C-Biscay S, Celtic-Biscay Shelf; Iberian C, Iberian Coastal; Mediterr, Mediterranean; Canary C, Canary Current; Benguela C, Benguela Current; Agulhas C, Agulhas Current; S China Sea, South China Sea; E China Sea, East China Sea; Kuroshio C, Kuroshio Current; S Japan/E S, Sea of Japan/East Sea; Oyashio C, Oyashio Current; W Bering S, West Bering Sea; Iceland S S, Iceland Shelf and Sea; Faroe P, Faroe Plateau

2006. Catches in years of cold and warm winters were compared for each of the eight most caught fish species. Generally, mean catches of polar and temperate species were higher in years of warm winters in the northern part of the species range and in years of cold winters in the southern part of their range; mean catches of subtropical species were higher in cold years in lower latitudes and in warm years in higher latitudes.

Several studies have focused on the prediction of shifts in species distributions in different future climate change scenarios (Cheung et al. 2009; Vinagre et al. 2011). The distribution of marine ectotherms tends to move poleward as the ocean warms up, which may result in an increase in species richness in high-latitude regions (Cheung et al. 2009). Hiddink and Hofstede (2008) showed that the rise of species richness of fish in the North Sea, observed in a 22-year period, was related to higher water temperatures. Vinagre et al. (2011) predicted a general increase in species richness by 2100 in the Portuguese coast, with the appearance of new subtropical and tropical species and the elimination of only a few species, and Gamito et al. (2013) have reported a recent increase in the relative importance of subtropical fish species in Portuguese fisheries. Bioclimate envelope models have predicted a redistribution of the global catch potential, with an increase of 30–70 % in high-latitude regions and a decrease of up to 40 % in tropical regions (Cheung et al. 2010). A different approach, using a physical-biogeochemical model coupled with a dynamic, size-based food web model, resulted in broadly similar predictions (Blanchard et al. 2012). Fish catches in slowly warming LMEs have decreased from 1982 to 2006. As most of the area occupied by slowly warming LMEs is located in tropical regions, this result may be indicative of a decline in catches in tropical fisheries, as predicted by several studies (Cheung et al. 2010; Blanchard et al. 2012). Nevertheless, this result also includes catches in high latitudes, and a similar declining trend was observed for rapidly warming LMEs. Although high-latitude LMEs may be increasing their species richness due to the arrival of subtropical and tropical species, the catches may not immediately reflect this change. Catches depend, among other factors, on the fishers decisions. The decision of fishers on whether to change target species and gear depends on several factors, such as resource abundance, commercial value, information from other fishers, weather conditions, distance to fishing grounds, cultural aspects and fisheries management measures (Christensen and Raakjær 2006). Thus, the adaptation of fisheries to the changes in the fish communities will not most likely be that fast. Also, the Sea Around Us Project database which was used in the present work includes only the species that were most caught in each LME. For that reason, an increase in other subtropical or tropical species not included in this database

may have occurred, without having been detected in the present analyses.

Generally, mean catches of polar and temperate species were higher in years of warm winters in the northern part of the species range and in years of cold winters in the LMEs located in the southern part of their range. *T. chalcogramma* had higher catches in warm years in the Northwest Pacific and in cold years in the Southwest Pacific. *M. villosus* also had higher catches in warm years in the LMEs located in the northern part of its range and in cold years in the south. SST is higher in the southern LMEs (East Asian Seas) than in the northern LMEs (e.g. Bering Sea, Gulf of Alaska, Sea of Okhotsk). Warmer winters may result in a shift of polar species to higher latitudes, as the temperatures in the southern LMEs may reach values higher than those species can tolerate. Another important factor influencing the catches is the ice-cover extent. The loss of ice cover in polar areas will strongly affect the ecology of those areas and will probably lead to positive effects in fisheries (MacNeil et al. 2010). As ice cover is lost, new open-water areas will probably show a strong increase in primary productivity, which will increase zooplankton abundance and thus fish biomass (Sherman et al. 2009; MacNeil et al. 2010). In the Bering Sea, the winter fishing season for *T. chalcogramma* takes place during the period of maximum seasonal sea-ice extent. However, fishers avoid fishing in ice-covered waters, because vessels cannot physically enter those areas. In warm years, fishing vessels can reach areas which they would generally avoid due to ice cover, resulting in a change in effort. This distribution of winter fishing may shift as the ice cover declines with climate change (Pfeiffer and Haynie 2012). *M. villosus* has previously been considered an early warning “canary” for climate change, as it appears to react quickly to environmental changes (Rose 2005a). In fact, changes in *M. villosus* distribution have been reported as drifting at larval stage and as active feeding or spawning range changes of juveniles and adults. Changes in temperature as small as 1 °C have been associated with changes in this species’ distribution over hundreds of kilometres, and larger changes in temperature may result in much larger shifts in distribution (Rose 2005a, b). Drinkwater (2005) has studied the response of *G. morhua* to climate change and predicted that, by the year 2100, stocks in the Celtic and Irish Seas would disappear and those in the southern North Sea and Georges Bank would decline. The same author also predicted that *G. morhua* would likely spread northwards along the coasts of Greenland and Labrador, occupy larger areas of the Barents Sea, and even extend onto some of the continental shelves of the Arctic Ocean. In fact, even though distributional shifts have not been visible in the present study—higher catches of *G. morhua* were found in cold years for every LME studied—warming has already

led to a northern range expansion of this species in Norway and Greenland (Drinkwater 2006, 2009). Climate change is expected to lead to fish invasions into high-latitude regions and particularly into the Arctic (Cheung et al. 2009). On the other hand, polar species generally have much narrower temperature limits than lower latitude species, making them highly sensitive to temperature change. Thus, despite the arrival of new species, polar regions may still be susceptible to climate change impact, in terms of biodiversity (Cheung et al. 2009). *C. harengus* has also had higher catches in warm years in the northern LMEs and in cold years in southern LMEs. Like polar species *M. villosus*, this temperate species is considered to react strongly and quickly to climate change due its physiological limits and potential for fast population growth (Rose 2005b). The same author observed that when Icelandic and Greenland waters warmed considerably in 1920–1940, *C. harengus*, *M. villosus* and *G. morhua* shifted north very quickly. Over the next 50 years, the value of fish production for the most important *C. harengus* stocks is expected to increase by 20 % in Iceland and 200 % in Greenland (Arnason 2007). Temperate species are generally distributed close to the centre of their thermal tolerance range and thus show a greater capacity to shift ranges (MacNeil et al. 2010). Changes in species composition in temperate regions will be caused by the departure of species moving to higher latitudes and the arrival of warm-water species from lower latitudes (Cabral et al. 2001; Henriques et al. 2007; MacNeil et al. 2010; Vinagre et al. 2011). Distributions of North Sea fishes have responded markedly to increases in sea temperature, with nearly two-thirds of species shifting in mean latitude or depth or both over 25 years (Perry et al. 2005). In biogeographic transition zones, between temperate and subtropical areas, these changes can also be detected in fisheries catches (Gamito et al. 2013). The East Asian Seas, the Subarctic Gyre and the European Seas have rapidly warmed from 1982 to 2006 (Belkin 2009). The Bering Sea has slowly warmed in 1982–2006 (Belkin 2009), and global climate models predict further warming and 40 % reduction in winter ice cover by 2050 (Overland and Wang 2007; Pfeiffer and Haynie 2012). The present results suggest a future poleward shift in the distribution of catches of polar and temperate species, due to their displacement to higher latitudes. In polar regions, a reduction in ice cover will also favour an intensification of fishing effort in new open-water areas.

In general, the present study showed higher mean catches of subtropical species in cold years in low latitudes and in warm years in higher latitudes. Although *S. sagax* is known to be more productive during warm-water regimes in the California and the Humboldt Currents (MacCall et al. 2005; Sumaila et al. 2011), the catches analysed in the present study did not reflect that trend for warm-winter years. In

fact, mean catch of *S. sagax* in those LMEs was lower in warm-winter years than in cold-winter years. Yet, this result when seen together with the other results obtained for this species agrees with a poleward movement of subtropical species in warm years. Both *T. lepturus* and *S. pilchardus* had higher catches in warm years. Although the analyses of the mean catches of *T. lepturus* included two temperate LMEs and a tropical LME, the results were not different for temperate and tropical LMEs. However, in the tropical LME—South China Sea—the difference between mean catches in cold and warm years was rather small. The analyses of *S. pilchardus* included catches from temperate/subtropical LMEs. In fact, these LMEs are located in a biogeographic transition zone, from temperate to subtropical areas. The northern and southern range limits of *S. pilchardus* are related with the average water temperature, which for this species should be between 10 and 20 °C (Garza-Gil et al. 2010). In the Portuguese coast, previous studies related decreasing trends in the recruitment of small pelagic populations in the 1980s and 1990s with the increase in upwelling events during winter (Santos et al. 2001). The Celtic-Biscay Shelf, the Iberian Coastal and the Mediterranean LMEs have rapidly warmed in 1982–2006. Garza-Gil et al. (2010) have predicted that if the SST in the Iberian-Atlantic fishing grounds followed the current warming trend, lower biomass and catches of *S. pilchardus* would be obtained and therefore the economic yield would also decrease. In the Humboldt Current, warming effects on upwelling dynamics and productivity, related with the El Niño Southern Oscillation, are associated with declines of *E. ringens* (Lehodey et al. 2006). Phases with mainly negative temperature anomalies parallel *E. ringens* regimes (Heileman et al. 2009). The results obtained in the present paper agree with those findings. In the Humboldt Current, the mean catch of *E. ringens* in cold years was higher than in warm years. The Humboldt Current has cooled from 1982 to 2006 (Belkin 2009). This LME is located in the East Pacific coastal upwelling zone, where the upwelling intensity is near its global maximum; the observed cooling in this LME suggests an increase in the upwelling intensity (Heileman et al. 2009). Upwelling in the Humboldt Current varies with the El Niño, decreasing in warm years and reducing the planktonic food sources for juvenile and adult *E. ringens* (Heileman et al. 2009). Since the frequency of regional climate anomalies, such as El Niño, is expected to increase (Timmermann et al. 1999), devastating consequences could arise for the *E. ringens* fishery.

As temperature influences several life stages of fish species (Pörtner et al. 2001; Pörtner and Peck 2010), the effects of changes in SST may not always be immediately visible in fisheries catches. The present study analysed fish catches of a large number of species throughout LMEs. If only a few species, with similar life cycles, had been

studied, this analysis could have considered a time lag between SST and catches. However, due to the large number of species considered, each with its particular life cycle, it was not possible to define a time lag adequate for every species. Also, the present study used catch data from the Sea Around Us Project database (Pauly 2007), which is based on the official landings reported annually by the Food and Agriculture Organization of the United Nations (FAO). Therefore, as they exclude unreported landings and discards, landings are in fact underestimates of catches. Also, the lack of information on fishing effort in these databases may be a source of bias in our analysis. However, reported landings are the only data that are collected and made publicly available for fisheries in about 80 % of all maritime countries (Pauly et al. 2013). Despite criticisms on the use of these data to detect and interpret trends in fisheries, several authors (e.g. Froese et al. 2012; Pauly et al. 2013) defend that when only catch data are available, fisheries researchers can and should use these data. In fact, several recent studies have used the Sea Around Us Project database (Christensen et al. 2009; Merino et al. 2012; Watson et al. 2013; Cheung et al. 2013).

The analyses of fish catches in the present study have agreed with a poleward shift of fish species in a warming ocean. A continued warming of the oceans will most likely result in further changes in catch composition throughout the world. The impact of these changes on fisheries may not always be negative, for new fishing opportunities may arise, particularly in temperate and polar regions. On the other hand, food security in tropical regions may be at risk.

Acknowledgments This study had the support of the Fundação para a Ciência e Tecnologia (FCT) (Pest-OE/MAR/UI0199/2011). Rita Gamito was funded with a PhD Grant (SFRH/BD/78363/2011) by the FCT. We thank Catarina Vinagre for discussions and comments on the manuscript.

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