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Nutrition and income from molluscs today imply vulnerability to ocean acidification tomorrow

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Abstract

Atmospheric carbon dioxide (CO_2) emissions from human industrial activities are causing a progressive alteration of seawater chemistry, termed ocean acidification, which has decreased seawater pH and carbonate ion concentration markedly since the Industrial Revolution. Many marine organisms, like molluscs and corals, build hard shells and skeletons using carbonate ions, and they exhibit negative overall responses to ocean acidification. This adds to other chronic and acute environmental pressures and promotes shifts away from calcifier-rich communities. In this study, we examine the possible implications of ocean acidification on mollusc harvests worldwide by examining present production, consumption and export and by relating those data to present and future surface ocean chemistry forecast by a coupled climate-ocean model (Community Climate System 3.1; CCSM3). We identify the 'transition decade' when future ocean chemistry will distinctly differ from that of today (2010), and when mollusc harvest levels similar to those of the present cannot be guaranteed if present ocean chemistry is a significant determinant of today's mollusc production. We assess nations' vulnerability to ocean acidification-driven decreases in mollusc harvests by comparing nutritional and economic dependences on mollusc harvests, overall societal adaptability, and the amount of time until the transition decade. Projected transition decades for individual countries will occur 10–50 years after 2010. Countries with low adaptability, high nutritional or economic dependence on molluscs, rapidly approaching transition decades or rapidly growing populations will therefore be most vulnerable to ocean acidification-driven mollusc harvest decreases. These transition decades suggest how soon nations should implement strategies, such as increased aquaculture of resilient species, to help maintain current per capita mollusc harvests.

Keywords Adaptability, aquaculture, food security, mollusc harvests, Ocean acidification, population growth

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[1]This included the following nations: Djibouti, Ecuador, Eritrea, Estonia, Fiji, Finland, Iran, Laos, Latvia, Lithuania, Luxembourg, Maldives, Malta, Marshall Islands, Mauritius, Morocco, Mozambique, Myanmar, Namibia, Netherlands, Pakistan, Peru, Poland, Romania, Saudi Arabia, Singapore, Slovak Republic, Somalia, Switzerland, Togo, Tonga, United Arab Emirates, Uruguay, Yemen.

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Introduction

Quantifying the effects of ocean acidification on human communities requires assessing its direct and indirect chemical impacts on valuable marine ecosystem services such as fisheries. Ocean acidification refers to a well-described progressive alteration of seawater chemistry owing to atmospheric carbon dioxide (CO_2) emissions from human industrial activities (Doney *et al.* 2009; National Research Council 2010b). Since the Industrial Revolution in the late 1800s, surface seawater pH has decreased from pH 8.2 to 8.1 (Caldeira and Wickett 2003), which represents a 26% increase in hydrogen ion concentration. At the same time, the carbonate ion concentration in surface seawater has decreased markedly, and this has also reduced the saturation state of calcium carbonate minerals (Ω) that are used by marine organisms like molluscs and corals to build hard shells and skeletons (Orr *et al.* 2005). Anthropogenic CO_2 emissions are expected to continue to rise for the next several decades as global populations and industries grow (Intergovernmental Panel on Climate Change (IPCC) 2007, pp.21–32), and coupled climate-ocean models forecast that the decline in ocean pH will accelerate worldwide (Orr *et al.* 2005).

By 2050, ocean acidification will have decreased the saturation states of carbonate minerals in surface seawater to levels well below preindustrial conditions (Feely *et al.* 2009), and these new chemical conditions are expected to affect many marine organisms by altering calcification, intracellular pH, respiration, photosynthesis, nitrogen fixation and by exerting selective pressure on juveniles (Doney *et al.* 2009). Organisms are believed to spend more energy for maintaining hard calcium carbonate shells or skeletons in lower-Ω or undersaturated ($\Omega < 1$) conditions (National Research Council 2010b, pp. 33–42). Ocean acidification may thus leave these calcifying species with fewer resources for other activities like reproduction and metamorphosis.

To date, studies of ocean acidification's effects on aquatic organisms have often focused on calcifying molluscs. Different species-specific responses among molluscs have been observed (e.g., Miller *et al.* 2009), but the majority of mollusc responses to ocean acidification are neutral to negative (Table 1). For example, shell thickness, area, and calcification rate of the Eastern oyster (*Crassostrea virginica*, Ostreidae) larvae and adults (Gazeau *et al.* 2007; Miller *et al.* 2009) decrease with increases in CO_2 and/or decreases in Ω_{ar} (the saturation state of aragonite, one of the most soluble calcium carbonate minerals). In the hard clam or quahog (*Mercenaria mercenaria*, Veneridae), *C. virginica* and

Table 1 Responses of economically or nutritionally important bivalve molluscs to elevated CO_2 and/or decreased pH.

Species	Calcification	Growth	Survival	Other	References
Atlantic bay scallop (*Argopecten irradians*)*	– (1)	– (1)	– (2)	Length: – (1); Delayed metamorphosis: (1)	Ries *et al.* (2009b); Talmage and Gobler (2009, 2010)
Suminoe oyster (*Crassostrea ariakensis*, Ostreidae)	0	0			Miller *et al.* (2009)
Pacific oyster (*Crassostrea gigas*)*	– (2)		– (1)	Reproduction: 0 (1)	Havenhand and Schlegel (2009); Kurihara *et al.* (2007); Gazeau *et al.* (2007)
Eastern oyster (*Crassostrea virginica*)*	– (4)	– (1)	– (1)	Length: – (1); Delayed metamorphosis (1); Metabolism: – (1)	Ries *et al.* (2009a); Talmage and Gobler (2009); Beniash *et al.* (2010); Miller *et al.* (2009); Waldbusser *et al.* (2010)
Smooth Australian abalone (*Haliotis laevigata*, Haliotidae)		–	–		Harris *et al.* (1999)
Blacklip abalone (*Haliotis rubra*, Haliotidae)		–	–		Harris *et al.* (1999)
Common periwinkle (*Littorina littorea*, Littorinidae)	P (1)		Metabolism: – (1); Calcification defence against predators: – (1); Avoidance of predators: +(1)		Ries *et al.* (2009b); Bibby *et al.* (2007)
Yellow periwinkle (*Littorina obtusata*, Littorinidae)			–	Altered behaviour AND physiology; Heart rate: –	Ellis *et al.* (2009)
Hard clam (*Mercenaria mercenaria*)*	– (3)		– (3)	Size: – (1)	Ries *et al.* (2009b); Talmage and Gobler (2009, 2010); G. Waldbusser *et al.* (2010)
Steamer clam (*Mya arenaria*, Myidae)*	–				Ries *et al.* (2009b)
Blue mussel (*Mytilus edulis*, Mytilidae)*	0 (1) – (1)	– (3)		Health: – (1); Size: – (1); Length: – (1); Metabolism: P(1); Shell thickness: – (1)	Beesley *et al.* (2008); Bechmann *et al.* (2011); Thomsen and Melzner (2010); Gazeau *et al.* (2007)
Mediterranean mussel (*Mytilus galloprovincialis*, Mytilidae)		–		Nitrogen excretion/protein degradation: +	Michaelidis *et al.* (2005)
Common limpet (*Patella vulgata*, Patellidae)		+ (1)		Radula damage: – (1)	Findlay *et al.* (2009); Marchant *et al.* (2010)
Pearl oyster, (*Pinctada fucata*, Pteriidae)		–		Strength: –	(Welladsen *et al.* 2010)

Table 1 (Continued).

Species	Calcification	Growth	Survival	Other	References
Sydney rock oyster (*Saccostrea glomerata*, Ostreidae)		– (2)			Parker *et al.* (2009, 2010)
Florida fighting conch (*Strombus alatus*, Strombidae)	–				Ries *et al.* (2009a)
Strawberry conch (*Strombus luhuanus*, Strombidae)		–	–		Shirayama and Thornton (2005)

Adapted from Kroeker *et al.* (2010) and updated with published studies through April 2011. Decreases are denoted by minus signs, increases by plus signs, no change by 0 and parabolic responses by 'P' (c.f. Doney *et al.* 2009). For species with multiple studies, numbers in parentheses following –, 0, + or P indicate the number of studies that showed that response. Within this list, the species that have been harvested commercially in the USA for the last four decades are noted with an asterisk (*).

the Atlantic bay scallop (*Argopecten irradians*, Pectinidae), three economically valuable North American species, larval mollusc development is delayed and mortality increases as Ω_{ar} decreases (Talmage and Gobler 2009; Green *et al.* 2009). Delayed development can increase mortality of planktonic juvenile molluscs by exposing them to water column predation for longer and by depleting energy reserves that may be required for metamorphosis and settlement. After settlement, smaller or weaker, thinner shells could increase mollusc mortality by providing less adequate defence against predation or physical damage; in addition, degraded shells could prolong the time until adults became harvestable. Even just the seemingly small 2.4% increase in daily mortality of *M. mercenaria* observed as Ω_{ar} decreases from 2.6 to 2.0 (Miller *et al.* 2009) could lead to dramatic population decreases, given that a 5% increase in daily mortality of *C. virginica* has been calculated to decrease larval recruitment by 89% (Kennedy *et al.* 1996). It is presently unknown whether ocean acidification could affect larval or juvenile forms more profoundly or in more long-lasting ways than it affects adults. Even though species-specific studies have not been performed on every mollusc species worldwide, these initial data (Table 1) imply that ocean acidification is likely to have negative overall impacts on many economically and nutritionally valuable mollusc populations.

In addition, ocean acidification is expected to alter marine ecosystems, in some cases leading to reduced biological diversity, by helping photosynthetic species even as it harms calcifiers. In coastal ecosystems with naturally lower pH and elevated CO_2 or with rapidly decreasing pH, benthic coastal ecosystems with calcifier-dominated populations gave way to non-calcifying populations and species diversity decreased (Hall-Spencer *et al.* 2008; Wootton *et al.* 2008; Russell *et al.* 2009). Ocean acidification will also occur in conjunction with other chronic and acute environmental pressures like eutrophication, temperature increases and trophic shifts (Fabry *et al.* 2008; Doney *et al.* 2009; Gooding *et al.* 2009; Russell *et al.* 2009), several of which have been shown to promote shifts towards algae-dominated communities (Hoegh-Guldberg *et al.* 2007).

Human communities will feel the effects of ocean acidification once it alters economically and socially important marine ecosystem services (Cooley *et al.* 2009). Calcifiers provide provisioning, supporting and cultural ecosystem services (Millennium Ecosystem Assessment 2005) that include economically and nutritionally valuable species for harvest, environmentally important marine habitat, food for marine predators, coastal protection, recreational opportunities, cultural identity and other more difficult-to-quantify benefits, like nutrient recycling. Quantifying the economic value of services with direct ecosystem benefits and market values, such as mollusc harvests, is the most logical first step to begin assessing the socioeconomic consequences of ocean acidification-driven changes in calcifier populations (e.g., Cooley and Doney 2009).

In this study, we use the vulnerability assessment approach (Intergovernmental Panel on Climate Change 2007) to examine the implications of ocean acidification and human population growth for future worldwide per capita mollusc protein availability. Our analysis gauges vulnerability by examining exposure, sensitivity and adaptive capacity (Intergovernmental Panel on Climate Change 2001). We quantify current mollusc production, consumption and export patterns (to estimate baseline sensitivity to present environmental conditions), and we relate those data to present and future surface ocean saturation state (to estimate exposure) and to human populations (to estimate adaptive capacity). We limit this pilot analysis to mollusc harvests for several reasons: the studies reviewed above suggest that molluscs may be more at risk than crustaceans and finfish; our present incomplete understanding of marine trophic interactions limits our ability to assess the ecosystem-level consequences of changes in mollusc populations; and values for the indirect and non-market ecosystem services that calcifiers provide (e.g., food for predators, cultural identity and habitat) are not well established. Even though mollusc harvests provide just a small fraction of consumed protein and export income for many nations, they represent a portion of the fishery sector that, at present, has the best-understood potential to be directly affected by ocean acidification. Our intent is not to forecast all possible impacts of ocean acidification on national protein consumption and income from fisheries, but instead to advance the assessment of what socioeconomic and environmental characteristics could place nations' current levels of well-being at risk in the future as ocean acidification progresses. Because of the present limitations in our understanding of marine ecosystems' total responses to ocean acidification, we restrict ourselves here to the better-understood subset of marine ecosystems.

After examining future trends in protein demand and mollusc production implied by population growth forecasts, we examine the vulnerability of individual nations to ocean acidification's potential impacts on molluscs. Because the mechanistic responses of locally important molluscs around the world to changes in Ω are still being resolved, we instead identify the 'transition decade' when future Ω_{ar}, as forecast by the National Center for Atmospheric Research (NCAR) Community Climate System Model 3.1 (CCSM3, P. E. Thornton *et al.* 2009), will be distinctly different from that of the present. After this time, molluscs will no longer be living in conditions equivalent to today's, and harvest levels similar to today's cannot be guaranteed if present ocean chemistry is a significant factor influencing today's mollusc populations. Finally, we gauge nations' vulnerability to mollusc harvest decreases from ocean acidification by comparing their nutritional and economic dependence on mollusc harvests (their sensitivity), their overall adaptability (their adaptive capacity) and the amount of time they have until the transition decade is reached (their exposure; Intergovernmental Panel on Climate Change 2001).

Methods

Datasets

In all cases, we used the most recent and updated data available. Specific years associated with each dataset are noted below. Because of the diversity of data types and sources used in this study, data from different years were compared in our analysis. However, every dataset and index in this study used information that was <10 years old.

Mollusc data

United Nations Food and Agriculture Organization (FAO) datasets cataloguing mollusc production and export for each nation were accessed using FishStat Plus software (Food and Agriculture Organization of the United Nations 2010b). In this study, the term 'mollusc' refers collectively to the commercially important mollusc families (e.g., conch, abalone, whelk, clam, oyster, scallop, mussel) and excludes cephalopods (e.g., squid, octopi). Mollusc data for a given region or condition therefore comprised the total sum of all data for these families. The FAO family-level classifications used here were considered to be most accurate because species-level errors do occur in aquaculture data upon submission (personal communication, X. Zhou, 2010), and we assumed this was also true for wild capture data. Appendix 1 lists the mollusc families included in this study. The FAO categories 'miscellaneous molluscs' and 'not elsewhere included molluscs (nei molluscs)' were included in our calculations; it is possible that some nations that harvest significant amounts of cephalopods may report these harvests in those two categories. We discuss those cases in the Results.

Mollusc production data for each nation were obtained using FishStat Plus software. Its Total Fisheries Production dataset sums the weights of capture harvests and aquaculture harvests from 2008 (Total Fishery Production 1950 2008 dataset, Food and Agriculture Organization of the United Nations 2010b). Capture harvests are the total wet live weight equivalent of wild molluscs collected for commercial, industrial, recreational and subsistence purposes. Aquaculture harvests are the total wet live weight of cultured molluscs (Capture production 1950 2008 dataset, Food and Agriculture Organization of the United Nations 2010b). Cultured molluscs are individually or corporately owned and have been reared using human intervention such as stocking, feeding or protection to increase yields (Food and Agriculture Organization of the United Nations 2010b).

Total mollusc export for each country for 2007 in US dollars (Food and Agriculture Organization of the United Nations 2010b) included the sum of exports and re-exports. Export included all commercial trade, food aid, donated quantities and estimates of unrecorded trade (Fisheries Commodities Production and Trade 1976–2007 dataset, Food and Agriculture Organization of the United Nations 2010b). For countries whose documented total production quantities were less than their export quantities, we replaced the total production values with the total export quantities.[1] This corrected for small mismatches between FAO Trade and Production datasets, although it also introduced the assumption that in each of these countries, the amount of molluscs produced must be greater than or equal to what was exported, and no imported molluscs were re-exported. For these countries, mollusc re-export is not a large industry, and the assumption seemed to be valid.

Food and Agriculture Organization food balance sheets reported national protein availability and seafood consumption per capita (Food Balance Sheets, SUA FBS domain dataset, Food and Agriculture Organization of the United Nations 2010b), but they did not explicitly separate seafood into taxonomic families. Therefore, total national per capita protein consumption from FAOSTAT (http://faostat.fao.org) was compared with national per capita protein from molluscs, which we determined using calculated mollusc consumption from this study (Mollusc and socioeconomic data) and United States Department of Agriculture average mollusc protein content (25 g protein per 100 g mollusc)(United States Department of Agriculture, Agricultural Research Service 2010).

Economic and governance data

We used datasets from several different sources to evaluate nations' economic dependence on molluscs and their adaptive capacities (Allison *et al.* 2009). Gross domestic product (GDP) data for 2010 were primarily from the World Bank (The World Bank 2010), but gaps were filled with data from the Central Intelligence Agency (CIA) World Factbook (Central Intelligence Agency 2010a). Per capita GDP adjusted for purchasing power parity (GDP PPP) data from 2009 were obtained from the CIA World Factbook (Central Intelligence Agency 2010b), and data gaps were filled with values from the International Monetary Fund (International Monetary Fund 2010). Life expectancy in years for 2008, which summarized citizens' overall health (Moss *et al.* 2001), was from the Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat and was accessed using the Climate Analysis Indicators Tool (CAIT, World Resources Institute 2009). Education data for 2000–2007 (variable by nation) from United Nations Educational, Scientific, and Cultural Organization Institute for Statistics (UNESCO 2008) were accessed from CAIT. An index quantifying governance over 1996–2008 was taken from the World Bank's Worldwide Governance Indicators (WGI) Project (Kaufmann *et al.* 2009). This index quantified six characteristics: voice and accountability, political stability, government effectiveness, regulatory quality, rule of law and control of corruption (Kaufmann *et al.* 2009).

Population projections

Current and future populations for each country through 2050 were from the United States Census Bureau (United States Census Bureau, Population Division 2010). Population estimates for 2100 were calculated using a compounding interest formula based on the projected rates of population growth at 2050 (United States Census Bureau, Population Division 2010). Nations whose populations were projected to decline were set to have constant population for this study so that future mollusc production (Mollusc and socioeconomic data) stayed constant at the present rate.

Ocean acidification data
Ocean chemistry conditions were calculated from the Community Climate System Model (CCSM3.1) case B31.161n with T31-gx3v5 resolution (Thornton *et al.* 2009). This coupled climate model includes historical atmospheric CO_2 emissions for the past and the Intergovernmental Panel on Climate Change (IPCC) A2 scenario ('business as usual') for the future. Monthly output fields of ocean surface temperature, dissolved inorganic carbon, total alkalinity and salinity were interpolated to a regular 2°× 2° grid from the variable model grid. The saturation state of aragonite (Ω_{ar}) for the surface ocean was calculated using these input fields, and the Lueker *et al.* (2000) refit carbonate system dissociation constants, KSO_4 from Dickson (1990), and the total pH scale in a polynomial solver for Matlab similar to that provided by Zeebe and Wolf-Gladrow (2001).

Analysis

Mollusc and socioeconomic data
Because FAO food balance sheets (Food and Agriculture Organization of the United Nations 2010b) do not quantify mollusc consumption, we examined the nutritional role of molluscs for each nation using production and trade data, population and nutritional data. First, we assumed that

(domestic consumption) = (domestic production) + imports − (exports + re-exports),

where all quantities were in metric tons per year, and all molluscs available domestically are consumed each year. Second, we calculated the implied mollusc protein consumption per capita per day from domestic consumption, average mollusc protein content and present population estimates.

We then determined the dietary importance of molluscs for citizens and the role of molluscs in meeting their protein needs by comparing mollusc protein consumed per capita per day to nationally available dietary protein consumed (Food and Agriculture Organization of the United Nations 2010a) and to the United States Department of Agriculture's 'protein sufficiency' baseline of 65 g protein per day for adults (United States Department of Agriculture, Agricultural Research Service 2010). For countries without nationally available protein per capita per day data, we assumed citizens receive 65 g capita^{-1} d^{-1} of total dietary protein.

To forecast future mollusc production requirements, we multiplied the current production rate per capita by future projected population. We assumed that nations will maintain approximately the same protein and mollusc consumption per capita patterns in the future, and that they will be able to increase the sum of wild and aquaculture harvests to meet future demands. Countries without any present mollusc harvests, aquaculture or imports (7 of the 193 nations listed in FAOSTAT datasets) therefore were excluded from the future projections in this analysis.

National adaptability indices were calculated as the average of four socioeconomic indicators (Allison *et al.* 2009): GDP adjusted for purchasing power parity, governance, literacy and life expectancy. We normalized each set of adaptive capacity indicators by subtracting the mean from all values and dividing the difference by the standard deviation of the set, normalizing each indicator set around a mean value of 0 and setting its standard deviation at 1. The average national adaptability was then calculated using the socioeconomic indicators available for that country. Because some countries did not have all four indicators and the mean values of all four indicators varied somewhat, the normalizing step avoided biasing the averaged national adaptability when one or more indicators were missing (countries with indicators = 219; 55 countries missing 1 indicator; 14 missing 2; 8 missing 3).

Ocean acidification data
We high-pass filtered gridded monthly average surface Ω_{ar} data calculated from CCSM3 model output (Ocean acidification data) by calculating the 120-month centred running mean. We then calculated decadal mean values from this filtered monthly dataset, generating maps of mean surface Ω_{ar} for the decades centred around 2010 and 2050. We calculated mean surface ocean chemistry parameters for FAO's major statistical fishery areas using the region boundaries from FAO (FAO GeoNetwork Team 2007). Exclusive economic zones were mapped using shapefiles from the Flanders Marine Institute Maritime Boundaries Geodatabase (Vlaams Instituut voor de zee 2008).

Changes in marine carbonate chemistry caused by anthropogenic CO_2 are irreversible on the human-relevant timescales of decades to centuries. From a signal-processing standpoint, quantifying ocean acidification can be challenging because it involves assessing both spatial and temporal variability in a signal that fluctuates around a changing baseline. Furthermore, no clear chemical 'tipping points' can be identified at present because neither the tolerances of marine ecosystems to variability nor the socioeconomic implications of changing ocean chemistry are fully known. To quantify when this progressive chemical change could be profound for marine communities, we chose to identify the time when future Ω_{ar} diverged in a statistically meaningful way from present conditions. We located this transition decade of large change in Ω_{ar}, or the time when present and future Ω_{ar} diverged considerably, by determining when the mean ± the root mean square of future Ω_{ar} ($\overline{\Omega}_{ar,future} \pm RMS_{\Omega ar,\ future}$), or 'envelope' of variability, no longer normally overlapped the present normal range of Ω_{ar} variability ($\overline{\Omega}_{ar,2010} \pm RMS_{\Omega ar,\ 2010}$), or envelope (Fig. 1). To calculate this, we removed the secular trend from monthly mean surface Ω_{ar} ($\overline{\Omega}_{ar}$) by subtracting from it the high-pass filtered monthly average surface Ω_{ar} data, leaving an anomaly around zero that describes the seasonal and high-frequency (<0.1 per year) changes in Ω_{ar}. We calculated the root mean square of this anomaly ($RMS_{\Omega ar}$) using a 120-month window centred around the time in question to quantitatively describe variance around $\overline{\Omega}_{ar}$ over time. Because Ω_{ar} is declining over time, the transition decade when the future change exceeds the envelope of modern-day variability was calculated as the first date when the following condition became true:

$$(\overline{\Omega}_{ar,2010} - RMS_{\Omega ar,2010}) - (\overline{\Omega}_{ar,future} + RMS_{\Omega ar,future}) > 0.$$

Vulnerability assessment

We developed a scale to rank nations' vulnerability to decreased mollusc harvests from ocean acidification. Countries were grouped by net import/export status and then were given one point for each of the following conditions: if molluscs provide more than 0.001% of the GDP (sensitivity); if the country is protein insufficient (sensitivity); if molluscs provide more than 1% of citizens' protein (sensitivity); if the required increase in production by 2050 is more than 100% (adaptive capacity); or if the country currently does not have mollusc aquaculture (adaptive capacity). Countries also

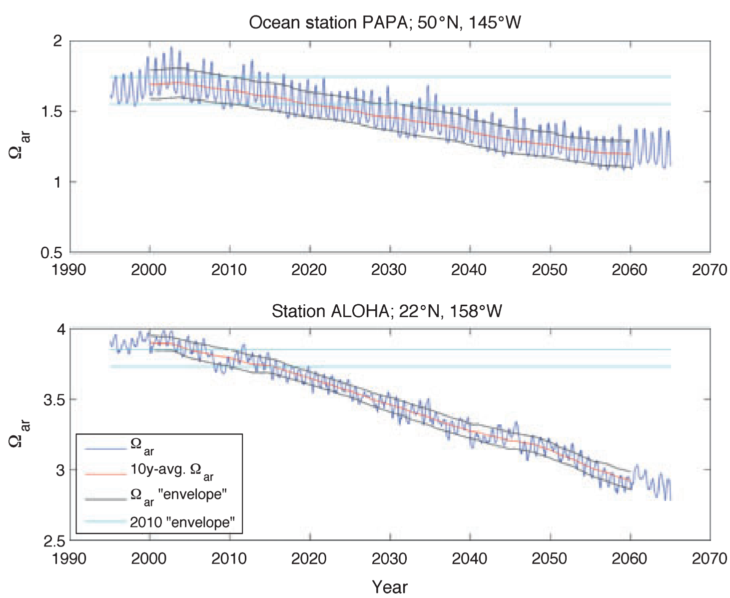

Figure 1 Sample time series of monthly mean Community Climate System 3-modelled surface Ω_{ar} (blue) for (top) high-latitude Station PAPA and (bottom) low-latitude Station ALOHA, with the 10-year running average (red) shown for reference. The normal range of annual variability (area between the black lines), or 'envelope,' will no longer overlap that of 2010 (area between the light blue lines) in approximately 2031 at Station PAPA and 2018 at Station ALOHA.

received points based on the rank of their average adaptabilities (adaptive capacity): those whose adaptabilities were below the 25th percentile (in the 1st quartile, Tables 4–6) received three points; the 26–50th percentile (or 2nd quartile), two points; the 51st–75th percentile (3rd quartile), one point; and the 76th percentile or greater (4th quartile), 0 points. Finally, each country received a fraction of a point based on the number of years until the Ω_{ar} transition decade (exposure):

Points = 1 − (years until transition decade within EEZ)/(maximum transition decade for all EEZs).

When the transition decade within a country's exclusive economic zone (EEZ) was not available because of lack of nearshore model detail, we substituted the average transition decade for the FAO region to which they belonged. For this measure, landlocked countries received zero points, and countries bordering the Mediterranean, which was not covered by the model, received 0.58 points, corresponding to the median global transition decade of 19 years from now. Countries with most 'hardship indicator' points were therefore most susceptible to difficulties caused by ocean acidification.

Results and discussion

Present conditions

Worldwide mollusc harvests in 2007 equalled approximately 16 million metric tons worth approximately $15 billion (Table 2) and supported about $5.1 billion in export value. Mollusc production per capita was unevenly distributed around the world and cannot be simply interpreted as a function of environment, economics, politics or culture alone (Fig. 2). Mollusc production per capita was high in North America and Europe as well as in the Caribbean, Peru, Chile, China, Korea, Japan,

Table 2 Present conditions grouped by Food and Agriculture Organization (FAO) statistical region*

Area #	Region	Total mollusc production (mt)	Regional aquaculture production (mt)	Domestically available molluscs (mt)	Proportion of molluscs in nationally available protein (%)	Average total protein consumption in 2008 (g person^{-1} per day)	Average Ω_{ar} in 2010	Decrease in Ω_{ar} from 1885 to 2010
87	SE Pacific	304 333	227 012	209 742	3.44	68	2.72	0.39
81	SW Pacific	112 617	107 782	66 670	10.85	99	2.44	0.43
77	E. Central Pacific	44 098	5999	4011	0.13	76	3.51	0.48
71	W. Central Pacific	739 613	571 431	667 278	1.24	70	3.80	0.52
67	NE Pacific†	61 863	42 943	–	–	–	1.68	0.35
61	NW Pacific	12 180 614	10 992 687	12 141 483	5.88	83	2.73	0.48
	NW Pacific excl. China	1 498 589	911 771	1769	0.86	82	2.73	0.48
57	E. Indian Ocean	134 988	78 078	131 054	0.11	67	2.77	0.43
51	W. Indian Ocean	7172	19 192‡	5026	0.01	65	3.27	0.50
47	SE Atlantic	2023	2012	4149	0.08	70	2.69	0.42
41	SW Atlantic	79 568	13 655	80 466	0.28	80	2.77	0.43
37	Medit. and Black Seas	288 623	178 456	315 339	0.57	95	–	–
34	E. Central Atlantic	17 393	225	12 448	0.05	70	3.47	0.50
31	W. Central Atlantic	271 866	94 971	124 112	0.49	73	3.67	0.54
27	NE Atlantic	766 552	479 699	931 772	2.03	100	1.55	0.37
21	NW Atlantic	696 553	52 892	731 503	1.66	88	1.79	0.33

*When mollusc and economic data are presented by FAO statistical regions, data for countries spanning more than one FAO region (e.g., Australia) are split so that the total is divided among regions according to (Food and Agriculture Organization of the United Nations 2010b)

†NE Pacific includes parts of United States and Canada only, and these countries' total production is included in other regional estimates.

‡India's aquaculture production is reported as 19 189 mt but this quantity is not reported in the FAO total production statistics, so total mollusc production for this region is likely low.

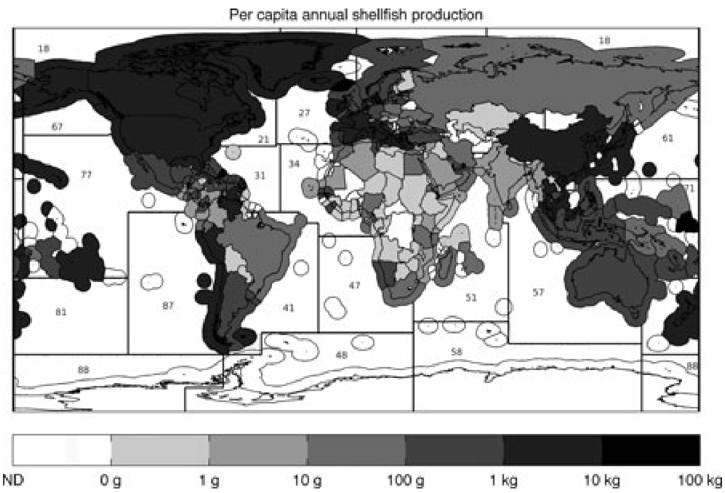

Figure 2 Mollusc production for 2007 (Food and Agriculture Organization of the United Nations 2010b) per person in 2010, with exclusive economic zones (EEZs) surrounding country coastlines. Ocean regions marked with straight black lines are Food and Agriculture Organization of the United Nations statistical regions, identified with numbers superimposed in ocean regions.

Southeast Asia, New Zealand and other Pacific islands. Nutritional dependence on mollusc protein (Fig. 3) was more clearly linked to culture and geography; for example, island nations with little agricultural land and a strong traditional emphasis on wild-caught seafood (e.g., Turks and Caicos Islands, Aruba, Faeroe Islands, Guernsey, Cook Islands, Isle of Man, Kiribati, Antigua and Barbuda, Greenland, St. Pierre and Miquelon, New Zealand, Thailand, France, South Korea and Chile) obtained more than 10% of their protein from molluscs. The economic benefit gained from exporting molluscs (Fig. 4) also strongly tracked overall per capita mollusc production (Fig. 2). Countries for whom mollusc exports contribute most to the GDP include St. Pierre and Miquelon (0.69%), Tonga (0.25%), Greenland (0.22%), New Zealand (0.15%), Vietnam (0.14%), Fiji (0.14%), Chile (0.12%) and Micronesia (0.11%). For some South Pacific nations like Tonga, Fiji and Micronesia, mollusc exports may include ornamental shell materials and not meat.

Aquaculture provided large proportions of several nations' mollusc production (Fig. 5) and about two-thirds of total global mollusc harvests (Food and

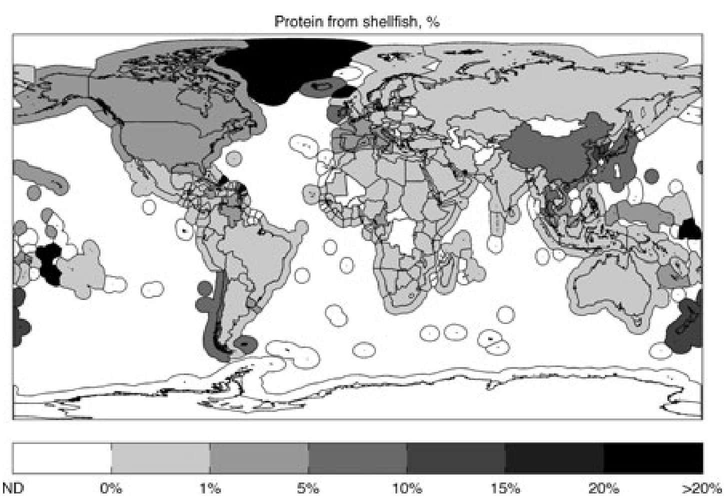

Figure 3 Dietary protein from molluscs (%), calculated as described in text.

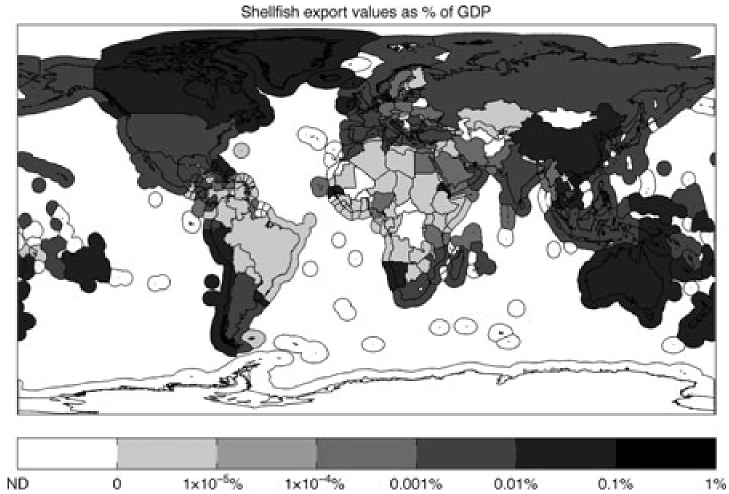

Figure 4 Mollusc export values as % of nations' GDPs (in 2007 dollars, Food and Agriculture Organization of the United Nations 2010b).

Agriculture Organization of the United Nations 2010c). Many of the countries that had the highest percentages of aquacultured molluscs, such as China, New Zealand, Philippines, Chile and nations around the Mediterranean and Western Europe, were also heavy producers (Fig. 2) and exporters (Fig. 4) of molluscs. However, many other countries do not currently have aquaculture operations (white or lightest grey, Fig. 5). Given that many of these countries produced, consumed or exported molluscs in 2007 (Figs 2–4), it seems reasonable to believe that those with appropriate conditions and resources might choose to begin aquaculture in the future as global or domestic populations grow and market demand for protein increases.

In some countries, citizens received <65 g total protein per person per day on average. The protein gap, or difference between 65 g d^{-1} $capita^{-1}$ and available protein, was greatest in the Republic of Congo, Liberia, Mozambique, Haiti and Angola (Fig. 6). Some of the countries with high protein insufficiency produced moderate amounts of molluscs per capita (e.g., Mozambique, Haiti, Togo, Madagascar, Eritrea, Tanzania, Djibouti, Gambia, Dominican Republic, Solomon Islands, Nigeria, Nicaragua, Cape Verde, Vanuatu, Fig. 7) and

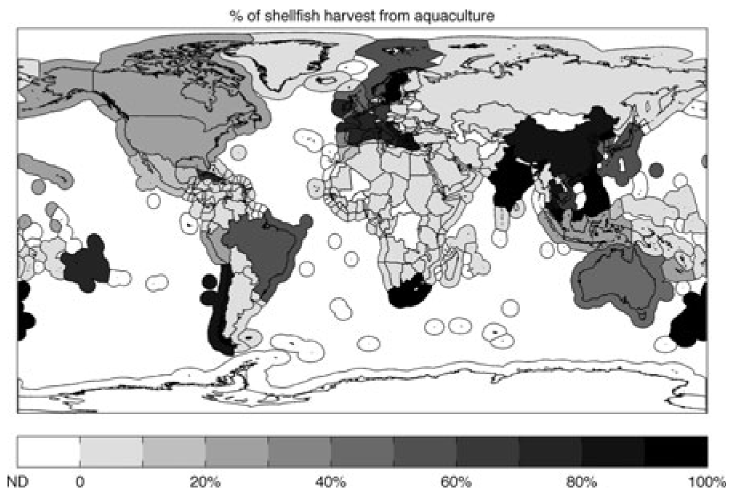

Figure 5 Per cent of mollusc harvest from aquaculture (Food and Agriculture Organization of the United Nations 2010b).

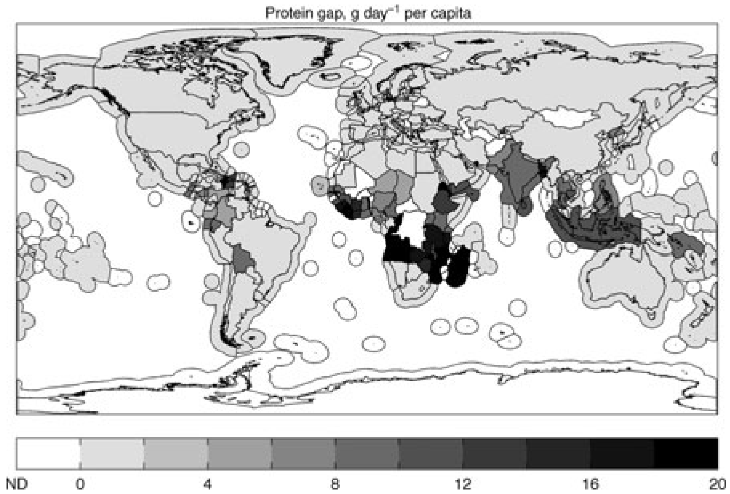

Figure 6 Protein insufficiency (grams/day/capita), or the additional protein required for citizens to receive the United States Department of Agriculture recommendation of 65 grams per day per capita.

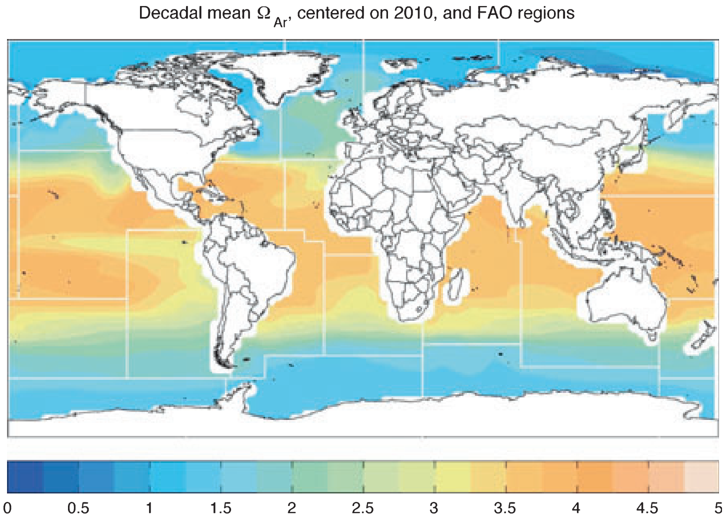

Figure 7 Mean Ω_{ar} for the decade centred around 2010, and Food and Agriculture Organization statistical regions marked in white.

derived moderate economic benefits (>0.1% GDP) from exporting these products (Fig. 4) but did not obtain much dietary protein from molluscs (<0.5%, Fig. 2) and did not seem to participate in mollusc aquaculture (Fig. 4). Furthermore, the quantities of molluscs exported from India, Yemen (likely cuttlefish, from aggregated mollusc numbers as discussed in Datasets), Mozambique, Togo, Eritrea, Pakistan, Djibouti and Bangladesh equalled the total amounts produced nationally, yet more than 20% of these populations were undernourished (Food and Agriculture Organization of the United Nations 2008). In some nations, low mollusc harvests reflect cultural preferences. Taken together, these statistics suggested that these countries may benefit from enhancing aquaculture capacity in the future, which would either provide domestically needed protein (where culturally acceptable) or generate a valuable export commodity.

In addition to the export and nutritional benefits examined in this study, countries may derive substantial economic benefits from domestic mollusc markets. Countries that either produced or consumed a great deal of molluscs in 2007 (Figs 2 and 4) are likely candidates for this. Domestic mollusc production could employ thousands of harvesters, wholesalers, processors, retailers and communities, whose activities would greatly add to national economies in excess of the dockside value of the molluscs. In one example of this, processing, wholesale and retail activities associated with the United States' $4 billion commercial ex-vessel harvest of all seafood contributed a substantial fraction of the total value added to the nation's gross national product (GNP) in 2007 ($34 billion), which depends on domestic catch and imports (Cooley and Doney 2009). Examining the domestic benefits of mollusc harvests worldwide, however, must be left for a future study.

Despite the variability among countries in mollusc production, consumption and nutrition, regional trends were apparent when data were aggregated according to FAO regions (Table 2; regions plotted on Fig. 2). The north-west Pacific Ocean had the highest value for many of the categories, largely because of the inclusion of data from China (Table 2). For all categories of fishery products, China's production values were the largest in the world, but these may be revised downwards in future datasets (Food and Agriculture Organization of the United Nations 2009). Residents of the south-west Pacific Ocean depended most heavily on molluscs for protein, but residents of the north-west Atlantic Ocean ate the most protein per capita. In general, the south-east Atlantic Ocean had the lowest mollusc production values. North and south Pacific nations tended to consume the largest proportion of mollusc protein, while the north-west Atlantic, the south-west Pacific, the west central Atlantic, south-west Pacific, the northeast Atlantic and the northeast Pacific ate the most protein overall, because the USA, Canada, Australia, New Zealand, European nations, Caribbean nations and Central American nations lead the world in protein consumption per capita.

The present saturation state of aragonite (Table 2, Fig. 7) was higher overall in tropical latitudes than it was near the poles, yet the change in saturation state from preindustrial times to the present was greater in tropical regions (Table 2). It is currently unknown whether all marine organisms experience changes in ocean carbonate chemistry the same way (Feely *et al.* 2009) – for example, we do not know whether a decrease of 1 unit of Ω_{ar} affects calcifiers living in Ω_{ar} = 4.0 and Ω_{ar} = 3.0 waters similarly. In the first environment, this represents a 25% drop in ambient carbonate ion availability, whereas in the second, it represents a 33% drop, even though the decrease is the same when measured on the Ω_{ar} scale. Despite this uncertainty about how organisms respond to ocean chemistry changes, it is clear that the change in Ω_{ar} from anthropogenic ocean acidification by 2050 will exceed natural variability in Ω_{ar} in most areas (Cooley *et al.* 2009). This will place calcifiers into chemical conditions very different from the ones they have grown accustomed to over many generations. In tropical open-ocean regions, natural variability in ocean chemistry is quite small, so small relative decreases (i.e., small per cent decreases) in Ω_{ar} in these regions with relatively high absolute values of Ω_{ar} will soon expose ecosystems to new chemical conditions.

It is especially difficult to quantify what constitutes 'normal' or 'harmfully altered' conditions for nearshore calcifier populations, because global models do not capture the small-scale biological and physical processes that cause most of the everyday chemical variability along coastlines. For now, we must use basin-scale trends as forecast by the global model to make conservative regional estimates. Nearshore observational studies show that short-to-medium temporal and spatial variabilities in pH, Ω_{ar}, and carbonate ion concentration are much higher than those in a global model like CCSM (e.g., Feely *et al.* 2008, 2010; Jiang *et al.* 2010), but anthropogenic factors such as eutrophication and pollution (Doney *et al.* 2007; Doney 2010), or simply regional circulation features (Feely *et al.* 2008) that are not included in global coupled models are often responsible for a large portion of observed natural variability. These processes exacerbate ocean acidification by adding CO_2 from respiration of organic matter, decreasing pH by dissolving acidic species, lowering Ω by discharge of river water or aggregating additional anthropogenic CO_2 via mesoscale circulation. Figure 1 illustrates how high variability tends to lead to later transition decades: higher pH, Ω or CO_2 variability in a nearshore region whose long-term mean was changing at the same rate as the offshore region would lead to a later transition decade nearshore compared with offshore. The transition decades we have defined may therefore provide conservative estimates of when regional ocean chemistry could be in an entirely different range compared with today. Adaptive planning completed in time for a conservatively calculated, or somewhat early, transition decade would simply prepare regions well in advance of ocean acidification and spread the socioeconomic burden of developing infrastructure or human capacity over a longer, more easily financed period of time.

Future conditions

Forecasting the effects of ocean acidification on future mollusc harvests required assuming that many conditions in the next several decades will roughly resemble those of today. First, we assumed that ocean acidification acts in tandem with climate change only to the extent that rising atmospheric CO_2 levels lead to rising ocean temperature over time as parameterized in CCSM3, and other thermally driven ecosystem responses (e.g., coral bleaching, ecosystem tipping points, trophic shifts, sea level rise, water shortages, etc.) and human responses (e.g., migration, profound changes in natural resource use, etc.) were absent. Second, we assumed that both wild and aquaculture harvest levels could increase to maintain the same per capita production rates. This may be unrealistic, especially for wild harvests, which have levelled off on a per capita basis (Food and Agriculture Organization of the United Nations 2009). Nevertheless, examining future production needs in the context of present rates helped identify where the biggest increases in production may be warranted. Third, this analysis also assumes that present per capita protein and mollusc consumption will remain constant in the future. The second and third assumptions, which treat production growth as a function of future population, set up this study to examine future mollusc demand rather than to model possible supply. In an in-depth study of global fisheries supply and demand, Delgado *et al.* (2003) noted that 'it is an open question as to whether supply or demand factors best explain' historical trends in fish consumption, consumption of high- vs. low-value items, and relationships among consumption patterns and consumers' wealth.

To further examine the precedent for demand-based projections, we considered historical trends of mollusc and fishery harvests. From a global perspective, historical trends show that total food fish supply has been growing at a rate of 3.6% per year since 1961, while the world's population has been expanding at 1.8% per year. Globally, the per capita availability of fish and fishery products has nearly doubled in 40 years, far outpacing population growth (World Health Organization 2011). Further supporting the argument that mollusc production will increase in the future, the FAO reported that between 1970 and 1997, mollusc consumption tripled, and this growth is expected to follow population growth patterns (Food and Agriculture Organization of the United Nations 2009, p.79). The stable per capita seafood supply has been driven by a number of factors, including investment in new aquaculture, application of new culturing techniques and selection of species that thrive in aquaculture.

Growth in mollusc harvests is primarily because of aquaculture expansion. In the past four decades, mollusc aquaculture has grown steadily from about 30% of global mollusc production in 1970 to 65% in 2008 (Food and Agriculture Organization of the United Nations 2010c). Meanwhile, global wild harvests of all fish products have declined, but aquaculture has continued to rise and this has maintained a steady per capita supply of fish for food (Food and Agriculture Organization of the United Nations 2009). Mollusc production from aquaculture has surpassed that from wild harvests in the past 10–15 years (Delgado *et al.* 2003), and assessments suggest that aquaculture continues to provide opportunities to expand mollusc production to respond to demand (Food and Agriculture Organization of the United Nations 2010c). As global terrestrial protein sources become exhausted or fully exploited in the future, growing populations may increasingly turn to marine sources of protein, particularly those that are cultured.

Seafood and mollusc harvests are likely to be affected by national development patterns, changing preferences among consumers, changing trade patterns and management (or over-exploitation) of wild populations. Animal product consumption grows fastest in countries with rapid population growth, rapid income growth and urbanization (Rae 1998; Delgado *et al.* 2001, 2003). Increases in developing-country fish consumption since the 1970s are consistent with this finding. In addition, as wealth increases in a country, protein consumption also rises, often accompanied by diversification or substitution from lower-priced calories to higher-priced protein sources, such as beef and other meats (Food and Agriculture Organization of the United Nations 2009, p.64). Once a country reaches 'developed' status, its protein consumption rates typically stabilize. This saturation of diets in developed countries, coupled with low rates of population and urban growth, consistently explains why total fish consumption in developed countries has stagnated, despite greater access to production technologies. In contrast, small developing island nations may never diversify to other protein sources because they lack alternative animal proteins and therefore depend heavily on fish/mollusc protein as part of their daily diet. Seafood is also generally the most inexpensive culturally preferred protein (Food and Agriculture Organization of the United Nations 2009, p.64). The instabilities seen in production trends in small developing island nations are usually because of stock exploitation or market volatility, as resource scales are permanently small.

With changes in the fishing sector and national development in different countries, future fishery/mollusc production trends are difficult to predict (Delgado *et al.* 2003). However, seafood production has in recent decades been driven primarily by population growth (World Health Organization 2011; Food and Agriculture Organization of the United Nations 2009, p.64), and our projections for future mollusc harvests are therefore driven by projections of population growth. Molluscs play a prominent role in global aquaculture; they are the second largest species group by weight and the third largest in value terms (Food and Agriculture

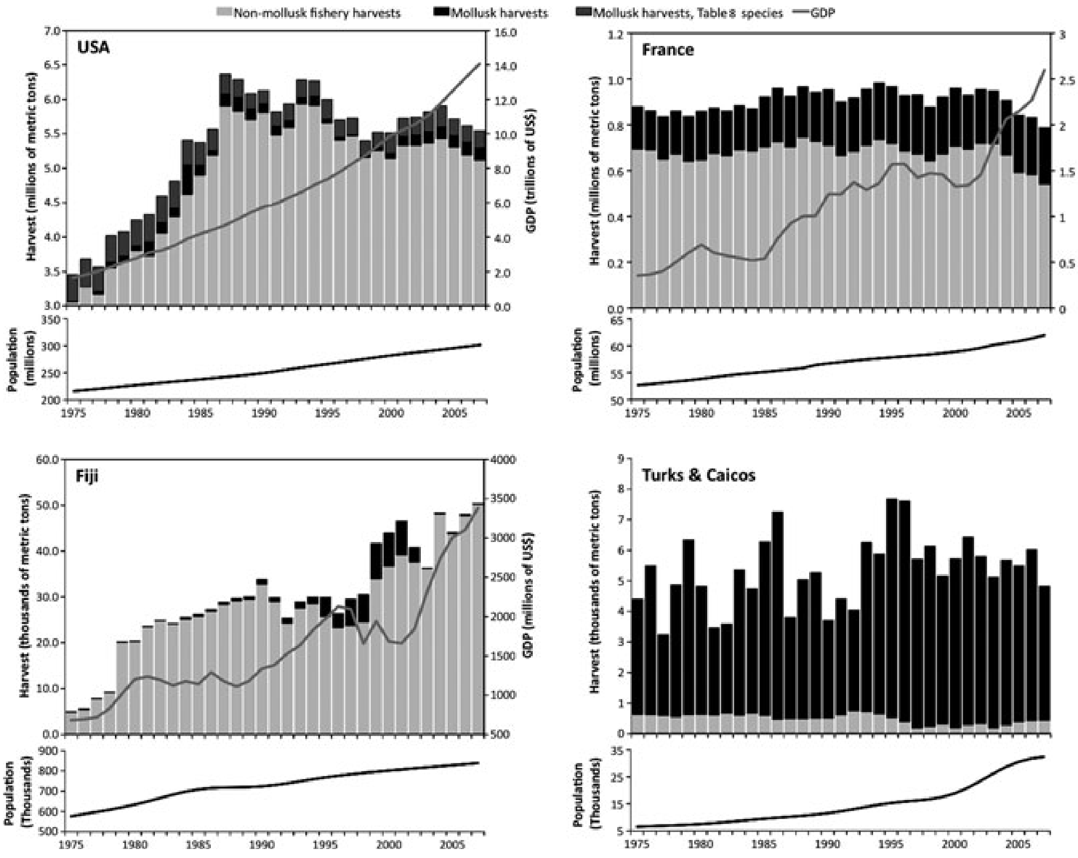

Figure 8 Historical mollusc and fishery harvests (left axes, bar charts) with gross domestic product (right axes) and population growth through time (secondary plot) for (top left) the United States and (top right) France, developed nations with stable protein consumption habits, and for (bottom left) Fiji and (bottom right) Turks and Caicos, both classified by the United Nations as 'small island developing states' (SIDS). Commercial mollusc harvests in the United States of species whose responses to OA have been studied (Table 1, starred species) are plotted with dark grey bars in the top-right plot (Food and Agriculture Organization of the United Nations, 2010b). Turks and Caicos have a well-developed queen conch fishery and primarily exports harvests (The World Bank, 2010; Food and Agriculture Organization of the United Nations, 2010b). Gross domestic product data were unavailable for Turks and Caicos.

Organization of the United Nations 2010c). Production grew at an average rate of 7% per year for the past four decades (Food and Agriculture Organization of the United Nations 2010c), and a growing list of countries is culturing shellfish commercially in response to growth in population, wealth and international trade demand.

Historical data for many nations with widely varying socioeconomic and natural characteristics show fishery and mollusc harvest increases that generally track population and wealth growth (Fig. 8). Production rises more quickly in developing nations compared with developed nations. At the same time, mollusc harvests have remained roughly constant or have increased over time (Fig. 8), with instabilities attributable to stock exploitation and market fluctuations. For countries where population decreases are expected, we assumed that mollusc production would remain at today's rate and more strongly supply international trade in place of a dwindling domestic market.

Population in 2050 multiplied by current mollusc production per capita (Fig. 2) provided a likely lower bound of total national mollusc production needed in 2050 (Fig. 9) to maintain the present per capita supply. China will need the greatest production because of its present high level of production and its anticipated large growth. Future production needed for most countries represents a moderate relative increase from current production because population growth will be small or because 2007 production was relatively large compared to needed increases (Fig. 10). On the other hand, some countries with low per capita current production in 2007 (Fig. 2) and rapid population growth forecasts need production to more than double to maintain current per capita production rates (e.g., Serbia-Montenegro, Madagascar, Somalia, Togo, Equatorial Guinea, Sudan and Mauritania; Fig. 10). Although doubling mollusc production in these countries still yields only modest total production compared with other nations (Fig. 9), these large relative domestic increases may nevertheless require substantial investments in aquaculture or fishery capacity. Some of the countries that will need to increase mollusc production by more than 80% by 2050 also currently generate more than 0.01% of GDP from mollusc export (e.g., Oman, Djibouti, Eritrea, Senegal and Madagascar; Fig. 4) and might therefore have an economic incentive to scale up production. Other countries requiring large relative increases in mollusc production (>80% increase by 2050) derive fewer economic benefits from exporting molluscs (<0.01% GDP; Fig. 4) but also have a protein gap (Fig. 6; Solomon Islands, Yemen, Mozambique, Gambia, Togo and Sierra Leone). These nations do not currently obtain much protein from molluscs (<0.5%, Fig. 3), but the datasets we used did not indicate whether supply or demand caused this situation. If a domestic demand for molluscs existed or could be cultivated, establishing basic mollusc aquaculture in any of these protein-insufficient countries could help them move towards protein sufficiency.

Some of the regions in which demand for molluscs is likely to rise the most are also regions

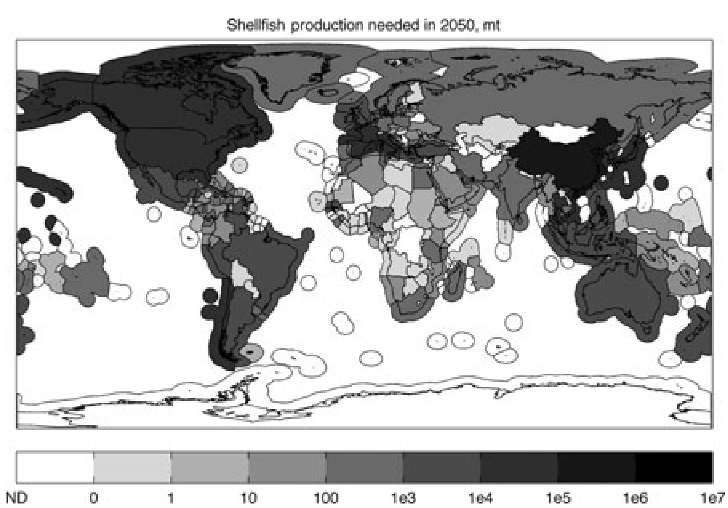

Figure 9 Mollusc production projected for 2050 if current supply will be maintained for future population levels.

in which the future Ω_{ar} will change the most or where transition decades will come the soonest (Table 3, Fig. 11). In the W. Central Pacific and the NE Pacific, population increases are likely to raise demand for molluscs by hundreds of thousands of metric tons by 2050. At the same time, Ω_{ar} will have decreased by 0.62 and 0.38, respectively, in those areas. Long before 2050, Ω_{ar} in many of these locations will have decreased to values that no longer overlap those of today (Fig. 11). Low-latitude regions like the western central Pacific will experience these unfamiliar chemical conditions at earlier transition decades (Table 3, Fig. 11) because seasonality is already low and interannual variability is small.

At present, the population- and ecosystem-scale responses of marine molluscs and other valuable marine resources to ocean acidification are not well-known, and forecasting harvest levels of specific calcifiers by 2050 is difficult. Nevertheless, both declining pH and Ω_{ar} have been associated with decreases in wild calcifier populations. In one study, Hall-Spencer *et al.* (2008) found statistically significant decreases in coralline algae, sea urchins, gastropods, limpets and barnacles with decreases in pH and Ω_{ar} (Fig. 2 in Hall-Spencer *et al.* 2008); however, the study was too short to assess seasonal and interannual variability effects of pH. In another study, a natural decrease in pH from 8.41 to 7.99 over 8 years in a coastal lagoon environment was associated with a more than 40% reduction in calcified benthic organism cover (Wootton *et al.* 2008). Although the mean pH decrease observed in Wootton *et al.*'s experiment was statistically significant (Fig. 1 in Wootton *et al.* 2008), the pH range at the end of their experiment still overlapped that of the beginning of their experiment. That study demonstrates especially clearly that profound shifts in marine ecosystems may occur even before our threshold criteria (lack of overlap between future and present conditions) are met. Therefore, it is likely conservative to conclude that calcifier populations worldwide will not change greatly until the transition decades we calculated.

Unlike aquaculture of some carnivorous finfish, which require fishmeal and oil supplements and may be limited by wild harvests from reduction fisheries, expansion of mollusc aquaculture is ultimately limited only by primary production and the supply of particulate organic nutrients in the water column. Molluscs presently account for about 30% of global aquaculture production in weight terms (Food and Agriculture Organization of the United Nations 2009), and there is extensive potential for expanded mollusc farming in many coastal oceans, including those of South America (as demonstrated by Chile's mussel industry) and parts of East Africa, where wild mollusc stocks have been harvested for centuries, and mollusc aquaculture is just beginning to be practiced (Crawford *et al.* 2010; Kite-Powell 2010). Some of the anticipated new aquaculture production in these regions may begin on small scales and for local consumption rather than as large export projects. Mollusc farming is relatively simple and inexpensive: A simple mollusc hatchery can be assembled for about $10 000.

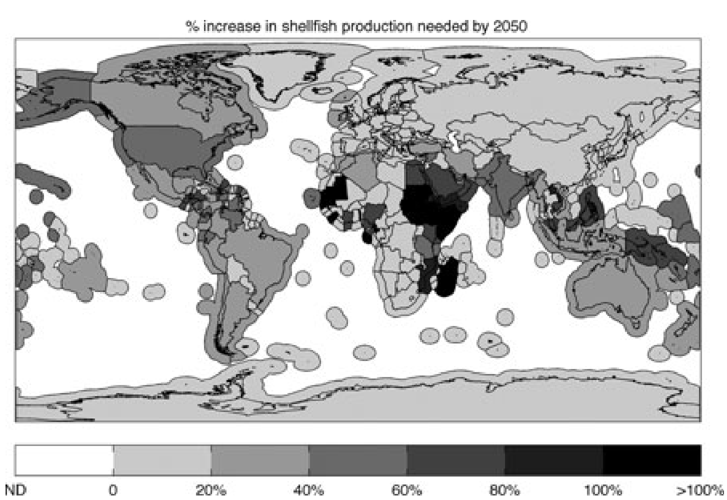

Figure 10 Per cent increase in mollusc production projected for 2050 to maintain current supply.

Table 3 Future conditions grouped by Food and Agriculture Organization statistical region.

Area #	Region	Necessary increase in total production to meet 2050 demands (2050–2007 production) per region (mt)	Necessary increase in aquaculture production to meet population demands (2020–2050) per region (mt)	Per cent increase of 2007 production to meet population demands per region	Mean Ω_{ar} 2050	Decrease in Ω_{ar} from 1885 to 2050	Years before transition decade ($\Omega_{ar} \neq \Omega_{ar,\ Jan.\ 2010}$)
87	SE Pacific	87 594	65 339	29	2.29	0.83	36
81	SW Pacific	25 082	24 005	22	1.98	0.89	38
77	E. Central Pacific	20 046	2727	45	2.96	1.03	30
71	W. Central Pacific	255 743	197 589	35	3.17	1.15	24
67	NE Pacific*	–	–	–	1.30	0.73	31
61	NW Pacific†	455 300	410 896	4	2.18	1.03	32
	NW Pacific excl. China	9135	93 258	1	2.18	1.03	32
57	E. Indian Ocean	6543	17 509	91	2.27	0.92	32
51	W. Indian Ocean	12	12	1	2.71	1.05	23
47	SE Atlantic	23 312	4001	29	2.23	0.89	33
41	SW Atlantic	83 457	51 602	29	2.28	0.91	39
37	Medit. and Black Seas	13 120	170	75	–	–	–
34	E. Central Atlantic	93 610	32 701	34	2.88	1.08	23
31	W. Central Atlantic	24 341	15 232	3	3.04	1.17	21
27	NE Atlantic	863 131	73 864	140	1.18	0.74	29
21	NW Atlantic	87 594	65 339	29	1.42	0.70	36

*NE Pacific includes parts of United States and Canada only, and these countries' total production is included in other regional estimates.

†This region's production is exceptionally high because of China's very high reported production (Food and Agriculture Organization of the United Nations 2010b), and this drives down the per cent increase required for 2050.

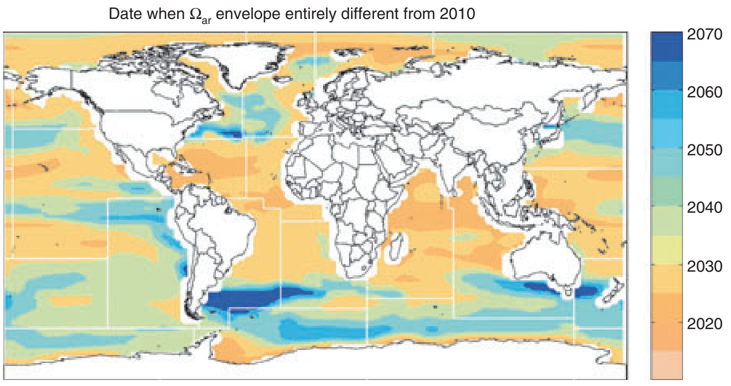

Figure 11 Transition decades when future surface Ω_{ar} will no longer overlap that of 2010.

Aquacultured mollusc species may be as susceptible as wild harvest species to ocean acidification, so research is needed to determine what mollusc species might thrive in a range of culture conditions. Over the past several years, United States oyster hatcheries in the Pacific Northwest-growing Pacific oysters (*Crassostrea gigas*, Ostreidae) in coastal seawater have experienced mass larval mortality during periodic upwelling events that accelerate ocean acidification's effects (Feely *et al.* 2008). Market demand for Pacific oysters is still strong, so these businesses are first determining whether they can protect their stocks by amending the seawater they use in culture tanks or by collecting it at other times or places. New or expanded mollusc aquaculture such as that suggested for developing nations above, however, might be able to choose ocean acidification-resilient species from the start (e.g., the Suminoe oyster instead of the Eastern oyster, as in Miller *et al.* 2009) and eliminate the need for expensive mitigation measures.

Present dependence and adaptability will affect future responses

Countries' economic dependence on molluscs may affect their experiences of ocean acidification. If global mollusc supply decreases from ocean acidification, prices will likely rise and net exporters of molluscs (blue tones, Fig. 12) could benefit at the expense of net importers of molluscs (orange tones, Fig. 12). Similarly, countries with higher adaptability indices (lighter oranges and blues) may weather economic and market changes better than those with lower indices (darker oranges and blues, Fig. 12) because their greater wealth, education, health and governmental stability provide their citizens with a greater degree of flexibility to pursue innovative solutions to new challenges. These possibilities could also occur within nations having large domestic mollusc markets: rising mollusc prices owing to scarcity could exclude poorer consumers, promoting a wealth gap between producers and consumers. This effect could be less pronounced in countries with higher adaptability indices, because consumers would have more options owing to greater wealth overall.

Nutritional status and dependence on mollusc protein will also shape countries' vulnerability to ocean acidification. Nations that obtain more than 1% of their protein from molluscs (Fig 3, and hatched countries, Fig 12) may experience shortages of molluscs if harvests decline (or do not grow to needed levels) because of ocean acidification. Countries that currently have a protein gap (Fig 6, and stippled countries, Fig 12) may increasingly seek protein from seafood as populations grow and agricultural land becomes fully utilized. Both conditions are true for some countries (cross-hatched countries, Fig. 12), and we expect those countries will suffer most if mollusc harvests decline.

Many of the countries with multiple indicators for experiencing hardship from mollusc declines (i.e., the darkest-coloured, hatched/stippled countries in Fig. 12) are located in areas where the transition decades for substantial changes in ocean chemistry are soonest (Fig. 12; Tables 4–6). Even though there is a short time remaining ($\sim$15 years) until the ocean acidification transition decades in these areas, some countries may still be able to institute basic mollusc aquaculture or increase what already exists. Once a mollusc aquaculture industry exists in a country at a scale that can meet some of the country's food demands, (e.g., Ahmed and Lorica 2002) techniques can be developed and refined to raise ocean acidification-resilient species or to amend culture enclosures in ways that protect vulnerable species or life stages. These steps would help alleviate some of the hardships associated with declining mollusc harvests from ocean acidification. Furthermore, by providing domestically or internationally valuable goods, these steps could also help improve national adaptability by contributing to GDP and health.

Countries' relative susceptibilities varied greatly (Tables 4–6). Some countries had over seven hardship indicator points, whereas others had slightly more than one. By this metric, the five exporting nations most susceptible to mollusc harvest declines from ocean acidification included: Senegal (this data may include octopus, as discussed in Mollusc data), Madagascar, Gambia, Mozambique and Haiti. Excluding the net importing nations with zero mollusc production and approximately zero consumption (this includes many landlocked countries), the five most susceptible importing nations included: Solomon Islands, Jamaica, Belize, Cook Islands and Sudan. Countries likely to suffer the least from ocean acidification-related mollusc harvest declines included: Austria, Hong Kong and United Kingdom (net exporters); and Slovenia, Switzerland, Sweden, Germany and Finland (net importers).

Even though ocean acidification can affect countries through economic and nutritional means, it is just one of the several stressors acting on marine ecosystems (e.g., Doney 2010). For example, rising nutrient runoff plus higher aquatic CO_2 levels and atmospheric deposition may counteract or supplement the effects of ocean acidification in nearshore regions (Doney *et al.* 2007; Russell *et al.* 2009;

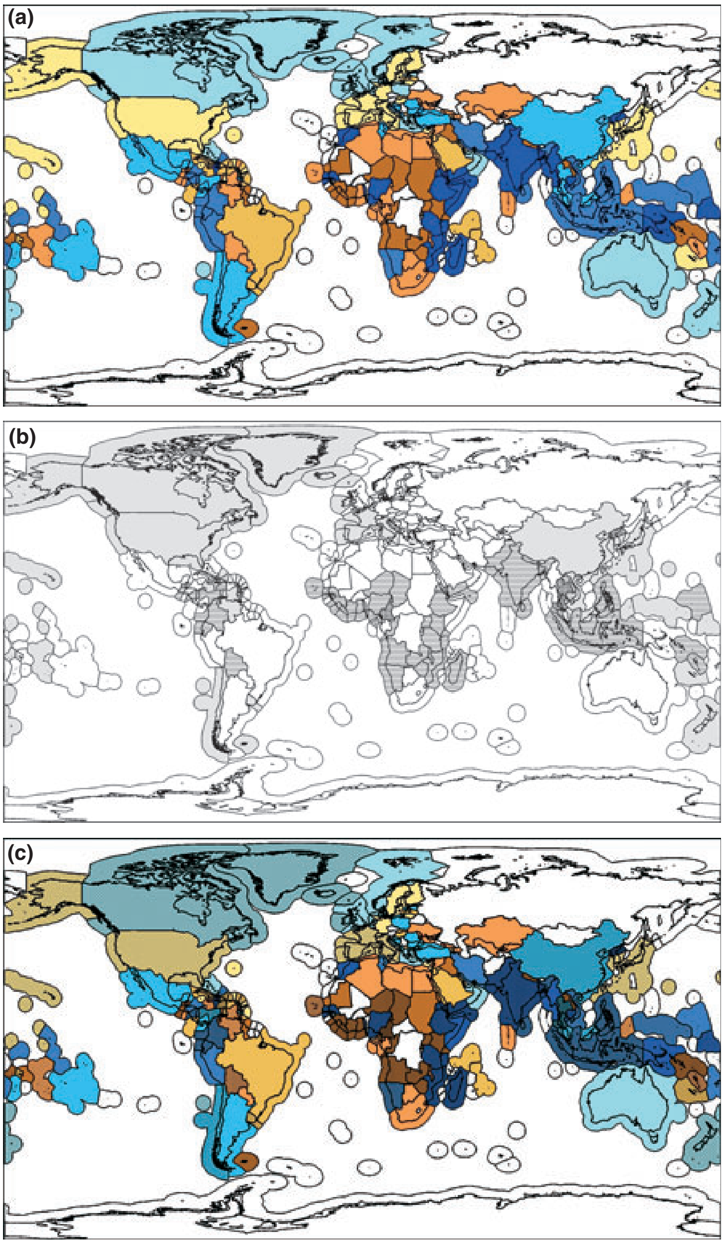

Figure 12 Summary of countries' vulnerability to ocean acidification effects on mollusc harvests. (a) Net exporters of molluscs are indicated with blue tones; net importers are indicated with oranges. Countries' adaptability index values are indicated by hue: the first quartile (least adaptable 25% of nations) is darkest; the fourth quartile (most adaptable 25%) is lightest. (b) Vertical hatching indicates countries that obtain more than 1% of their protein from molluscs. Stippling indicates countries that currently have a protein gap. Cross-hatching indicates countries where both conditions are true. (c) Both (a) and (b) are overlaid; darkest countries with cross-hatching have most risk factors, and lightest countries with no hatching/stippling have the fewest risk factors.

Borges and Gypens 2010). Increasing temperature is expected to have a range of effects on marine ecosystem makeup and function (Hoegh-Guldberg and Bruno 2010). Changes in freshwater cycling associated with climate change or human use patterns will alter carbonate chemistry, circulation and other environmental gradients in estuaries or on continental shelves (Salisbury *et al.* 2008; Miller

Table 4 Vulnerability of nations examined in this analysis with net mollusc export.

Country	Present mollusc production (kg person^{-1})	Gross domestic product contribution from export (%)	Dietary protein (g person^{-1} per day)	Mollusc protein as % of available protein	Total mollusc production to meet 2050 demands (mt per year)	Mollusc aquaculture to meet 2050 demands (mt per year)	Increase in present production to meet 2050 demands (%)	Adaptability	Adaptability quartile	Years until Ω_{ar} transition decade	Total hardship points
Senegal	0.8	0.061	55	0.7	24407	90	124	−0.726	1	16	7.7
Madagascar	0.0	0.016	46	0.0	1062	NA	166	−0.499	1	19	7.6
Gambia	0.4	0.004	50	0.5	1479	NA	116	−0.477	1	21	7.6
Mozambique	0.0	0.003	41	0.0	250	NA	99	−1.173	1	18	6.6
Haiti	0.0	0.003	42	0.0	525	NA	75	−0.733	1	19	6.6
Togo	0.0	0.000	46	0.0	156	NA	140	−0.885	1	22	6.5
Djibouti	0.0	0.026	49	0.0	17	NA	88	−0.642	1	23	6.5
Eritrea	0.0	0.061	46	0.0	126	NA	96	−0.809	1	23	6.5
North Korea (Dem)	2.6	0.030	59	2.8	62283	62283	4	−0.515	1	45	6.0
India	0.0	0.001	56	0.0	9879	27097	41	−0.378	1	15	5.7
Somalia	0.0	0.000	65	0.0	3	NA	157	−1.161	1	16	5.7
Micronesia	1.4	0.111	65	1.3	150	NA	0	−0.169	2	16	5.7
Nicaragua	0.1	0.017	59	0.1	1208	NA	58	−0.243	2	16	5.7
Yemen	0.0	0.000	53	0.0	339	NA	95	−0.729	1	16	5.6
Turks and Caicos Islands	183.0	0.026	65	176.6	7871	NA	79	−0.055	2	17	5.6
Tanzania (plus Zanzibar)	0.0	0.001	48	0.0	1902	NA	60	−0.592	1	19	5.6
Kiribati	34.1	0.052	72	32.3	4773	NA	41	−0.051	2	20	5.6
Pakistan	0.0	0.001	59	0.0	1517	NA	56	−0.704	1	20	5.6
Nigeria	0.0	0.000	59	0.0	4976	NA	74	−0.917	1	22	5.5
Cambodia	0.1	0.002	54	0.1	3087	2104	62	−0.568	1	24	5.5
Bangladesh	0.0	0.000	48	0.0	405	NA	48	−0.764	1	32	5.3
St. Pierre and Miquelon	17.3	0.694	65	15.6	104	NA	0	−0.224	2	36	5.2
Ecuador	0.0	0.003	56	0.0	197	NA	43	−0.140	2	41	5.1
Indonesia	0.3	0.006	53	0.4	103388	25331	29	−0.039	2	14	4.7
Sri Lanka	0.1	0.011	54	0.0	1200	7	16	0.068	2	16	4.7
Papua New Guinea	0.0	0.032	65	0.0	463	2	67	−0.833	1	16	4.7
Colombia	0.0	0.000	61	0.0	117	NA	27	0.141	2	16	4.7
Honduras	0.0	0.010	65	0.0	240	NA	62	−0.179	2	16	4.6
Philippines	0.4	0.006	58	0.5	75700	74349	72	0.022	2	17	4.6
Myanmar	0.0	0.001	66	0.0	180	NA	32	−0.505	1	17	4.6

Table 4 (Continued).

Country	Present mollusc production (kg person^{-1})	Gross domestic product contribution from export (%)	Dietary protein (g person^{-1} per day)	Mollusc protein as % of available protein	Total mollusc production to meet 2050 demands (mt per year)	Mollusc aquaculture to meet 2050 demands (mt per year)	Increase in present production to meet 2050 demands (%)	Adaptability	Adaptability quartile	Years until Ω_{ar} transition decade	Total hardship points
Marshall Islands	0.0	0.010	65	0.0	2	NA	56	−0.253	2	18	4.6
Thailand	5.9	0.060	57	6.4	410524	348723	5	0.148	3	20	4.6
Fiji	0.7	0.136	79	0.1	989	NA	51	−0.250	2	21	4.5
Viet Nam	2.8	0.137	67	2.6	316378	211001	24	−0.061	2	24	4.5
Namibia	0.2	0.026	64	0.2	467	13	1	−0.142	2	27	4.4
Morocco	0.0	0.004	88	0.0	1559	246	33	−0.336	1	27	4.4
Russia	0.1	0.002	92	0.1	11338	105	0	0.036	2	15	3.7
Greenland	23.9	0.223	65	20.3	1389	NA	0	0.846	4	15	3.7
Panama	0.4	0.009	68	0.1	1849	NA	42	0.352	3	16	3.7
Oman	0.0	0.012	65	0.0	84	NA	82	0.582	3	16	3.6
Romania	0.0	0.002	110	0.0	482	NA	0	0.350	3	19	3.6
Tunisia	0.1	0.016	90	0.0	1583	152	18	0.113	2	19	3.6
St. Vincent and the Grenadines	0.0	0.005	75	0.0	4	NA	0	0.345	3	20	3.6
Bahrain	1.4	0.005	65	0.0	1396	NA	33	0.695	3	23	3.5
Estonia	0.5	0.007	88	0.1	659	NA	0	0.642	3	23	3.5
Iran	0.0	0.000	87	0.0	1218	NA	22	−0.138	2	23	3.5
Faeroe Islands	105.1	0.057	65	107.7	5991	NA	16	1.328	4	24	3.5
Chile	13.5	0.115	85	10.0	261964	245677	16	0.715	3	24	3.5
Malaysia	2.3	0.007	77	1.6	98547	116387	65	0.405	3	32	3.3
China	8.0	0.026	91	5.9	11174711	10545878	5	0.155	3	32	3.3
Peru	2.6	0.095	70	0.1	100638	19124	29	0.049	2	46	3.0
Mexico	0.8	0.006	92	0.5	111774	9629	32	0.287	3	16	2.6
Bahamas	1.3	0.019	83	0.4	493	NA	20	0.812	4	17	2.6
Iceland	16.8	0.019	127	7.6	5882	11	14	1.251	4	19	2.6
Albania	0.4	0.001	97	0.3	1493	1043	10	0.266	3	19	2.6
Bosnia and Herzegovina	0.1	0.015	86	0.0	363	70	0	0.204	3	19	2.6
Bulgaria	0.7	0.017	79	0.4	4681	595	0	0.378	3	19	2.6
Canada	4.2	0.020	105	2.1	170774	37426	22	1.239	4	19	2.6
Croatia	0.8	0.002	74	0.7	3637	3000	0	0.559	3	19	2.6

Table 4 (Continued).

Country	Present mollusc production (kg person^{-1})	Gross domestic product contribution from export (%)	Dietary protein (g person^{-1} per day)	Mollusc protein as % of available protein	Total mollusc production to meet 2050 demands (mt per year)	Mollusc aquaculture to meet 2050 demands (mt per year)	Increase in present production to meet 2050 demands (%)	Adaptability	Adaptability quartile	Years until Ω_{ar} transition decade	Total hardship points
Turkey	0.8	0.003	96	0.5	84678	254	30	0.208	3	19	2.6
French Polynesia	8.1	0.069	99	0.5	3181	2573	35	0.401	3	20	2.6
Ireland	14.9	0.029	114	6.2	80248	58226	27	1.209	4	21	2.5
United Arab Emirates	0.3	0.001	101	0.2	2074	NA	61	0.880	4	23	2.5
Tonga	5.2	0.246	65	0.5	981	2	53	0.195	3	23	2.5
New Zealand	25.4	0.150	92	11.7	131827	126280	22	1.045	4	26	2.4
Belgium	1.0	0.012	98	0.0	10877	NA	0	1.087	4	29	2.4
Denmark	10.8	0.024	110	3.4	60179	1756	1	1.179	4	29	2.4
Netherlands	3.5	0.032	104	1.4	61320	39203	3	1.228	4	29	2.4
Poland	0.0	0.001	100	0.0	941	NA	0	0.615	3	29	2.4
Argentina	1.3	0.016	93	0.8	70125	304	29	0.285	3	34	2.3
Norway	0.7	0.002	104	0.3	3592	2065	6	1.505	4	15	1.7
Australia	1.6	0.022	106	1.0	47670	21733	35	1.240	4	17	1.6
Greece	2.2	0.013	117	0.4	23390	21099	0	0.833	4	19	1.6
United Kingdom	1.4	0.008	104	0.7	87211	36400	4	1.107	4	21	1.5
Hong Kong	1.0	0.024	91	0.3	7169	1156	3	1.342	4	32	1.3

NA, no aquaculture; LL, landlocked.

Table 5 Vulnerability of nations examined in this analysis with net mollusc import.

Country	Present mollusc production (kg person^{-1})	Gross domestic product contribution from export (%)	Dietary protein (g person^{-1} per day)	Mollusc protein as % of available protein	Total mollusc production to meet 2050 demands (mt per year)	Mollusc aquaculture to meet 2050 demands (mt per year)	Increase in present production to meet 2050 demands (%)	Adaptability	Adaptability quartile	Years until Ω_{ar} transition decade	Total hardship points
Solomon Islands	0.0	0.002	57	0.1	42	NA	82	−0.450	1	18	6.6
Jamaica	1.7	0.001	77	1.5	5994	NA	25	0.086	2	16	5.7
Belize	6.3	0.001	75	6.2	3400	NA	73	0.133	2	18	5.6
Cook Islands	0.9	0.005	65	49.6	10	NA	0	−0.213	2	19	5.6
Ivory Coast	0.0	0.000	50	0.0	2	NA	76	−1.228	1	21	5.5
Equatorial Guinea	0.0	0.000	65	0.0	22	NA	119	−0.479	1	22	5.5
Vanuatu	0.5	0.005	64	0.5	155	NA	41	−0.008	2	22	5.5
Sudan	0.0	0.000	75	0.0	16	NA	110	−0.896	1	23	5.5
Guatemala	0.0	0.000	57	0.1	17	NA	70	−0.300	1	38	5.2
Belarus	0.0	0.001	88	3.5	348	NA	0	0.053	2	LL	5.0
Laos	0.0	0.000	63	0.0	2	NA	89	−0.525	1	LL	5.0
Palau	0.7	0.006	65	1.6	15	2	10	0.016	2	16	4.7
Dominican Republic	0.1	0.001	52	0.3	2037	NA	50	0.066	2	17	4.6
Cape Verde	0.0	0.000	63	0.0	1	NA	46	0.136	2	18	4.6
Venezuela	2.0	0.000	66	2.0	79157	NA	48	−0.025	2	19	4.6
Sao Tome and Principe	0.1	0.000	59	0.1	23	NA	76	−0.199	2	22	4.5
Uruguay	0.7	0.050	84	2.7	2809	NA	9	0.548	3	34	4.3
Maldives	0.0	0.000	106	0.8	2	NA	12	0.058	2	15	3.7
Anguilla	0.7	0.000	65	5.2	18	NA	80	0.605	3	19	3.6
Antigua and Barbuda	5.9	0.000	74	25.0	731	NA	41	0.682	3	19	3.6
Egypt	0.0	0.000	94	0.0	4691	NA	71	−0.233	2	19	3.6
Georgia	0.1	0.000	77	0.1	600	NA	0	−0.040	2	19	3.6
St. Kitts and Nevis	1.8	0.000	81	1.6	101	NA	12	0.391	3	19	3.6
Ukraine	0.0	0.000	86	0.1	487	NA	0	0.039	2	19	3.6
Netherlands Antilles	0.0	–	94	0.3	6	NA	11	0.646	3	20	3.6
South Africa	0.0	0.011	76	0.1	1570	2011	1	−0.209	2	20	3.6
New Caledonia	1.3	0.036	84	1.5	365	85	27	0.228	3	23	3.5
Samoa	1.0	0.000	77	1.3	255	NA	28	0.321	3	23	3.5
Latvia	0.0	0.001	87	0.1	87	NA	0	0.520	3	29	3.4
Lithuania	0.2	0.007	110	0.1	583	NA	0	0.557	3	29	3.4

Table 5 (Continued).

Country	Present mollusc production (kg person^{-1})	Gross domestic product contribution from export (%)	Dietary protein (g person^{-1} per day)	Mollusc protein as % of available protein	Total mollusc production to meet 2050 demands (mt per year)	Mollusc aquaculture to meet 2050 demands (mt per year)	Increase in present production to meet 2050 demands (%)	Adaptability	Adaptability quartile	Years until Ω_{ar} transition decade	Total hardship points
El Salvador	0.1	0.000	67	0.1	507	NA	2	0.009	2	32	3.3
Luxembourg	0.2	0.001	124	1.3	111	NA	45	1.896	4	LL	3.0
Mauritius	0.1	0.007	80	0.1	87	2	11	0.400	3	17	2.6
United States	2.5	0.002	116	1.6	1088987	219758	42	1.259	4	18	2.6
Algeria	0.0	0.000	86	0.0	111	6	28	−0.209	2	19	2.6
Italy	2.7	0.006	113	2.2	157350	123010	0	0.831	4	19	2.6
Grenada	0.3	0.000	73	0.3	30	NA	6	0.169	3	20	2.6
St. Lucia	0.3	0.000	94	0.4	41	NA	1	0.405	3	20	2.6
Japan	6.4	0.011	91	5.4	807827	417300	0	1.120	4	20	2.6
Saudi Arabia	0.0	0.000	84	0.0	109	NA	71	0.346	3	23	2.5
France	3.8	0.007	116	3.0	266161	203666	8	1.082	4	23	2.5
Taiwan	2.9	0.003	65	3.6	66454	88320	1	0.805	4	24	2.5
Singapore	0.6	0.027	65	3.1	2866	1640	9	1.288	4	24	2.5
Portugal	0.6	0.005	114	1.1	7033	2432	1	0.779	4	26	2.4
Spain	5.6	0.010	110	4.2	228457	185157	0	0.926	4	26	2.4
Macao, China	0.5	0.005	91	0.4	281	NA	9	0.798	4	32	2.3
South Korea (Rep)	11.3	0.013	86	10.6	558903	351051	1	0.794	4	34	2.3
Slovak Rep.	0.0	0.000	72	0.0	8	NA	0	0.595	3	LL	2.0
Costa Rica	0.0	0.000	70	0.2	28	1	34	0.510	3	16	1.7
Cuba	0.2	0.000	78	0.2	2310	1594	1	0.261	3	16	1.7
Brazil	0.1	0.000	85	0.1	29507	17396	30	0.194	3	17	1.6
Cyprus	0.0	0.000	99	0.5	4	NA	26	0.921	4	19	1.6
Malta	0.0	0.001	116	0.8	8	NA	3	0.839	4	19	1.6
Qatar	0.1	0.000	65	0.2	69	NA	33	1.548	4	23	1.5
Brunei	0.2	0.000	93	0.5	118	NA	62	1.074	4	24	1.5
Finland	0.0	0.000	104	0.1	2	NA	0	1.175	4	29	1.4
Germany	0.1	0.001	99	0.3	10625	6982	0	1.116	4	29	1.4
Sweden	0.1	0.001	107	0.2	1235	1913	0	1.226	4	29	1.4
Switzerland	0.0	0.000	91	0.4	42	NA	2	1.370	4	LL	1.0
Slovenia	0.2	0.001	102	0.3	304	224	0	0.903	4	19	0.6

Table 5 (Continued).

Country	Present mollusc production (kg $person^{-1}$)	Gross domestic product contribution from export (%)	Dietary protein (g $person^{-1}$ per day)	Mollusc protein as % of available protein	Total mollusc production to meet 2050 demands (mt per year)	Mollusc aquaculture to meet 2050 demands (mt per year)	Increase in present production to meet 2050 demands (%)	Adaptability	Adaptability quartile	Years until Ω_{ar} transition decade	Total hardship points
Congo, Republic of	0.0	0.000	23	0.0	0	NA	NP	−0.621	1	29	NP
Liberia	0.0	0.000	33	0.0	0	NA	NP	−1.162	1	16	NP
Angola	0.0	0.000	42	0.0	0	NA	NP	−1.008	1	25	NP
Rwanda	0.0	0.000	45	0.0	0	NA	NP	−0.807	1	LL	NP
Zambia	0.0	0.000	48	0.0	0	NA	NP	−0.830	1	LL	NP
Zimbabwe	0.0	0.000	49	0.4	0	NA	NP	−0.877	1	LL	NP
Guinea	0.0	0.000	54	0.0	0	NA	NP	−1.326	1	14	NP
Malawi	0.0	0.000	54	0.0	0	NA	NP	−0.702	1	LL	NP
Ghana	0.0	0.000	55	0.0	0	NA	NP	−0.449	1	21	NP
Uganda	0.0	0.000	56	0.0	0	NA	NP	−0.669	1	LL	NP
Cameroon	0.0	0.000	57	1.2	0	NA	NP	−0.844	1	23	NP
Niger	0.0	0.000	60	0.0	0	NA	NP	−1.181	1	LL	NP
Chad	0.0	0.000	61	0.1	0	NA	NP	−1.403	1	LL	NP
Nepal	0.0	0.000	61	0.0	0	NA	NP	−0.713	1	LL	NP
Iraq	0.0	0.000	65	0.0	0	NA	NP	−0.704	1	23	NP
Swaziland	0.0	0.000	66	0.0	0	NA	NP	−0.685	1	LL	NP
Bolivia	0.0	0.000	57	0.0	0	NA	NP	−0.264	2	LL	NP
Botswana	0.0	0.000	65	1.0	0	NA	NP	−0.097	2	LL	NP
Paraguay	0.0	0.000	68	0.0	0	NA	NP	−0.074	2	LL	NP
Azerbaijan	0.0	0.000	73	0.0	0	NA	NP	0.015	2	LL	NP
Moldova, Republic	0.0	0.000	73	0.0	0	NA	NP	0.011	2	LL	NP
Libyan Arab Jamahiriya	0.0	0.000	74	0.0	0	NA	NP	0.080	2	19	NP
Uzbekistan	0.0	0.000	74	0.0	0	NA	NP	−0.221	2	LL	NP
Gabon	0.0	0.000	81	0.0	0	NA	NP	−0.268	2	27	NP
Lebanon	0.0	0.000	86	0.0	0	NA	NP	0.034	2	19	NP
Kazakhstan	0.0	0.000	95	0.0	0	NA	NP	0.087	2	LL	NP
Kyrgyzstan	0.0	0.000	101	0.0	0	NA	NP	−0.177	2	LL	NP
Trinidad and Tobago	0.0	0.000	68	0.0	0	NA	NP	0.419	3	20	NP
Armenia	0.0	0.000	70	0.0	0	NA	NP	0.193	3	LL	NP
Jordan	0.0	0.000	73	0.0	0	NA	NP	0.216	3	LL	NP

Table 5 (Continued).

Country	Present mollusc production (kg person^{-1})	Gross domestic product contribution from export (%)	Dietary protein (g person^{-1} per day)	Mollusc protein as % of available protein	Total mollusc production to meet 2050 demands (mt per year)	Mollusc aquaculture to meet 2050 demands (mt per year)	Increase in present production to meet 2050 demands (%)	Adaptability	Adaptability quartile	Years until Ω_{ar} transition decade	Total hardship points
Macedonia, Fmr Yug Rp of	0.0	0.000	74	0.0	0	NA	NP	0.274	3	LL	NP
Seychelles	0.0	0.000	78	0.5	0	NA	NP	0.384	3	15	NP
Dominica	0.0	0.000	90	0.0	0	NA	NP	0.278	3	19	NP
Hungary	0.0	0.000	90	0.0	0	NA	NP	0.625	3	LL	NP
Aruba	0.0	0.000	65	137.8	0	NA	NP	0.748	4	20	NP
Cayman Islands	0.0	0.000	65	0.0	0	NA	NP	1.187	4	16	NP
Bermuda	0.0	0.000	75	0.3	0	NA	NP	1.816	4	18	NP
Kuwait	0.0	0.000	87	0.0	0	NA	NP	0.841	4	23	NP
Barbados	0.0	0.000	88	0.6	0	NA	NP	0.739	4	20	NP
Israel	0.0	0.000	126	0.0	0	NA	NP	0.832	4	19	NP

NA, no aquaculture; NP, no production; LL, landlocked.

Table 6 Vulnerability of nations examined in this analysis whose mollusc import/export status is not known.

Country	Present mollusc production (kg person^{-1})	Gross domestic product contribution from export (%)	Dietary protein (g person^{-1} per day)	Mollusc protein as % of available protein	Total mollusc production to meet 2050 demands (mt per year)	Mollusc aquaculture to meet 2050 demands (mt per year)	Increase in present production to meet 2050 demands (%)	Adaptability	Adaptability quartile	Years until Ω_{ar} transition decade	Total hardship points
Sierra Leone	0.2	0.000	47	0.3	2397	NA	159	−1.392	1	14	6.7
Kenya	0.0	0.000	57	0.0	340	NA	63	−0.687	1	18	5.6
Wallis and Futuna	1.9	0.000	65	2.0	29	NA	0	−0.345	1	21	5.5
Mauritania	0.0	0.000	83	0.0	16	NA	104	−0.728	1	30	5.3
US Virgin Islands	4.0	0.000	65	4.2	436	NA	0	0.459	3	18	3.6
Syria	0.0	0.000	79	0.0	194	NA	52	−0.135	2	19	3.6
Puerto Rico	0.2	0.000	65	0.2	849	NA	2	0.603	3	18	2.6
Guadeloupe and Martinique	3.1	0.000	65	3.2	1250	NA	0	0.962	4	19	2.6
Serbia-Montenegro	0.0	0.000	75	0.0	24	24	1101	0.146	3	19	2.6
American Samoa	0.0	0.000	65	0.0	1	NA	48	0.289	3	23	2.5
Isle of Man	44.8	0.000	65	47.2	3586	NA	4	0.831	4	29	2.4
Guernsey/Channel Islands	62.7	0.000	65	66.0	3822	2042	110	1.188	4	29	2.4
Falkland Islands	5.1	0.000	65	5.4	16	NA	0	0.846	4	34	2.3
British Virgin Islands	0.4	0.000	65	0.4	12	NA	36	1.057	4	18	1.6

NA, no aquaculture.

et al. 2009; Yamamoto-Kawai *et al.* 2009). Overfishing and physical destruction often accompany chemical and thermal stresses where human populations are dense (Bryant *et al.* 1998). In marine ecosystems, these multiple stressors act synergistically or antagonistically in ways that have not yet been fully resolved, making it difficult for managers to plan for the future. Protecting against socioeconomic losses triggered by ocean acidification will require the development of plans that account for the possibility of multiple stressors and indirect effects.

Nevertheless, it is clear from considering our results that vulnerability to ocean acidification alone could take many forms, and countries with similar geographic characteristics could be at risk of socioeconomic impacts for different reasons. These risks could also depend on the effects of other stressors as discussed earlier. Countries with significant nutritional interests in molluscs could experience hardships if ecosystem shifts even partially related to ocean acidification occur, which decrease the overall availability or nutritional quality of mollusc protein (not to mention other ocean creatures that depend on molluscs as prey). Countries with significant economic dependence on molluscs could experience difficulties if effects of ocean acidification and other stressors decrease the size, appeal or numbers of specific desirable species in ways that depress mollusc prices on the global market. In addition, we cannot easily predict humans' responses to these factors or how they will affect global mollusc consumption and trade. The adaptive strategies appropriate for each country will likely be at the fishery level, and they will necessarily vary depending on each country's particular mix of economic and nutritional dependence and its risk factors, especially given present production and aquaculture and the timescale over which ocean conditions will be significantly different. Strategies will also vary depending on the species of interest and the availability of resistant substitute species.

Outlook for the future

Since the Industrial Revolution, the ocean's pH and aragonite calcium carbonate saturation state (Ω_{ar}) have declined just a small amount to present conditions (Table 2), but they are expected to decline more quickly in the next four decades (Table 3). Ocean chemistry will move outside the present range of natural variability in many regions beginning in about 2025, depending on the existing natural variability in Ω_{ar} in a given area. When ocean chemistry in an area becomes entirely different from present-day conditions, we postulate that the range of ecosystem services provided by marine organisms will also change significantly in those regions, and wild mollusc harvests in particular may decline measurably. Countries with low adaptive capacities, high nutritional or economic dependence on molluscs, rapidly approaching dates of significant chemical change or rapidly growing populations will therefore be most at risk of losing important ecosystem-related services, including mollusc production. These changes could occur on the order of decades.

While ocean acidification progresses, other anthropogenic factors such as climate change, wild harvests and terrestrial runoff will also be affecting marine ecosystems (Doney 2010). Although this particular study aims to provide a preliminary assessment of ocean acidification's possible implications for nations that depend on molluscs for nutrition and income, future investigations should include these other anthropogenic factors. However, to date there have been relatively few studies of ocean acidification's interactive effects with other environmental stressors and those completed have been for just a few marine species, so such future studies of OA's effects in context with multiple stressors may be data-limited for some time. Similarly, identifying ocean acidification's effects on all marine ecosystem services is an ultimate goal to achieve, but a great deal of research is required before even preliminary estimates can safely be made.

Even though ocean acidification promises to be just one stressor acting on marine mollusc populations, we propose that the transition decades for Ω_{ar} should also be the dates by which nations and regions have developed new plans to maintain current per capita mollusc harvests in the face of rapidly occurring environmental change and are preparing, where possible, to make up for wild capture decreases by increasing aquaculture. Strategies to respond and adapt to ocean acidification (and other stressors) must be developed and implemented for each region to account for local species, economies and mollusc use patterns. National adaptive strategies will also likely need to account for the different responses of other harvestable marine resources such as crustaceans and finfish.

Once the population-scale responses of molluscs and other harvestable marine resources to lower pH and Ω environments are clearer, a similar but expanded analysis may be needed to provide decision support for planners as they develop regional plans that incorporate a broader range of species and market behaviours.

Aquaculture operations may have an advantage over wild capture mollusc fisheries in that they tend to be confined to relatively small areas where it may be possible to manage environmental conditions for mollusc growth and/or to select for production species and individuals that tolerate lower-pH conditions. These advantages, combined with the high nutritional, economic and social benefits that mollusc aquaculture offers, should serve as a starting point for building action-oriented climate change/ocean acidification adaptation plans that feature aquaculture expansion.

Most of the mollusc culture in the vulnerable areas is currently performed on a small scale, and this form of extensive mollusc rearing can be responsibly enhanced using native species, organic farming and proper site selection (National Research Council 2010a). Mollusc culture in general is an inexpensive, biogeochemically benign, form of aquaculture that is also not resource intensive. If ocean acidification reduces wild populations and harvest volumes, it may be necessary to increase aquaculture production even faster in the future to maintain mollusc supply and to focus on species that are more tolerant of low-pH conditions, or to manipulate ocean chemistry around mollusc farming sites. Furthermore, it may be necessary to plan for certain changes in mollusc physiology (like weaker shells or delayed development) during aquaculture if meat harvests are unchanged. Plans should be made to invest in aquaculture facilities that promote research and produce high-valued species to cater to high-end markets and/or versatile or resistant species. Efforts to diversify mollusc species and incorporate mollusc culture in other types of aquaculture operations (e.g., polyculture) may also increase coping capacity. Where possible, hatchery development and shifting to intensive farms (with careful consideration of resource overuse and habitat carrying capacity) may prove to be the best strategy for assuring mollusc production in areas most affected by waters harmfully altered by ocean acidification. Until the direct links between individual effects from ocean acidification and ecosystem responses are fully understood, a range of planning and adaptive efforts such as these must be conducted so that mollusc-dependent nations and regions will be ready to meet the dates when Ω_{ar} will become entirely different with plans for sustainable mollusc harvests in place.

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Appendix 1

Phylum	Class	Family	Species with highest global production
Mollusca	*Gastropoda*	*Strombidae* (conch)	*Strombidae gigas* (queen conch)
		Haliotoidae (abalone)	*Haliotis rubra*
		Buccinidae (whelk)	*Buccinum undatum*
	Bivalvia	*Veneridae* (clam)	*Spisula solidissima* (Atlantic surf clam)
		Crassostrea (oyster)	*Crassostrea virginica* (Eastern cupped oyster)
		Pectinia (scallop)	*Patinopecten yessoensis* (Yesso scallop)
		Mytilidae (mussel)	*Mytilus edulis* (blue mussel)

Phylogenetic table illustrating the commercially important mollusc species and families summed in this study. (Food and Agriculture Organization of the United Nations 2010b).