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ABSTRACT

The rising demand of ecosystem services, due to the increasing human population in coastal areas, and the subsequent need to secure healthy and sustainable seas constitute a major challenge for marine ecosystems management. In addition, global anthropogenic changes have transformed the marine realm, thereby challenging ecosystem health and the services necessary for human welfare. These changes have opened ecological space for opportunistic organisms, such as jellyfish, resulting in ecosystem-wide and economic implications that threaten marine ecosystem services. Here, we used a comprehensive dataset of jellyfish hazards over the period 1960–2019 to track their dynamics and implications for human welfare. Our results revealed that their large-scale patterns have been mainly enhanced in human-perturbed Large Marine Ecosystems, although the contribution of jellyfish Class to hazard type changed across ocean regions. The long-term variability of these events suggests that their temporal patterns mirror the pace of ocean warming and ocean health degradation nurtured by global anthropogenic changes in recent decades. These results warn of the wide socioecological risks of jellyfish hazards, and their implications advocate for transboundary, regional cooperation to develop effective ecosystem-based management actions. Failure to integrate jellyfish into ocean surveys will compromise coastal ecosystem services governance.

Classification: Social Sciences/Sustainability Science, Biological Sciences/Ecology.

1. Introduction

Global environmental changes have transformed the marine realm, posing unprecedented risks to marine biodiversity and ecosystem functioning, ultimately threatening human welfare (Hoegh-Guldberg and Bruno, 2010; IPBES, 2019; IPCC, 2019). In addition, interactions among overfishing, coastal nutrient over-enrichment, and habitat degradation (hereafter referred as anthropogenic stressors) magnify climate change impacts on marine ecosystems and result in widescale environmental changes. The consequences of these processes have shaped patterns of resource distribution and biogeochemical fluxes in the world ocean. These impacts are projected to increase along with the pace of ocean warming, and there is great uncertainty about how this might impact ocean health, ecosystem services, and human wellbeing (Halpern, 2020). Warming is one of the most pervasive drivers of ocean dynamics (Rosenzweig et al., 2008), as it shapes the water column structure, vertical mixing and nutrient availability for primary producers in the euphotic layer (Roxy et al., 2016). Warming also affects the metabolic rates of plankton, their productivity, and ecological interactions, thereby regulating food web dynamics and carbon export (Boero et al., 2016; O'Connor et al., 2009). At larger scales, warming has fostered environmental shifts, i.e., contractions and expansions of hydrographic patterns, thus altering the distributions of marine taxa (Beaugrand, 2015; Kleisner et al., 2017) and reducing biodiversity, while promoting the proliferation of opportunistic organisms, such as jellyfish (Roxy et al., 2016). These events have been further ascribed to

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the decline in the number of predators and competitors through overfishing, habitat modification, and eutrophication (Purcell, 2012).

In semi-enclosed marginal seas, the increasing number of jellyfish outbreaks threatens socioecological systems and challenges regional and global conservation efforts, including the aim of Good Environmental Status by the EU Marine Strategy Framework Directive and the Sustainable Development Goal 14 to conserve and sustainably use oceans, seas, and marine resources (IOC-UNESCO and UNEP, 2016). Indeed, jellyfish proliferation events heavily affect broad ecosystem services through their impact on trophic dynamics and carbon fluxes, tourism and fishery industries, and human health, as some species cause envenomation and severe injuries (Gershwin et al., 2010; Graham et al., 2014). For instance, the toxins produced by jellyfish in the Class Cubozoa, e.g., *Chirodropids* spp., *Chironex* spp., *Chiropsalmus* spp., may be fatal to sea users (Fenner, 1996; WHO, 2003; Cegolon et al., 2013). The wide impacts of jellyfish have triggered serious monetary losses in diverse ocean regions and major semi-enclosed marginal seas in recent decades, i.e., the Gulf of Mexico (Boero et al., 2016), Southern Brazilian Bight (Nagata et al., 2009), East Asian waters, i.e., Japan, China and Korea (Kawahara et al., 2006; Dong et al., 2010; Kim et al., 2012), West Pacific waters, i.e., Bangladesh, Indonesia, Malaysia, Philippines, Singapore, Thailand, and Vietnam (Tan et al., 2019), California Current (Conley and Sutherland, 2015), southern Peruvian coast (Quiñones et al., 2013), and Mediterranean Sea (Ghermandi et al., 2015; Tomlinson et al., 2018). Such economic losses are mainly due to the impact of jellyfish in productive fishery grounds, i.e., reducing fish recruitment and interfering in varied fisheries activities (Borsh-Belmer et al., 2021 and references therein). Similarly, massive jellyfish blooms hamper coastal facilities operation, such as blocking inlets of cooling systems, e.g., powerplant, energy generators, ships (reviewed in Richardson et al., 2009). The economic losses are further ascribed to the influence of jellyfish emergence in tourist hotspots, where they create a negative perception on sea-users and visitors. For instance, in Israel the estimated monetary markdown of such events has reached up to € 6.2 million due to the decline of annual tourism (Ghermandi et al., 2015).

These threats may increase in coastal regions due to the projected enhancement of anthropogenic stressors that favor jellyfish proliferation (Brotz et al., 2012; Purcell, 2012). Hence, bearing in mind the widespread impacts of jellyfish on socioecological systems (hereafter referred as hazards), they are considered not only as warnings of prominent changes in the state of marine ecosystems (Brodeur et al., 2016), but also as a novel variable that threatens provisioning and cultural ecosystem services (Johnson, 2015; Rothe, 2020). However, mainstream research on jellyfish has focused on underlying causes of their proliferation (Richardson et al., 2009; Graham et al., 2014), while less attention has been given to implications across systems from a socioecological perspective.

Here, we use a comprehensive dataset of jellyfish hazards covering the period 1960 to 2019 to investigate (i) decadal biogeographic changes in jellyfish hazards in the world ocean, (ii) to track the temporal trend of jellyfish hazards and its link with the human imprint in the marine environment, and (iii) to assess the associations between spatial patterns of jellyfish hazards and ocean health degradation in large marine ecosystems (LMEs). We hypothesize that jellyfish hazards track spatiotemporal patterns of the human imprint on marine ecosystems and on overall ocean health. Therefore, we combine these data with relevant global data of anthropogenic forces acting on marine ecosystems to examine whether jellyfish hazards mirror marine ecosystem degradation. A thorough understanding of the foundations of jellyfish hazards and their spread in LMEs is imperative if we are to protect the biodiversity, resilience, and sustainable use of marine ecosystems.

2. Methods

2.1. Data of jellyfish hazards records

We collected quantitative information on four major detrimental socioeconomic factors associated with jellyfish based on the number of hazard reports. These data do not reflect the magnitude of each hazard case in the specific number of patients or estimated economic loss, instead they provide insights into the evolution of the phenomenon over the last decades: (i) *fatal cases*, i.e., deaths after envenomation by jellyfish; (ii) *sting cases*, i.e., geographic spread in the frequency of stung sea-users that received medical treatment; (iii) *fishery industry*, i.e., events of fishery gear damage, spoiling fish catches, and fish mortality in aquaculture; and (iv) *coastal power plants*, i.e., jellyfish-induced clogging of cooling systems indicating disturbance events due to jellyfish.

Envenomation data (i.e., both fatal and sting cases) and data related to fishery industry and power plant damage were retrieved from a bibliographic search of peer-reviewed literature through the Web of Science and Google Scholar. The bibliographic search was based mainly on English terms, which limits number of information sources. The dataset used, however, is the most comprehensive information to explore the relationship between ocean health degradation and jellyfish hazards. As such, it provides a necessary baseline for science-based management actions.. Jellyfish hazards data were gathered by bibliographic search of peer-reviewed literature using the Web of Science and Google Scholar. To do so, we used keywords related to jellyfish (e.g., cnidarians, medusae, gelatinous carnivore zooplankton) and then we combined terms to build a new query based on the hazard types that included keywords associated to their consequences (e.g., fatal, injury, fishery mortality, powerplant clogging). We further included ancillary information gathered from media sources, when available. The bibliographic search used mainly English terms, which limits the number of information sources. An integrate list of the keywords and searching formula used is provided in Supplementary information. Fig. A.1a.

The collected data were sorted by date and jellyfish Class and were georeferenced. Details of these records are displayed as a subset in Appendices B-E, which contain the full compilation of jellyfish hazards record since 1884. In our analyses, we excluded data prior 1960 to enhance the reliability and because this period overlaps with the accelerated human influences on the Earth System, the Anthropocene (Steffen et al., 2015). Data selection followed the PRISMA protocol, which is provided in S. Fig. A.1b.

2.2. Data of environmental and anthropogenic factors

To assess covariations between jellyfish hazards and human imprint in marine ecosystems, we compiled data on anthropogenic stressors contributing to jellyfish proliferation, thus enhancing the probability of hazard events. We used data on sea surface temperature (SST) as a proxy for plankton's physical environment, marine fish capture and aquaculture production, which alter the food web structure and contribute to marine ecosystem deterioration favoring jellyfish (Pauly et al., 2008). In addition, we used two factors associated with anthropogenic pressures in coastal ecosystems: the influx of nitrogen (N), as a proxy for excess nutrients, and maritime trading, as a proxy for environmentally harmful influences, including transport of invasive species and coastline changes by artificial infrastructures in the marine ecosystem. These data were retrieved for the period 1990–2010, except for maritime trading, for which the data start in 1970. Details of these data are described in Table G.1.

2.3. Statistical analyses

Goal 1: Decadal biogeographic changes in jellyfish hazards in the world ocean

Data were pooled geographically by LME to track the decadal spread of hazard types. The analysis focused on the period 1960 to 2019 due to the reliability of data, and because the second half of the twentieth century featured rapid growth of ocean threats and global socioeconomic trends that have become a prime driver of change in the Earth's system (Steffen et al., 2015; Halpern, 2020; Heinze et al., 2021). We assessed the cumulative jellyfish risk (hereafter jelly-risk) by means of a qualitative index that consider the cumulative jellyfish hazard events occurring in a specific LME. The index was scaled from jelly-risk 1 (occurrence of one hazard type within an LME) to jelly-risk 4 (co-occurrence of four hazard types within an LME). Decadal changes of jelly-risk were then mapped by LME to track their geographic expansion in the world ocean. Details of jellyfish hazards in LMEs are shown in supplemental Table A.1 – A.4. We further identified the dominant jellyfish Class by hazard type and by region.

Goal 2: Tracing the temporal trend of jellyfish hazards and human imprint in the marine environment

We hypothesize that the cumulative number of jellyfish hazards tracks marine environment deterioration. The long-term trend of the human imprint on marine ecosystems and overall ocean health was approached by means of a matrix composed by the following anthropogenic stressors: SST, marine fish catch, aquaculture production, N inputs to coastal waters, and maritime trading. To do so, we removed linear temporal trends from all variables by regressing chronological observations against time, and residuals were retained for analysis. We then applied Principal Component Analysis (PCA). The first principal component (PC1) was used as a proxy for the human imprint, as it captures the main pattern of variability of the human imprint matrix. The relationship between indicators of the human imprint on marine ecosystems (e.g., PC1 and SST) and the jellyfish hazards time series was assessed by means of Pearson product moment correlation using a bootstrap resampling which involved a random pairwise sampling with replacement, where each time series was resampled 1000 times. To account for temporal autocorrelation in the time series, we adjusted the degrees of freedom in the statistical test following the two previous developed methods (Chelton, 1984; Pyper and Peterman, 1998). Furthermore, to minimize the likelihood of committing a type I error when identifying statistical links, we used a conservative alpha level of 0.01.

Goal 3: Assessment of the associations between spatial patterns of jellyfish hazards and ocean degradation

To assess covariation between ecosystem degradation and jellyfish hazards in LMEs that have experienced jellyfish hazards since 1960 ($n = 36$), we confronted the cumulative jelly-risk to the Ocean Health Index (OHI, https://www.oceanidex.org) and warming rate experienced by LME. To do so, we used alluvial diagrams, which allow assessing relationships in categorical data through flow lines displaying varying widths that correspond to the strength of relationships. Here we use it to quantify the extent to which jellyfish hazards are concomitant with the LME perturbation state and global warming. All variables were assigned to parallel vertical axes and were clustered in four categories. Column 1 depicts the ocean warming rate (℃/decade) based on the net SST change per LME and per decade (Belkin, 2009). We retained the same categories, except "slow warming" and "cool" were merged into one category. The warming scale denotes the SST increase as follows: superfast warming 0.96–1.35 ℃, fast warming 0.67–0.89 ℃, moderate warming 0.3–0.6 ℃, and slow warming −0.1–0.28 ℃. Column 2 denotes the rescaled ocean health risk, which deduced OHI. The OHI we used consisted of seven ecological components relevant to environmental quality: food provisioning (subgoals: mariculture, fisheries), coastal protection, tourism and recreation, clean waters, and biodiversity (subgoals: species, habitat). OHI scores are given in a range of 0–100, where lower scores correspond to perturbed systems, while higher scores denote healthier systems. The categories used are classified according to thresholds of OHI scores as follows: highest risk ≤ 62, $62 <$ high risk ≤ 65.25, $65.25 <$ medium risk ≤ 68.5, and $68.5 <$ low risk. These risk categories were defined by Halpern et al. (2016). Last, column 3 corresponds to the cumulative jelly-risk, from 1 to 4, over the period 1960–2019.

Tools used for data mining

Geographical locations of jellyfish hazards were retrieved by Geoplaner version 2.7 (https://www.geoplaner.com), and data were sorted by LMEs and country from the LME portal (https://lme.edc.uri.edu). Data analysis and visualization were performed using R 3.5.3 (R core team 2019), QGIS 3.14 (QGIS.org 2020), and Grapher 16 (Grapher™ from Golden Software). Maps were created using the R packages sp (Pebesma and Bivand, 2005; Bivand et al., 2013) and pheatmap (Kolde, 2019). The alluvial diagram was drawn with RAW Graphs (https://rawgraphs.io). The workflow of our approach is displayed in Fig. 1.

3. Results

3.1. Long-term biogeographic changes in the jelly risk

Decadal biogeographic patterns of jelly risk have steadily spread over the last six decades, 1960 s − 2010 s (Fig. 2a), with a prominent increase after the 1980 s. During the 1960 s, such events were mainly confined to eight LMEs located in East Asia and northeastern Australia, while few events were reported for the eastern U.S. continental shelf. Jellyfish hazards increased in the 1970 s in European waters, mainly in the Mediterranean and Black seas, although events were also reported in the Norwegian Sea. Additionally, these events increased in northeastern Australia and East Asian marginal seas, i.e., the East China Sea and East Sea/Sea of Japan, which faced cumulative hazards reaching jelly-risk levels 3 and 4. In the 1980 s, the number of LMEs affected by jellyfish hazards increased to 17 (Fig. 2b). These areas were mainly clustered along the eastern U.S. Atlantic coast, northeastern and southeastern Atlantic waters, western Indian Ocean, and southeastern Asian waters. During the 1980 s, jellyfish hazards further increased in the Mediterranean Sea, East Asian Seas, and northeastern Australian waters. Such geographic expansion lasted over the last three decades and has been biased toward the Northern Hemisphere (see Fig. 3). Over this period, 1990–2019, the LMEs most affected were the East Sea/Sea of Japan, Mediterranean Sea, and Yellow Sea, which faced the co-occurrence of several hazard types, thus reaching the highest scores (jelly-risk level 4). These LMEs were followed by the Kuroshio Current, East China Sea, Northeast Australian Shelf, and Southeast US continental shelf, which displayed sustained high scores and jelly-risk level 3. Likewise, we found high scores for the Celtic-Biscay Shelf, Gulf of Mexico, Arabian Sea, and Humboldt Current during the 1990 s − 2010 s.

The decadal jellyfish hazard events increased from 36 in the 1960 s to 156 in the 2000 s and displayed a progressive spatial spread over the last decades. Indeed, the number of LMEs affected rose from 8 in the 1960 s to 29 in the 2000 s (see Fig. F.1). Envenomation and impairing fishery industry appeared to be the most recurrent threats, and their intensity markedly increased from the 1990 s. In addition, jellyfish envenomation has steadily affected new areas with notable stinging cases in the Northern Hemisphere. These included the first fatal events in middle and high latitudes, e.g., Italy (2010) and South Korea (2014), and the first severe jellyfish sting events in Sweden in 2018 (see Tables B.1 and C.1).

In addition, the contribution of jellyfish groups to hazard types vary across geographic areas. Species responsible for sting envenomation differ among regions, with Cubozoa main caused group inducing fatality in the entire Oceans (79.84 %). In sting event, Hydrozoa dominating in the sting events although Cubozoa shown over 50 % contribution in the Indo-Pacific Ocean and South Pacific Ocean and Scyphozoa dominating the North Atlantic Ocean (47.37 %).In turn, fisheries and powerplant operation damages were dominated by Scyphozoa species accounted for 82.47 % and 100 %, respectively, in all regions (Table 1).

Jellyfish hazards parallel the human imprint in marine ecosystem deterioration.

The observed close covariation between the human impacts on

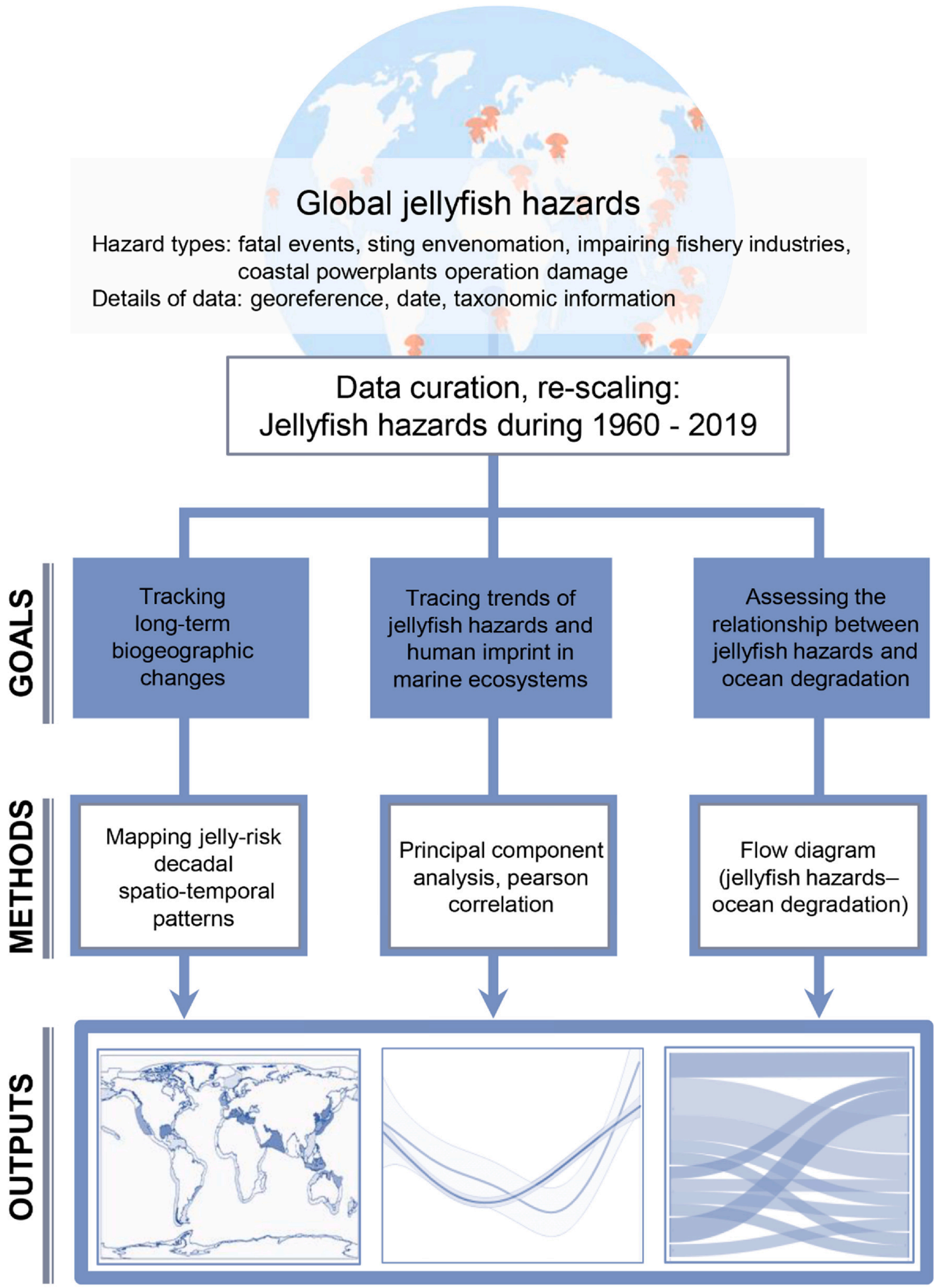

Fig. 1. Schematic representation of the data mining procedure used in this study.

marine ecosystems, as depicted by the first principal component (PC1 92 % of the total variance), and jellyfish hazards (jellyfish hazard = -0.380 + human imprint * 0.674 + 0.441 * pow (human imprint, 2); R = 0.66; $p < 0.001$; Fig. 4a) highlights that these events can be a valuable proxy to track marine environmental health deterioration, thereby supporting other indices of human ocean impact. The general trend of the human imprint, as depicted from PC1, primarily represents the influence of sea surface temperature, aquaculture production and world sea bone trading, followed by marine fisheries catches and coastal nutrient over-enrichment (see Table G.2). In addition, the long-term variability of jellyfish hazards shifted after the 1990 s toward larger variations (see Fig. 4b) The observed shift was concurrent with the enhanced pattern of human imprint in marine ecosystems, thus supporting the use of jellyfish hazards as a proxy for the state of the environment. In agreement with this, our results confirmed the close connection between jellyfish hazards and ecosystem degradation, as

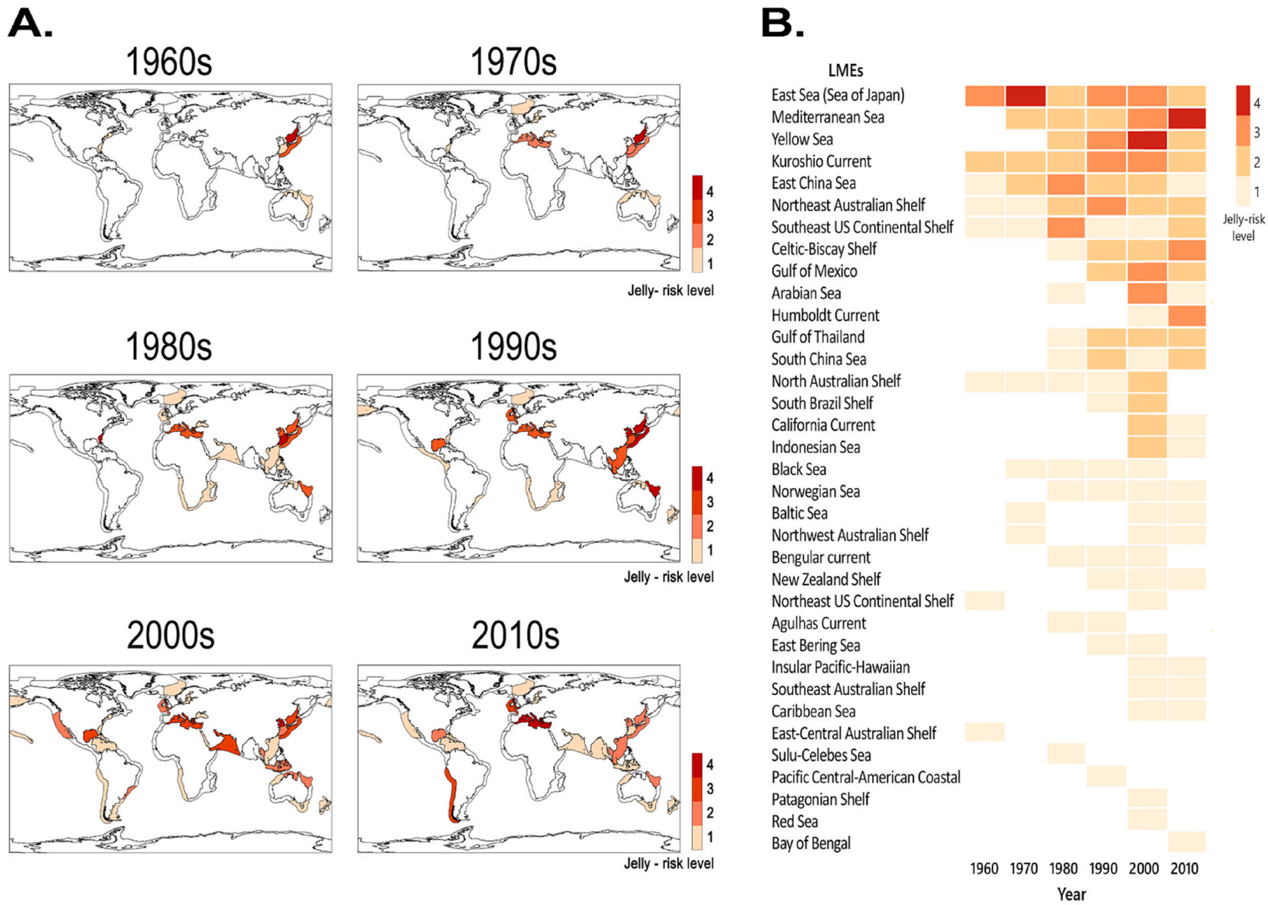

Fig. 2. (a) Large scale variability of jellyfish hazards in Large Marine Ecosystems (LMEs) over the period 1960 – 2019. The jelly-risk denotes the cumulative occurrence of jellyfish hazards in LMEs. The magnitude of jelly-risk from level 1 to 4 is displayed from light to dark red, respectively; (b) Decadal variability of jelly-risk sorted by LME. The jelly-risk denotes the cumulative occurrence of jellyfish hazards in LMEs, where the magnitude goes from 1 to 4 and is displayed from light to dark red, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

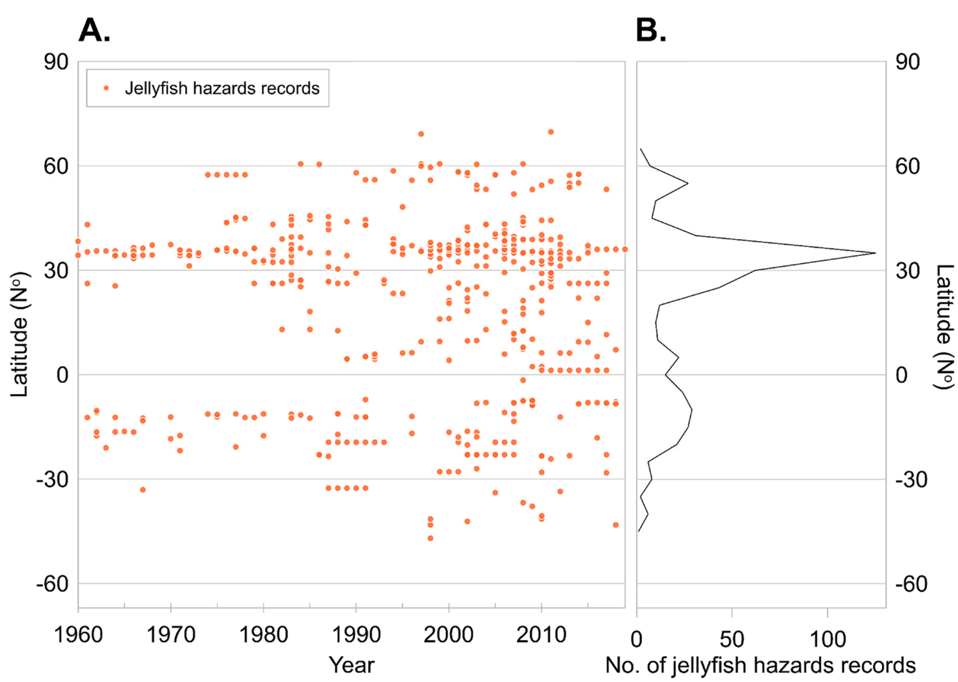

Fig. 3. Global distribution of jellyfish hazards records from 1960 to 2019. (a) Temporal spread of records by latitude, and (b) latitudinal overall pattern shown by the sum of records smoothed by 5-degree latitude.

Table 1
Dominant jellyfish Class by hazard type in ocean regions. The relative contribution (%) and number of events (in parentheses) by region are indicated. No records are denoted by the dashed line.

	Fatal event			Sting envenomation		
Region	Scyphozoa	Hydrozoa	Cubozoa	Scyphozoa	Hydrozoa	Cubozoa
North Pacific Ocean	35.00 (7)	30.00 (6)	35.00 (7)	37.21 (16)	44.19 (19)	18.60 (8)
Indo-Pacific Ocean	9.52 (2)	14.29 (3)	76.19 (16)	9.52 (2)	33.33 (7)	57.14 (12)
South Pacific Ocean	–	2.56 (2)	97.44 (76)	–	42.86 (6)	57.14 (8)
North Atlantic Ocean	16.00 (4)	4.00 (1)	–	47.37 (9)	15.79 (3)	36.84 (7)
South Atlantic Ocean	–	–	–	–	100.00 (3)	–
Total sum	10.48 (13)	9.68 (12)	79.84 (99)	27.00 (27)	38.00 (38)	35.00 (35)
	Impairing industrial fisheries			**Powerplant operation damage**		
Region	Scyphozoa	Hydrozoa	Cubozoa	Scyphozoa	Hydrozoa	Cubozoa
North Pacific Ocean	94.83 (45)	3.45 (2)	1.72 (1)	100.00 (45)	–	–
Indo-Pacific Ocean	100.00 (2)	–	–	100.00 (4)	–	–
South Pacific Ocean	100.00 (4)	–	–	–	–	–
North Atlantic Ocean	56.25 (18)	40.63 (13)	3.13 (1)	100.00 (3)	–	–
South Atlantic Ocean	100.00 (1)	–	–	–	–	–
Total sum	82.47 (80)	15.46 (15)	2.06 (2)	100.00 (52)	–	–

Note: These records do not consider information relative to salps (e.g. *Salpa fusiform*) and ctenophores (*Bolinopsis* spp. and *Mnemiopsis leidyi*). We provide such information in Table D.1 and Table E.1.

indexed by the OHI (Halpern et al., 2012), and ocean warming (Fig. 5). Indeed, the highest jelly-risk (level 4) was connected to the lowest ocean health scores (higher ecosystem degradation) and was further concurrent with superfast/fast warming rate clusters. Most LMEs within high and medium jelly-risk clusters (level 3 and level 2) showed connections to the highest and high categories of ocean degradation and to clusters of superfast and fast ocean warming. In clear contrast, we found that less perturbed ecosystems (i.e., a low ocean degradation level and a slow ocean warming rate) were associated with the low jelly-risk cluster.

4. Discussion

4.1. Global anthropogenic changes shape biogeography of jellyfish hazards

Our results support the current concern regarding the geographic spread of jellyfish species to temperate regions (Boero et al., 2016; Poloczanska et al., 2013). This phenomenon is shaped by multiple factors affecting marine environmental conditions. Besides the effects of warming on planktonic organisms' physical environment, anthropogenic activities, such as the increase of artificial structures associated with the exponential growth in shipping, aquaculture, and coastal protection, provide habitat for benthic life stages, and are hypothesized as major drivers of jellyfish blooms in recent decades (Duarte et al., 2013; Lo et al., 2008; Yoon et al., 2018). Partly favored by these vectors, alien jellyfish have increased in new areas and have been linked to local biodiversity losses and ecosystem disturbances (Bayha and Graham, 2014; González-Duarte et al., 2016; Jaspers et al., 2020). Moreover, alien jellyfish in semi-enclosed seas have affected aquaculture and tourism activities. This is the case for the Mediterranean Sea, where the Indo-Pacific jellyfish species, e.g., *Rhopilema nomadica* together with the native *Aurelia aurita*, are responsible for approximately fifty percent of local fishery disturbance cases caused by jellyfish (Bosch-Belmar et al., 2020). A further implication of global change impacts on marine ecosystems is the modification of large-scale biogeographic patterns of plankton assemblages, which is among the fastest and largest ecological responses to global anthropogenic pressures (Beaugrand et al., 2002; Chivers et al., 2017) Indeed, in the North Atlantic Ocean, warmer-water plankton shifted northwards by 10° latitude concurrently with a similar retreat of colder-water plankton over the last 50 years, thus impairing plankton production and biodiversity, and ultimately affecting fisheries (Beaugrand et al., 2002; Edwards et al., 2020). In agreement with this, we observed that the decadal patterns of jellyfish hazards displayed a spread towards high latitudes (see Fig. 3a), also noticed in the large-scale changes of the jelly-risk in LMEs (see Fig. 2). These trends unveil that decadal biogeographic patterns of jellyfish hazards echo the intensified anthropogenic pressures in coastal regions. It is worth noting that this phenomenon does not constitute a global rise of jellyfish populations, supporting previous global analyses (Brotz et al., 2012; Condon et al., 2012), instead it reflects consistent deterioration in semi-enclosed marginal seas.

4.2. Challenges for semi-enclosed marginal seas

Marine environments are facing unprecedented challenges due to the cumulative anthropogenic stress and may cross critical thresholds if ecosystem health degradation continues (IPCC, 2019). In line with previous global analysis showing decadal trends (1950–2010) of jellyfish populations in LMEs (Brotz et al., 2012), our results showed that the higher incidence of jellyfish hazards was mainly clustered in perturbed, semi-enclosed temperate seas, e.g., the East Sea (Sea of Japan), Mediterranean Sea, and Yellow Sea, that are exposed to multiple stressors, such as rapid warming (Belkin, 2009; Sherman et al., 2009), high marine activity (Hoagland and Jin, 2008), and coastal eutrophication (Sherman and Hempel, 2008). This is likely due to ecological advantages jellyfish have over fish in the exploitation of ecological spaces opened by anthropogenic disturbances. Indeed, through their large, water-laden bodies moving through the water sufficiently slowly, they increase prey contact rates. This, together with their high potential for growth and reproduction, favor them to functionally replace several overexploited commercial stocks of planktivorous fishes (Acuña et al., 2011; Schnedler-Meyer et al., 2016).

Abrupt and persistent changes in the ecosystem state have been documented at multiple sites around the globe and have been ascribed to the combined effects of anthropogenic perturbations and climate phenomena (Reid et al., 2016; Kim, 2020). Degraded ecosystems lose properties that aid in maintaining resilience and are therefore more vulnerable to sudden, strong climatic and cumulative anthropogenic pressures. We found that the jelly-risk was enhanced after the occurrence of ecosystem shifts in the Black Sea, western Mediterranean and Adriatic Sea (Conversi et al., 2010; Llope et al., 2011; Molinero et al., 2008). Likewise, rapid jellyfish proliferations have been reported in the northern Benguela ecosystem after the sardine collapse caused by overfishing (Lynam et al., 2006) and in the Mediterranean Sea, where synergies of overfishing and climate change favored the successful invasion and massive blooms of *Cotylorhiza tuberculata* (Prieto, 2018). Our

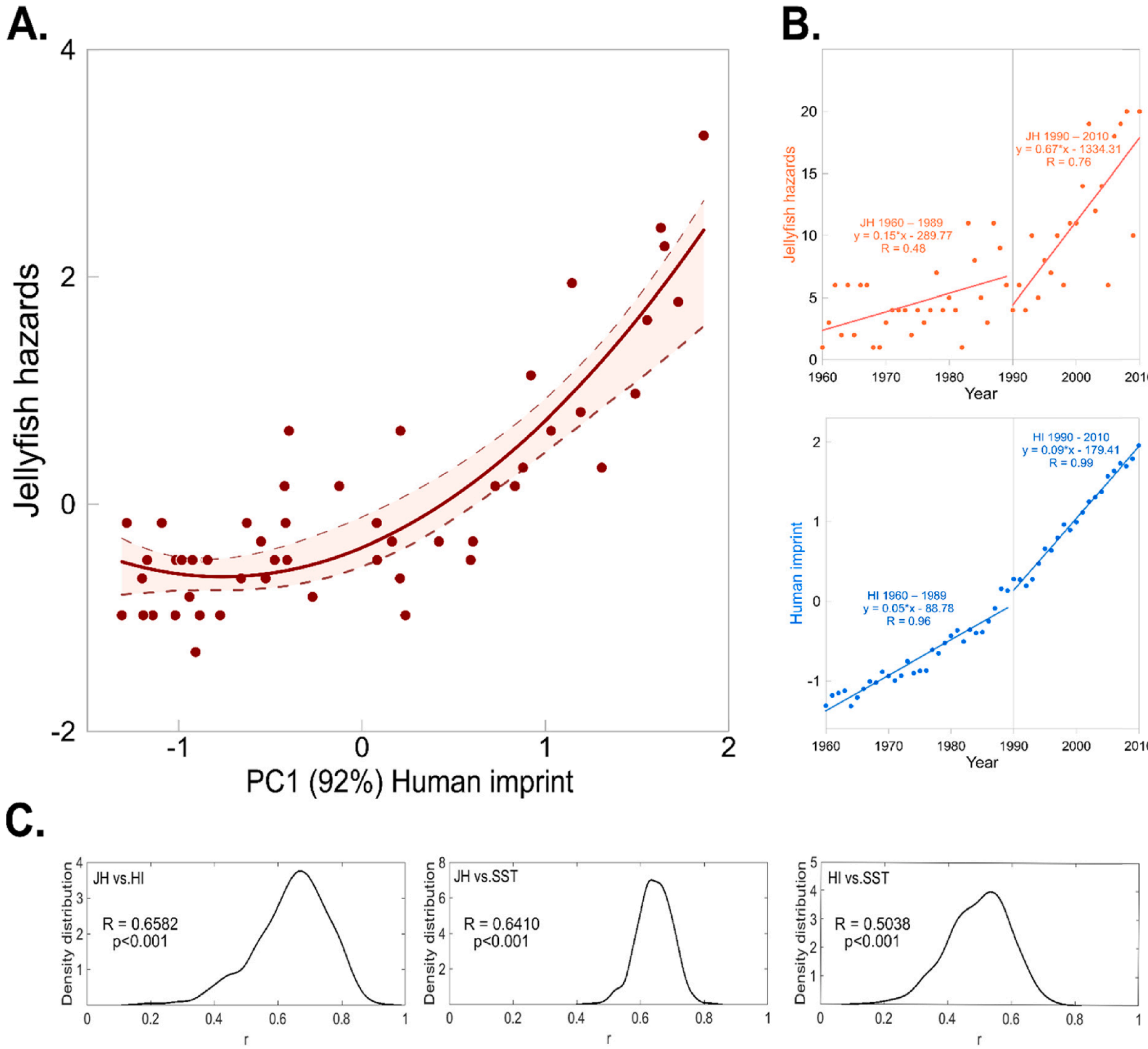

Fig. 4. (a) Relationship between human imprint (PC1) in the marine environment and anomalies of jellyfish hazards ($R^2 = 0.66$, $p < 0.01$) over the period 1960–2010. PC1 encompass five anthropogenic factors: sea surface temperature, marine fish capture, global aquaculture production, nitrogen in coastal zone, world seabone trading economic. Coefficients are shown in Table G2. (b) Relationship between jellyfish hazards and time (in red), and human imprint and time (in blue). Thick lines indicate the linear fit. Notice the increase of slope during the period 1990–2010. (c) Density distribution of correlation coefficients of the relationship between jellyfish hazards and ocean health indicators (HI – Human imprint, SST- Sea surface temperature, and JH – anomalies of jellyfish hazards). The density distribution was obtained by bootstrap resampling (1000 times). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

results therefore provide quantitative support to a former seminal hypothesis pointing towards the concurrence of jellyfish blooms with anthropogenic driven environmental perturbations (Purcell, 2012). Indeed, our findings reveal that recurrent jellyfish hazards are valuable warning signals of less healthy marine ecosystems, and they should be considered if we are to implement effective ecosystem-based management. This further suggests that these organisms might become prominent players in future ocean scenarios, thus interfering with provisioning and recreational ecosystem services for human welfare and regulating services (e.g., carbon export).

The highest jelly-risk regions turn out semi-enclosed seas, such as the Mediterranean and East Asian marginal seas, which simultaneously experience jellyfish transboundary nuisances that cannot be solved through a single country's efforts; instead, they should be approached through regional cooperation. For example, the giant jellyfish *Nemopilema nomurai* has a major nursery area in the western Yellow Sea where individuals are spread by mesoscale currents throughout the East China Sea and East Sea/Sea of Japan, thus affecting Korea and Japan and causing severe regional socioeconomic damage. The economic threats posed by such proliferation fostered regional cooperation between China, Japan, and Korea to mitigate local damages produced by jellyfish and warrant further platform building for joint efforts to secure sustained ecosystem services. For instance, annual meetings take place to address the "Jellyfish monitoring and Network Establishment in the Yellow Sea" (NIFS, 2006). Similarly, in the Mediterranean Sea transboundary collaborative jellyfish-related citizen science programs have recently gained momentum and have strengthened societal initiatives to support academic research. Indeed, citizen science has emerged as valuable and cost-effective tool for tailored management strategies that mitigate jellyfish impacts on Mediterranean socioecological systems, while endorsing marine conservation plans, e.g., Blue Growth (Marambio et al., 2021). In addition, recent efforts have provided cost-effective protocols to incorporate gelatinous monitoring in existing fishery surveys to improve the EU's Marine Strategy Framework Directive (Aubert et al., 2018). In agreement with this, we emphasize the need to survey jellyfish and their effects on socioeconomic activities as key indicators to assess the status and trends of social-ecological marine systems, and ultimately to reduce uncertainties of ecosystem responses

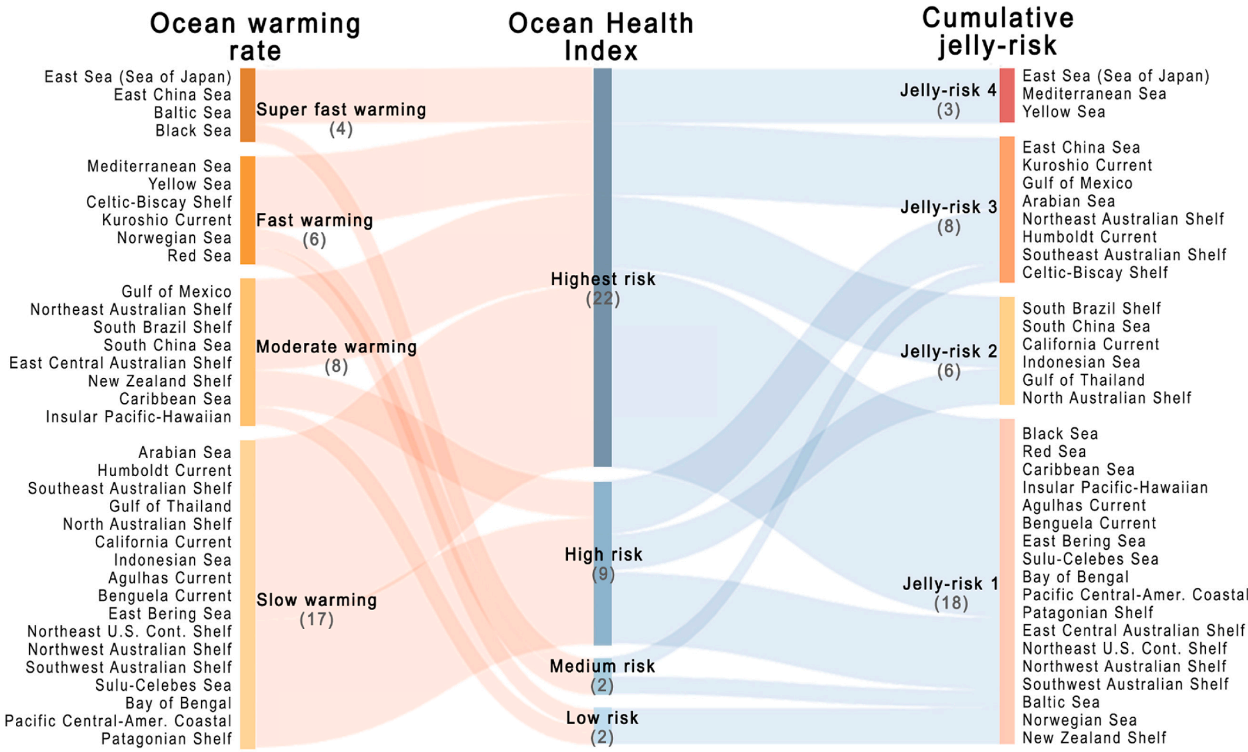

Fig. 5. Linkages between ocean degradation and jellyfish hazards shown by alluvial diagram. Ocean indicators and jellyfish hazards were assigned to parallel vertical axes and each variable was clustered in four categories, from 1 to 4, over the period 1960–2019. Column 1 depicts the ocean warming rate based on the net SST change per LME and per decade (Belkin, 2009). Column 2 denotes the rescaled ocean health risk, which encompasses seven ecological components relevant to environmental quality (Halpern et al., 2016), and Column 3 corresponds to the cumulative jelly-risk. Alluvial diagram shows correlations between categorical dimensions representing them as flows, visually linking categories with shared items, while their width is proportional to their value. Alluvial diagram was drawn with RAW Graphs (https://rawgraphs.io).

to global anthropogenic changes. Therefore, the inclusion of these holistic indicators is crucial to support the Integrated Ecosystem Assessment and consent to main principles for implementing Ecosystem Based Management (Boero et al., 2016; Levin et al., 2009).

The present study has revealed the implications of jellyfish hazards through the analysis of both quantitative and qualitative historical data gathered from a variety of sources, i.e., peer reviewed scientific surveys and technical reports. In some areas, however, these data are not exempt from uncertainties, particularly in regions where these organisms have long been overlooked and under-reported, for which our results might show only part of the entire picture. In such a case, however, the magnitude of this phenomenon may be larger. Notwithstanding these caveats, the observed biogeographic patterns are in line with current knowledge on plankton biogeographic changes, as well as with previous global analysis on the long-term trends of jellyfish in LMEs. Moreover, our results further highlight the value of jellyfish as indicators of marine ecosystem changes and the need to include them in coastal health monitoring.

5. Conclusions

Although new forms of regional cooperation are emerging, they are not doing so rapidly enough to match the pace of environmental health degradation. As growing coastal societies and projected high population densities predict a larger demand for marine ecosystem services in the future, jellyfish may affect the fulfillment of such needs, thus becoming prominent players in provisioning, cultural, and supporting services. Hence, our results advocate for their inclusion in multidisciplinary research beyond regional scales and call for investing in this group through systematic surveys. Such low cost, but strategic investments, might result in a high return due to the impacts of this group on ecosystem services. Failure to integrate jellyfish hazards into ocean surveys will yield a misleading picture of ocean health and will further compromise the good environmental status and the achievement of the UN Sustainable Development Goals (SDGs) related to ocean health.

Glossary

Anthropocene: describes the most recent period in Earth's history when human activity has significantly impacted the planet's climate and ecosystems.

Anthropogenic factors: these factors are referred as deterministic causes of environmental modifications resulting from the influence of human activities, i.e., warming, overfishing, habitat modification, coastal eutrophication.

Hazard: extreme events in the Earth and its ecological system that may cause adverse consequences for ecosystem services and human welfare.

Jellyfish hazard: refers to the negative consequences triggered by jellyfish proliferations. Here we assessed four hazard types, namely envenomation sting, fatal envenomation, fisheries and coastal power plant damages.

Jelly-risk: denotes the recurrence of a hazard caused by jellyfish proliferations. The jelly-risk shows four categories that indicate the co-occurrence of hazard in a same large marine ecosystem (LME), from 1 when only one hazard-type occurs to 4, when all hazards are reported in the same LME: envenomation sting, fatal envenomation, fisheries, and coastal power plant damages.

Human imprint: human impacts on the environment and natural resources from the impressions and dynamic effects and subsequent economic effects

Ocean Health Index: The index provides a robust, widely applicable tool to assess the current status and likely future state of ten widely held public goals for ocean ecosystems. It combines a number of indicators into an informative set that is repeatable and comparable through time.

Warming rate index: The index denotes the increase of long-term trend of annual sea surface temperature over the period 1957-2006 and is reported by Large Marine Ecosystem (LME). This index provides a classification based on the long-term linear trends estimated using annual SSTs for each LME: super-fast warming, fast warming, moderate warming.

CRediT authorship contribution statement

Sun-Hee Lee: Conceptualization, Data curation, Formal analysis, Writing – original draft. **Li-Chun Tseng:** Writing – review & editing. **Yang Ho Yoon:** Writing – review & editing. **Eduardo Ramirez-Romero:** Formal analysis, Writing – review & editing. **Jiang-Shiou Hwang:** Data curation, Funding acquisition, Supervision. **Juan Carlos Molinero:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be uploaded to data repository.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envint.2022.107699.

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