Tropical Marginal Seas: Priority Regions for Managing Marine Biodiversity and Ecosystem Function

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Annu. Rev. Mar. Sci. 2014. 6:415–37

First published online as a Review in Advance on October 2, 2013

The *Annual Review of Marine Science* is online at marine.annualreviews.org

This article's doi:
10.1146/annurev-marine-010213-135042

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Keywords

coral reef, fisheries, pelagic, deep sea, transboundary, management

Abstract

Tropical marginal seas (TMSs) are natural subregions of tropical oceans containing biodiverse ecosystems with conspicuous, valued, and vulnerable biodiversity assets. They are focal points for global marine conservation because they occur in regions where human populations are rapidly expanding. Our review of 11 TMSs focuses on three key ecosystems—coral reefs and emergent atolls, deep benthic systems, and pelagic biomes—and synthesizes, illustrates, and contrasts knowledge of biodiversity, ecosystem function, interaction between adjacent habitats, and anthropogenic pressures. TMSs vary in the extent that they have been subject to human influence—from the nearly pristine Coral Sea to the heavily exploited South China and Caribbean Seas—but we predict that they will all be similarly complex to manage because most span multiple national jurisdictions. We conclude that developing a structured process to identify ecologically and biologically significant areas that uses a set of globally agreed criteria is a tractable first step toward effective multinational and transboundary ecosystem management of TMSs.

INTRODUCTION

TMS: tropical marginal sea

EBSA: ecologically and biologically significant area

MPA: marine protected area

The tropical ocean globally covers 50% of open water and 30% of the continental shelf (Longhurst & Pauly 1987). Tropical marginal seas (TMSs)—basins a few thousand kilometers in extent that are connected with the open ocean and bounded by at least one island arc (Mazarovich 2011)—form natural subregions within tropical seas. TMSs share a suite of characteristics that are important to global efforts to conserve marine biodiversity. Each has complex bathymetry ranging from the deep sea, seamounts, and canyons to emergent coral reefs and island chains, all supporting the high biodiversity characteristic of the tropics. Many elements of this biodiversity, such as tropical coral reefs, deepwater suspension-feeder communities (e.g., cold-water corals), and charismatic megafauna (e.g., sea turtles, cetaceans, large sharks, and manta rays), are inherently sensitive to anthropogenic pressures. TMSs also share a common suite of natural resource management challenges that stem from historical overexploitation of their biodiversity and, in most cases, their proximity to large human populations experiencing rapid economic growth. In Southeast Asia, where most TMSs are located, more than 60% of the human population of 557 million lives within 60 km of the coast. On the coastal margin, urbanization, development, shipping, and habitat destruction threaten the health of marine ecosystems with pollution and species introductions (marine pests).

TMSs provide global focal points for conservation efforts because their natural boundaries define a set of marine ecosystems characterized by high overlap of diversity, vulnerability, and anthropogenic pressure. The challenges of managing TMSs are substantial, because these seas are typically surrounded by developing nations that have pressing economic and social priorities but few resources to support the scientific research needed to underpin management.

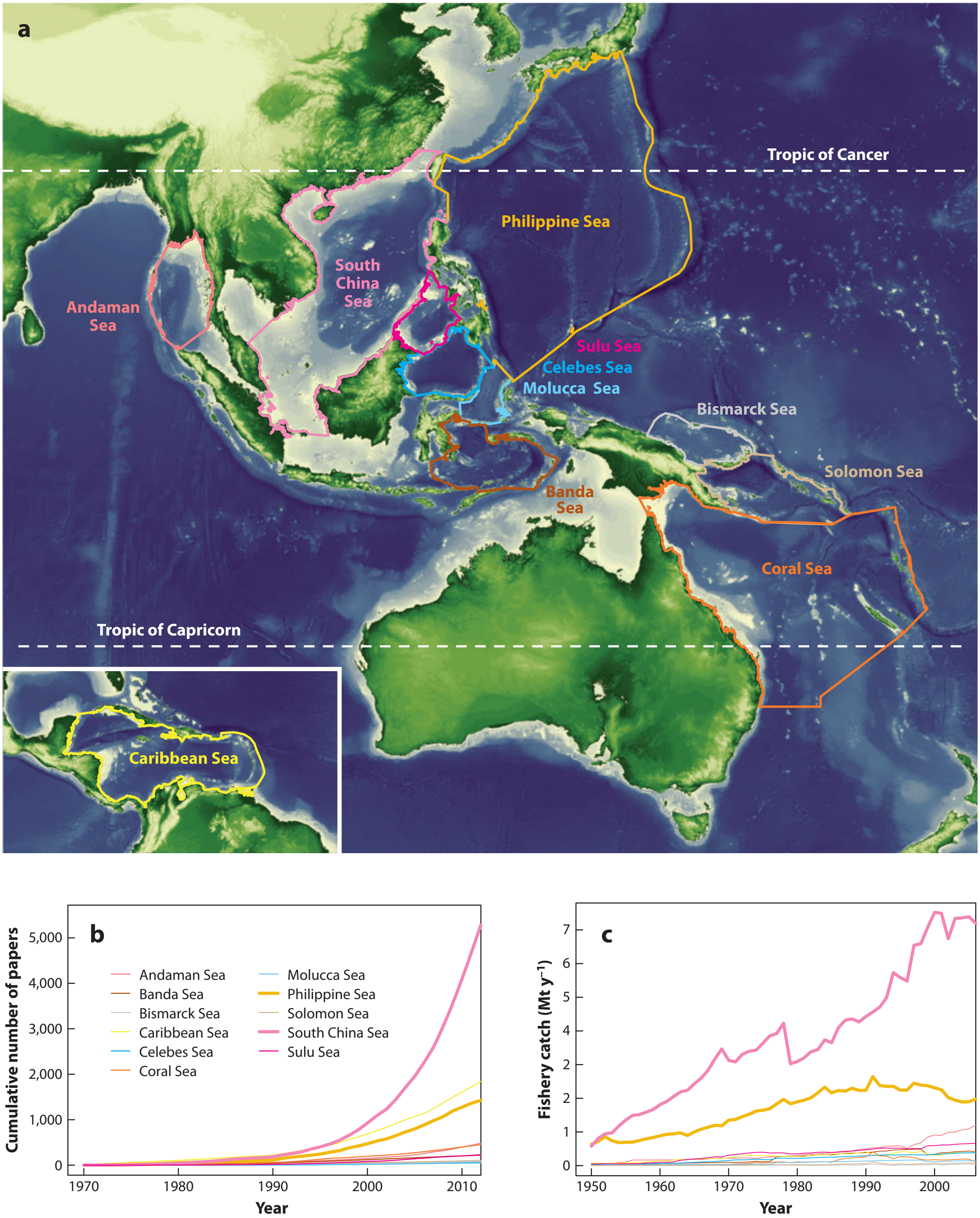
In the face of increasing threats and governance challenges to the maintenance of marine biodiversity, it is timely to review current knowledge available to support integrated management of TMS biodiversity and ecosystem services. In this review, we synthesize current ecosystem knowledge of 11 TMSs, of which the largest and best known are the South China Sea (SCS), the Caribbean Sea, and the Coral Sea (**Figure 1*a***). Our examples provide a strong contrast: The Coral Sea is nearly pristine (Ceccarelli et al. 2013), and the Australian territorial component has recently been declared a marine reserve, whereas the SCS (Han et al. 2012) and the Caribbean Sea are heavily affected by fishing, oil and gas extraction, mining, and eutrophication (Halpern et al. 2008). We focus on three primary oceanic ecosystems common to all TMSs—coral reefs and emergent atolls, deep benthic systems, and pelagic biomes—to demonstrate the need for effective ecosystem-based management that considers multiple human uses. We argue that the identification of ecologically and biologically significant areas (EBSAs) is an important and tractable step for establishing values and supporting sustainable management, and that templates developed for the successful management of TMSs could be widely applied.

APPROACHES TO MANAGING REGIONAL MARINE BIODIVERSITY

In 2002, the World Summit on Sustainable Development agreed to implement a comprehensive system of marine protected areas (MPAs) by 2012 (UN 2002), and in 2004, the Convention on

Figure 1

(*a*) The major tropical marginal seas of the world. The names and boundaries are as defined by the International Hydrographic Organization and recognized by the International Maritime Organization, shown here using a basin mask from Marine Regions (**http://www.marineregions.org**). (*b*) The knowledge base for each sea, based on a meta-analysis of published research output in Web of Science from 1970 to 2012. The number of publications for each sea is the result of a search for the name in quotation marks (e.g., "Caribbean Sea") as of October 11, 2012. (*c*) Fishery catches in each sea from 1950 to 2006. Abbreviation: Mt, megatonne.


a
Tropic of Cancer
Philippine Sea
South China Sea
Andaman Sea
Sulu Sea
Celebes Sea
Molucca Sea
Bismarck Sea
Solomon Sea
Banda Sea
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THE AICHI BIODIVERSITY TARGETS

The Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–2020 lists 20 targets within five strategic goal areas. Those most relevant to TMSs are as follows:

- Strategic goal B: Reduce the direct pressures on biodiversity and promote sustainable use.
- Target 6: By 2020, all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally, and by applying ecosystem-based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species, and vulnerable ecosystems and impacts of fisheries on stocks, species, and ecosystems are within safe ecological limits.
- Strategic goal C: Improve the status of biodiversity by safeguarding ecosystems, species, and genetic diversity.
- Target 11: By 2020, at least 17% of terrestrial and inland water and 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative, and well-connected systems of protected areas and other effective area-based conservation measures, and are integrated into the wider landscapes and seascapes.

Biological Diversity (CBD) committed to cooperate in areas beyond national jurisdictions for the conservation and sustainable use of biodiversity, including the establishment of MPAs (UNEP 2004). These goals are formalized in the Aichi Biodiversity Targets, which identify two important targets for marine areas (see sidebar The Aichi Biodiversity Targets). Targets 6 and 11 both require the implementation of marine spatial planning and integrated ocean management, providing a framework for improved decision making underpinned by ecosystem-based management. The targets emphasize links between land, freshwater and marine ecosystems, and their human uses (Secr. CBD & GEF Tech. Adv. Panel 2012). TMSs provide a subset of tropical systems that have many similar characteristics, features, and threats, and thus might be considered appropriate units for identifying habitats for conservation. Although in theory the CBD approach can be applied to the transboundary resources of TMSs, this has not yet been widely done. TMSs generally have low protection (MPAs comprise <5% of the total area of these seas, with the exception of the Coral Sea; **Table 1**), and for most it will be a challenge to achieve target 11 or to implement transboundary agreements that would meet target 6.

Gregr et al. (2012) compared classification schemes for the protection of marine biodiversity and concluded that the EBSA criteria initially developed by Fisheries and Oceans Canada are the most comprehensive and applicable to coastal, shelf, deep-ocean, and high-seas realms. The Global Ocean Biodiversity Initiative (**http://www.gobi.org**) recognizes the need for protection of the high seas, acknowledging that the deep sea and open ocean are the least understood areas, and advocates the application of EBSA criteria. The CBD has adopted and further developed EBSA criteria as foci for identifying areas of high ecological and biological value, potentially leading to enhanced management.

EBSAs are currently identified through a set of seven criteria (see sidebar What Are Ecologically and Biologically Significant Areas?). Although official EBSAs can be agreed upon only by the CBD Conference of Parties, there is no limit to the application of the criteria within national waters or within TMSs. The value of EBSAs lies not only in their identification but also in their use as a tool to engage all stakeholders and identify valued aspects of a system without specifying how they might be managed. In this way, the application of EBSA principles can help achieve transboundary conservation of biodiversity assets and assist TMS management.

CBD: Convention on Biological Diversity

WHAT ARE ECOLOGICALLY AND BIOLOGICALLY SIGNIFICANT AREAS?

The Convention on Biological Diversity promotes biodiversity conservation and sustainable development. One of its roles has been the development of seven criteria that can be used to identify ecologically and biologically significant areas in marine areas both within and outside of national waters (UNEP 2008):

1. Uniqueness or rarity
2. Special importance for life history stages of species
3. Importance for threatened, endangered, or declining species and/or habitats
4. Vulnerability, fragility, sensitivity, or slow recovery
5. Biological productivity
6. Biological diversity
7. Naturalness

The EBSA identification process relies on methods that incorporate scientific information systematically and robustly and that account for situations where knowledge is lacking. Although we anticipate that EBSAs will be evaluated at a variety of spatial scales, from extensive high-seas regions to smaller areas within exclusive economic zones, it will be important to define the precise boundaries of each area to be evaluated. The size of the areas examined will influence the availability and resolution of data sources and may influence how criteria are interpreted, and well-sampled regions will have many data available. TMSs provide suitable units for EBSA evaluation because they are precisely and naturally defined; are typically focal areas for scientific study, and are often areas where key elements of ecological structure or function have been reviewed or could be represented by surrogates or predictive models; and are of appropriate spatial scales (**Table 1**) for relevant data to be available.

TROPICAL MARGINAL SEAS IN PERSPECTIVE

In defining the scope of this review, we have used the names and boundaries of marginal seas in the tropics as defined by the International Hydrographic Organization. The Philippine Sea is separated from the SCS by the Philippine archipelago, and together these two seas form the western margin of the Pacific Ocean. The Sulu, Sulawesi, Molucca, and Banda Seas are contiguous and can be generally considered Indonesian seas, located within the Pacific transitional zone as defined by Mazarovich (2011). To the east of New Guinea, the Bismarck Sea is separated from the Solomon Sea by the islands of New Britain, but these seas have a close association with the Coral Sea to the south. Mazarovich (2011) does not separately consider the Solomon Sea or Bismarck Sea and regards the Coral Sea as part of the East Australian Basin, which includes the Coral, Tasman, and Fiji Seas. The Andaman and Caribbean Seas are discrete geographic entities, i.e., do not have a common boundary with another TMS. We acknowledge that our choice of TMSs is a matter of definition; for instance, the lack of a deep central basin has discounted some marginal seas, such as the Java, Timor, and Arafura Seas.

To create a proxy for existing knowledge of each TMS, we performed a meta-analysis of published research output in Web of Science from 1970 to 2012 (**Figure 1*b***). The SCS has the largest research base of any TMS (**Table 1**) and has an order of magnitude more literature than the other TMSs except for the Caribbean and Philippine Seas. The Bismarck, Celebes, Molucca, and Solomon Seas are the least known TMSs, with <110 publications each. The Coral Sea has been

Table 1 Key attributes of major tropical marginal seas

Sea	Surface area (km²)[a]	Area in depth range (%)[a] 1–200 m	200–2,000 m	>2,000 m	Number of seamounts[b]	Productivity (g C m^{-2} y^{-1})[a,c]	Fishery catch in 2006 (t)[d]	MPA area (km², along with% of total area)[e]	Number of publications[f]
Andaman Sea	608,941	37	40	23	70	222	1,203,674	2,685 (0.4)	470
Banda Sea	694,329	10	21	69	198	153	409,992	32,610 (4.7)	217
Bismarck Sea	359,440	6	61	33	82	132	45,673	375 (0.1)	79
Caribbean Sea	2,882,083	14	26	60	588	132	375,737	113,908 (4.0)	1,864
Celebes Sea	473,575	12	12	75	47	128	382,350	15,415 (3.3)	59
Coral Sea	4,051,683	12	26	62	513	116	112,959	839,491 (20.7)	455
Molucca Sea	218,396	8	36	55	27	137	138,133	6 (0.1)	44
Philippine Sea	5,710,564	3	8	90	2,515	79	1,976,619	37,905 (0.7)	1,407
Solomon Sea	739,508	10	26	64	255	113	62,172	995 (0.1)	104
South China Sea	3,341,521	49	21	29	351	195	7,197,101	66,512 (2.0)	5,099
Sulu Sea	332,871	33	32	34	36	154	665,701	8,830 (2.7)	233

Abbreviations: MPA, marine protected area; t, tonne.

[a]Area and depth statistics were derived from the Marine Gazetteer (**http://www.marineregions.org/gazetteer.php**).

[b]Numbers of seamounts were derived from Yesson et al. (2011).

[c]Productivity data were derived from remote sensing data on chlorophyll using the vertically generalized production model (VGPM) of Behrenfeld & Falkowski (1997) for 2005, which had a multivariate El Niño–Southern Oscillation index relatively close to zero. MODIS-AQUA satellite chlorophyll concentrations, MODIS-AQUA sea-surface temperature data, and MODIS cloud-corrected incident daily photosynthetically active radiation were used as inputs.

[d]Annual fishery catch data were estimated using the Sea Around Us database (**http://www.seaaroundus.org**). Fishery catches and fishing effort data were derived primarily from the UN Food and Agriculture Organization database (**http://www.fao.org/fishery/statistics**). These data were then mapped to a grid of 30-ft-by-30-ft spatial cells using a rule-based approach based on original spatial information, the operation of fleets in the exclusive economic zones of maritime countries (e.g., through documented access agreements), and the known habitat-driven distribution of the reported marine taxa (Watson et al. 2004).

[e]Total area of each sea that is in an MPA, along with the percentage of that sea's total area that is in an MPA.

[f]Number of publications in Web of Science from 1970 to 2012 resulting from a search of the sea name in quotation marks (e.g., "Caribbean Sea") as of October 11, 2012.

studied extensively by Australian and French scientists but ranks only fifth in research output. The Andaman Sea has now overtaken the Coral Sea in terms of research output, and the knowledge base is growing fastest in the Andaman, Caribbean, Philippine, and South China Seas. For comparison, the North Sea, which is the most studied marginal sea in the world and is similar in size to the TMSs reviewed here (750,000 km²), has had more than three times the research output of the SCS (17,535 publications for the North Sea compared with 5,099 for the SCS). However, the annual research output is growing more rapidly for the SCS: In the 1970s, the North Sea had 20 times more publications annually than the SCS did, but since 2000 it has had only twice as many.

TMSs vary in size from 332,871 km² (the Sulu Sea) to 5,710,564 km² (the Philippine Sea) (**Table 1**). By definition, TMSs are characterized by the presence of archipelagos, seamount chains, coral reef systems, and ocean ridges, all of which influence oceanographic and ecosystem processes as well as biodiversity. The Philippine Sea is dominated by abyssal habitats (90% of its area is >2,000 m in depth); includes the deepest point in the ocean, the Mariana Trench; and has 2,170 seamounts peaking within 2,000 m of the sea surface (Yesson et al. 2011). By contrast, the SCS is predominantly shallow, with 49% of its area at <200 m depth. The TMSs in the Indonesian region are critical to the Earth's climate system because the Indonesian Throughflow connects waters of the Pacific and Indian Oceans and plays an important role in global thermohaline circulation (Sprintall et al. 2009). The Coral and Philippine Seas enclose the complex partition of the westward

THE CORAL TRIANGLE INITIATIVE

The Coral Triangle Initiative, first suggested by Indonesian president Susilo Bambang Yudhoyono in 2006, was endorsed in 2007 by the Association of Southeast Asian Nations and has the following goals:

1. Design and effectively manage priority seascapes
2. Fully apply an ecosystem approach to the management of fisheries and other marine resources
3. Establish and effectively manage marine protected areas
4. Achieve climate change adaptation measures
5. Improve the status of threatened species

Pacific flows between the equator and the western boundary currents. Further flow trajectories to and from the equator (and the Pacific–Indian throughflow) pass through the Solomon, Bismarck, South China, Sulu, Celebes, and Molucca Seas. The Caribbean Sea provides the source waters for the Gulf Stream. Finally, the Andaman Sea represents a more limited regional circulation system adjoining the Indian Ocean (for current trajectories, see Tomczak & Godfrey 1994). TMSs in Southeast Asia have the warmest sea-surface temperatures in the ocean (>30°C) and are warming rapidly (Lough 2012). TMSs are generally oligotrophic, with primary productivity ranging from 79 to 222 g C m^{-2} y^{-1} (**Table 1**). No TMS has an area of active upwelling, but many have large tropical rivers that introduce terrigenous materials and local stratification.

The Coral Triangle (which includes all or portions of the Banda, Bismarck, Celebes, Molucca, Philippine, Solomon, and Sulu Seas) is the global center of marine biodiversity (Burke et al. 2011), despite comprising predominately oligotrophic seas. This region is defined primarily by high species diversity of corals (almost 600) and reef fish (>2,000) (Veron et al. 2011), and it contains 76% of the world's coral species and a number of endemics of various coral reef taxa. Southeast Asian coral reefs, most of which are found within Indonesian TMSs, comprise 34% of the world's coral reefs (hosting 600 species of hard corals and 1,300 species of reef-associated fishes). This biodiversity is particularly vulnerable to climate change because many species are near their thermal maxima (Tewksbury et al. 2008), and as oceans warm, species will need to either move large distances to remain within their current thermal preferences (Burrows et al. 2011) or adapt to warmer temperatures. TMSs also have important demersal (multispecies trawl) and pelagic (tuna and billfish) fisheries critical for the food security of many nations (GESAMP & Advis. Comm. Prot. Sea 2001). The Coral Triangle Initiative recognizes this area as a global priority for biodiversity conservation (see sidebar The Coral Triangle Initiative).

We have estimated primary production and fishery catches of each TMS using protocols described in **Table 1**. Although these protocols make various assumptions and include implicit errors, they are the only means available to present comparable data for all TMSs. Fishery catches scale with primary production, with the exception of the seas with the two highest catches: the SCS [7 megatonnes (Mt)] and the Philippine Sea (2 Mt) (**Table 1**). The SCS is the shallowest TMS, with 49% of the total area at <200 m depth and within reach of demersal trawlers. Conversely, the Philippine Sea is the deepest TMS and has the lowest primary production, though it has the most seamounts (**Table 1**). The Caribbean Sea yielded a total commercial catch of only 376,000 t, approximately 1/20th that of the SCS, despite the two seas being similar in geographic area, in part because only 14% of the Caribbean Sea is <200 m in depth. Fishery catches increased in all TMSs from 1950 to 2006, but the greatest increases have been in the SCS and the Philippine Sea (**Figure 1*c***).

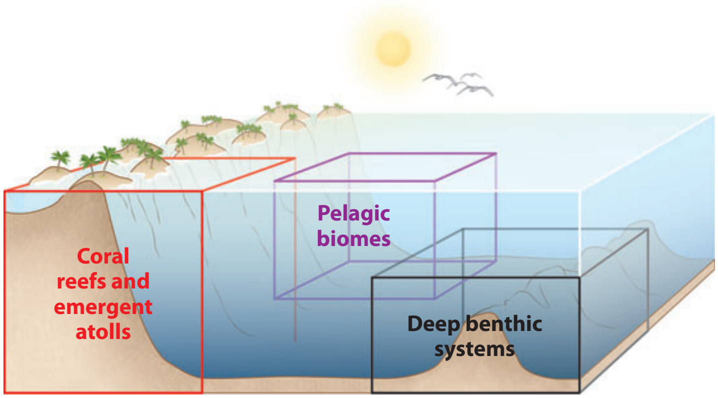

Figure 2

Spatial context of the three major biomes of tropical marginal seas: coral reefs and emergent atolls, deep benthic systems, and pelagic biomes.

KEY HABITATS AND THEIR DRIVERS

Here, we focus on three key ecosystem types—coral reefs and emergent atolls, deep benthic systems, and pelagic biomes (**Figure 2**)—to summarize drivers of biodiversity and ecosystem function in TMSs that are most relevant for management along with the threats to these drivers. These ecosystems do not exist in isolation; each is linked to the others via exchange of biota and materials and is exposed to the same climatic (oceanographic) forcing, although they may be subject to different threats. For instance, charismatic megafauna such as turtles utilize coral cays to breed yet range widely in the open sea, requiring conservation at multiple spatial scales (Wallace et al. 2011), and epipelagic fishes and megafauna "raid the larder" presented by rich seamount communities (Pitcher & Bulman 2007), highlighting linkages between benthic and pelagic ecosystems.

Coral Reefs and Emergent Atolls

Coral reefs are the most biodiverse of all marine ecosystems; although they occupy <1% of the ocean's surface area, they host 25% of marine species (Knowlton et al. 2010). Corals and coral reef fish reach a peak of biodiversity in the Indo-Australian archipelago as a result of the combined effects of geological history that have led to a proliferation of relatively recent habitats (Cowman & Bellwood 2013) and overlapping species ranges (mid-domain effect) (Bellwood et al. 2005). Globally, the largest coral reef complexes are located along the continental shelf of eastern Australia (the Great Barrier Reef), in the Caribbean, and in Southeast Asia, and most of these reefs are close to coastlines.

Beyond the continental shelves of bordering nations, TMS coral reefs usually occur in isolated oceanic settings, providing islands of structure and productivity in otherwise relatively featureless and nutrient-poor habitats. These oceanic reefs are therefore biodiversity hot spots and dispersal stepping stones within individual TMSs, often attracting aggregations of marine megafauna (**Figure 3**). Oceanic coral reefs are strongly coupled to atmospheric forcing through mixing induced by surface waves and swell (Lowe et al. 2005) and via strong diurnal insolation cycles and accompanying cycles in photosynthesis and modification of local water chemistry (Anthony et al. 2011). Dissipation of wave energy and wave-induced currents drive nutrient uptake by benthic communities (Zhang et al. 2011), but extreme wave events, generally associated with

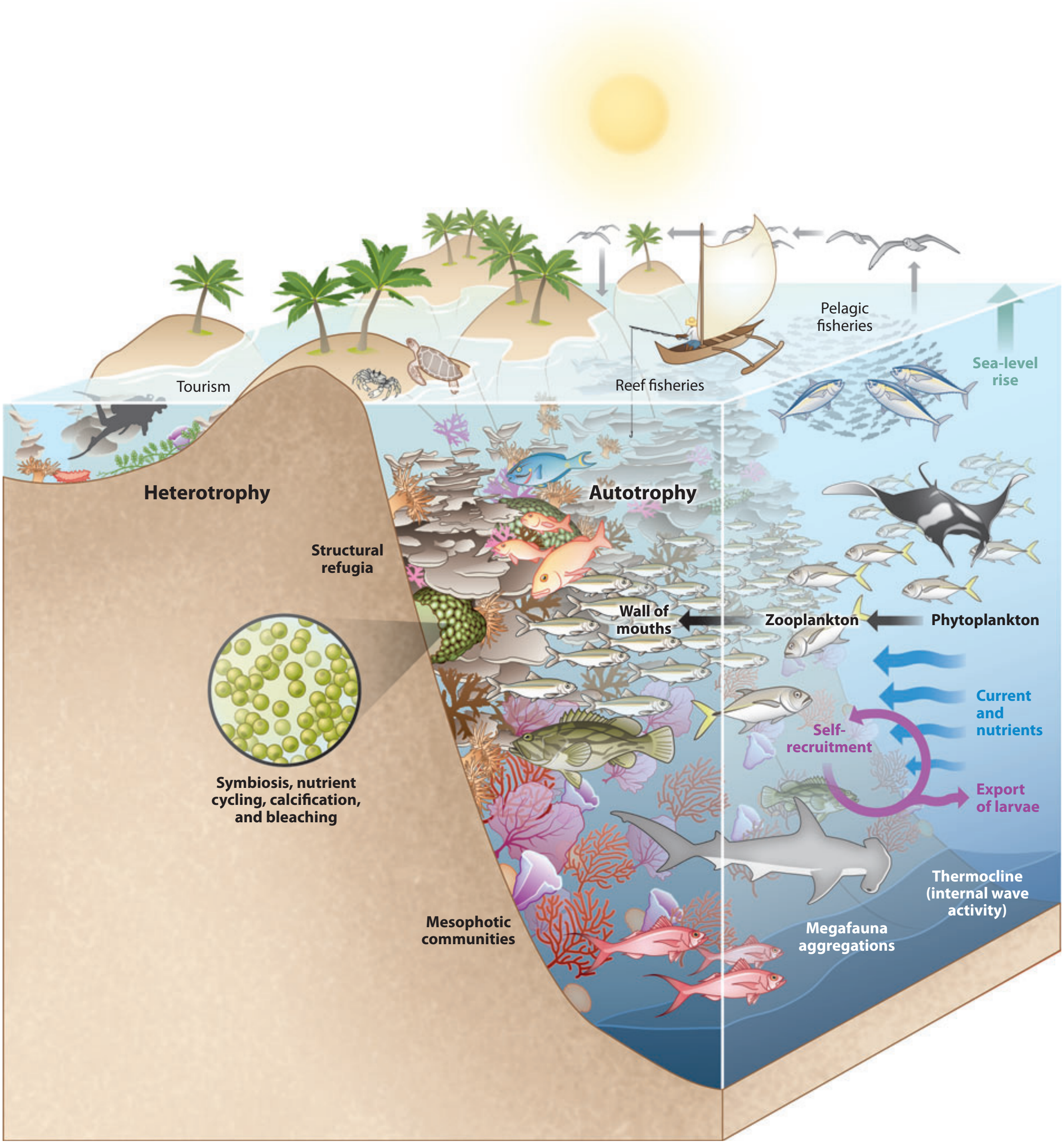

Figure 3

Biodiversity assets and ecosystem processes of coral reefs and emergent atolls in tropical marginal seas. See **Figure 2** for spatial context.

tropical storms, cause mechanical disturbance such as dislodgment of coral colonies and scouring of sediments (Massel & Done 1993, Fabricius et al. 2008). Isolated reefs generate large reef-scale lee eddies that enhance local water residence times and facilitate self-seeding.

Coral reefs grow through calcification by reef-building (scleractinian) corals containing symbiotic zooxanthellae. Symbiosis is critical to the growth of hard and soft corals and other phototrophic organisms such as sponges and ascidians, facilitating the efficient transfer of autotrophic production to host organisms and therefore effectively bypassing respiratory losses imposed by trophic transfer (herbivory, carnivory). Mass-transfer theory accounts for the transfer of dilute nutrients from the oligotrophic ocean to the reactive surfaces of benthic autotrophs by the velocity of water impinging on the reef system (Atkinson 2011). In the same way, constant flow brings plankton to a "wall of mouths" on the reef face (Hamner et al. 1988), which comprises communities of benthic suspension feeders and planktivorous fishes that use the complex structure of the reef front as shelter from marauding predatory fishes. Remineralization of nutrients by planktivores drives autotrophic production on the reef fronts and reef flats, whereas these nutrients are exhausted on the back reefs, resulting in these areas being predominately heterotrophic (Kinsey 1991). Other sources of nutrients to reef systems include rivers on fringing reefs (Furnas 2003).

Benthic primary production from crustose and turf algae, phototrophic corals, and other sessile invertebrates supports mobile benthic invertebrates and demersal fish, which in turn are prey for larger predators. As a general rule, on coral reefs herbivorous fish facilitate the competitive dominance of corals over algae (Hughes et al. 2007). Oceanic reefs in TMSs have lower coral cover and species diversity than reefs in shallower waters, and they may be more vulnerable to warmer ocean temperatures than reefs routinely exposed to greater temperature ranges. These reefs may be less resilient to disturbances, as they must rely on self-recruitment to a greater extent than larger and more well-connected reef systems (Graham et al. 2006).

Some oceanic reefs have associated sand islands that provide resting places and rookeries for migrating seabirds and turtles. Seabird guano contributes seeds and nutrients, increasing the likelihood of plant development. Vegetation on oceanic cays is typically dominated by pioneer species adapted to harsh environmental conditions (Ceccarelli et al. 2013). The species composition of flora influences species of seabirds able to use the cays for nesting and rearing chicks. Seabirds create an effective link between marine and terrestrial systems (McCauley et al. 2012) as they feed on pelagic fish, disturb the vegetation of the cays through their nesting activities, and deposit guano and carrion that in turn increase nutrient flow into surrounding waters. Climate and oceanography affect the growth and survival of terrestrial plant communities, the timing and success of migrations and nesting, and the abundance and distribution of the forage fish that seabirds prey on.

Mesophotic coral reefs occur at depths of 30–150 m. These are increasingly recognized as important refugia for shallow-water coral communities under threat from bleaching and storm damage (Lesser et al. 2009). The extent of these ecosystems may currently be greatly underestimated, but it can be predicted from high-quality bathymetry (Bridge et al. 2012). As light diminishes with depth, the dominance of autotrophs gradually transitions to the dominance of filter-feeding heterotrophs at 75–140 m.

TMSs have the largest number of threatened coral reef ecosystems in the world, primarily because of exploitation by high-density human populations that favor destructive fishing practices such as poisoning and dynamite fishing (Burke et al. 2011). Coastal regions of TMSs are also subject to sedimentation, eutrophication, and climate effects such as warming and the associated coral bleaching, acidification, sea-level rise, and hurricane/cyclone damage (Wilkinson 2008, Miloslavich et al. 2010, Hoegh-Guldberg 2011). These threats affect coral reefs in all TMSs, though the oceanic reef systems farthest from the region's coasts and islands may be largely pristine (e.g., Coral Sea reefs). The increasing wealth of China is driving demand for high-value reef fish, shark fins, and shellfish, resulting in pronounced changes in coastal livelihoods throughout Southeast Asia (Fabinyi et al. 2012). There has been a 30–60% loss of seagrass habitats and >50% loss of mangroves, increasing the vulnerability of coastlines to tsunamis and cyclones (Wilkinson 2008). Fish constitute 27.8% of the animal protein in the total human diet (GESAMP & Advis. Comm. Prot. Sea 2001) but 60–70% in the diets of countries reliant on TMSs, such as the Philippines, Indonesia, and Malaysia (DeVantier et al. 2004). Fisheries in TMSs, especially on Southeast Asian coral reefs, are either at maximum levels of exploitation or overfished (Swartz et al. 2010). Pest species such as crown-of-thorns starfish in the Indo-Pacific (Wilkinson 2008) and ornamental reef fishes (Semmens et al. 2004) and lionfish (Frazer et al. 2012) in the Caribbean perturb coral reefs.

Apart from the management of coral reef fisheries and climate change mitigation, the establishment of spatial management practices such as MPAs has been a successful conservation method for many coral reefs (Graham et al. 2011). Oceanic coral reefs are spatially discrete—more so than large, interconnected continental shelf or fringing reefs—and their largely self-seeding nature (Graham et al. 2006) means that connectivity to other reefs may be of lower priority than the individual coral reef complexes themselves. EBSA principles are useful in identifying areas worthy of protection, but TMS coral reefs are usually hot spots of biodiversity by virtue of being islands of complexity in otherwise relatively featureless oceanic settings. This would automatically identify all TMS coral reefs as EBSAs, raising the issue of how to choose which reefs might be more deserving of EBSA status than others. A possible solution to this problem may lie in the approach used by the Representative Areas Program to create a zoning system for the multiple-use Great Barrier Reef Marine Park. This marine park is widely considered the most sophisticated and extensively implemented example of marine zoning (Ruckelshaus et al. 2008, McCook et al. 2010). Under this program, roughly one-third of the park was zoned as a no-take area. More important, the park was divided into 70 bioregions based on existing biological and geomorphological knowledge, and the program achieved protection for 20% of each bioregion (Fernandes et al. 2005). Many TMSs are large enough to allow scope for bioregionalization (knowledge gaps notwithstanding), presenting an opportunity for a more stratified application of the EBSA criteria to TMS coral reefs. Under this model, representative coral reefs within each TMS subregion might be chosen as significant areas for conservation and management.

Deep Benthic Systems

Deep benthic systems make up the largest areas of almost all TMSs but remain relatively unsurveyed compared with shallow-water systems. Unsurprisingly, there are many gaps in knowledge of biological composition and structure and connectivity between communities, especially at fine taxonomic and spatial scales. However, general patterns can be determined from characteristics shared between TMSs and other deep systems and from reviews of some TMSs, e.g., the Coral Sea (Young et al. 2012).

The characteristically complex geomorphology of TMSs (**Figure 4**, **Table 1**) is described by bathymetric data sets available at a global scale (e.g., the General Bathymetric Chart of the Oceans; **http://www.gebco.net**), and seabed geomorphic features have been widely used as fine-spatial-scale surrogates of benthic biodiversity (e.g., Anderson et al. 2011, Harris & Baker 2011). Seabed feature maps provide underlays for many spatial analyses based on EBSA criteria; for example, a predictive global mapping of seamounts and their depth ranges (Yesson et al. 2011) enables the numbers, locations, and depth ranges of seamounts to be estimated for all TMSs.

Similarly, knowledge of depth-related patterns in biodiversity distribution and physical environmental parameters helps researchers understand and evaluate deep-sea diversity and productivity in relation to EBSA criteria. The interaction of oceanic currents with seamount, plateau,

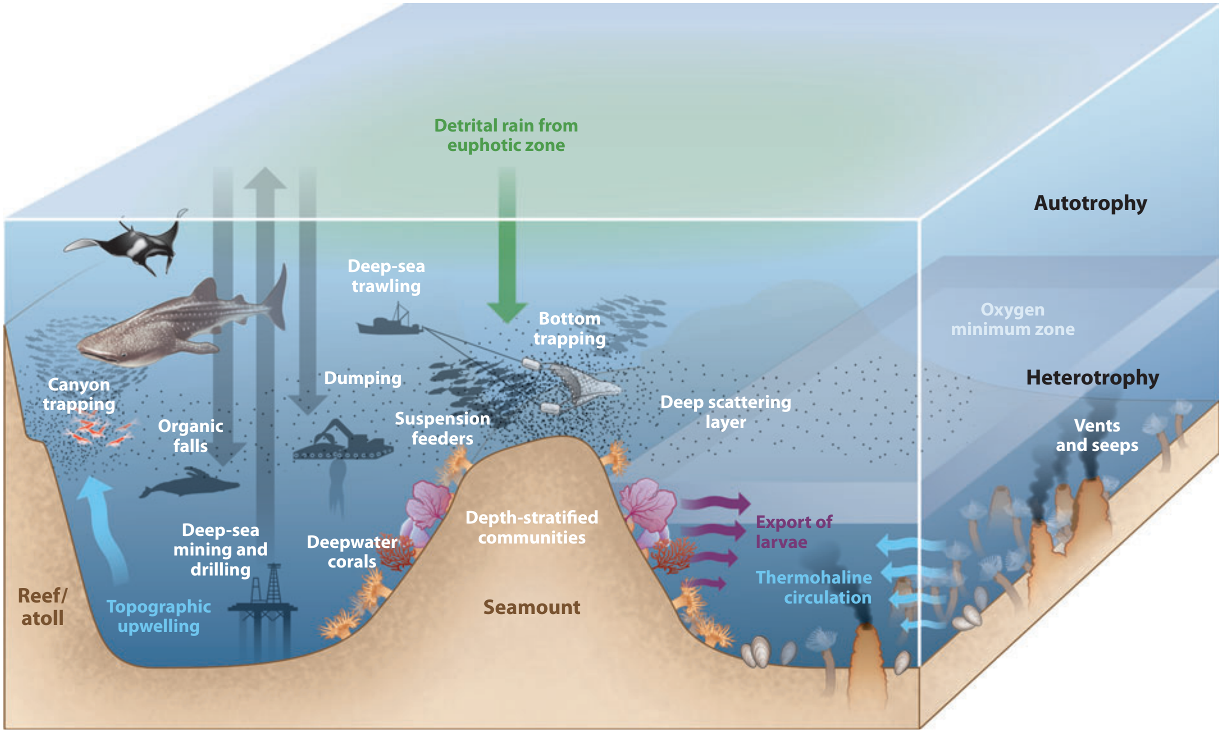

Figure 4

Biodiversity assets and ecosystem processes of deep benthic systems in tropical marginal seas. See **Figure 2** for spatial context.

and island topography gives rise to a large spectrum of effects and processes that influence the surrounding ocean (Roden 1987). These include amplification of tidal currents and resonant excitation of seamount-trapped waves through tidal forcing; baroclinic instabilities and eddy generation, with associated perturbations of density surfaces; the potential creation of Taylor column/cap formations; and the generation of internal waves (White & Mohn 2004). Most of these processes alter background turbulence levels and enhance vertical mixing, altering vertical fluxes of heat, momentum, nutrients, and biological material.

Beneath the euphotic zone (~200 m), the rain of detritus forms the primary source of energy for deepwater organisms, the only exception being chemoautotrophs associated with hydrothermal vents and cold seeps. At intermediate depths (200–2,000 m) on continental margins and seamounts, the interaction of vertical structure in the water column arising from hydrographic structure, oxygen minimum zones, and the interaction of different water masses forms "benthic layer cakes" of community structure (Levin & Sibuet 2012). Submarine canyons entrain and channel detrital export from continental margins, forming productive and diverse benthic communities (De Leo et al. 2010) and aggregations of micronekton and fish (Genin 2004). These in turn may attract tuna (Morato et al. 2010) and megafauna (Rennie et al. 2009). Some seamounts represent oases of biomass in the deep sea (Rowden et al. 2010), and seamount chains may be stepping stones for the dispersal of benthic organisms. Vertically migrating zooplankton and micronekton may have their downward migrations intercepted by seamounts, falling prey to benthic predators (Genin 2004), though Hirch & Christiansen (2010) found that the horizontal advection of smaller zooplankton is a more important food source. As is the case for shallow-water benthic systems, fluxes of allochthonous carbon from currents impinging on seamounts may provide the trophic subsidy necessary to sustain these biodiverse habitats in oligotrophic waters. Accumulations of long-lived fishes (such as pelagic armorheads) reliant on allochthonous plankton can result in large biomasses on seamounts in a storage effect that is easily disrupted by fishing (e.g., Somerton & Kikkawa 1992).

Bathyal and abyssal regions have low biomass and productivity because the organic supply declines exponentially with depth and the temperatures tend to be $<5°C$. Episodic import of organic material through sunken wood, whale falls, and even dumping of livestock carcasses can form hot spots of scavenger/decomposer activity that may last for years (Lundsten et al. 2010). Habitat heterogeneity also diminishes with depth, resulting in the tendency for organisms to use one another as substrates (Buhl-Mortensen et al. 2010). Despite this, the biodiversity of the deep sea is now recognized as among the highest on the planet (Ramirez-Llodra et al. 2010), even though trophic roles are limited to suspension feeding, scavenging, detritivory, and carnivory (e.g., Priede et al. 2006).

Human impacts in the deep sea may be long lasting or permanent (Williams et al. 2010). Ramirez-Llodra et al. (2011) showed that the footprint of anthropogenic activity in deep-sea areas is increasingly obvious despite their relatively large separation from human populations, owing to waste disposal, exploitation of deep-sea resources (fishing, oil and gas, pipelines and cables, acoustics), and climate effects (acidification, temperature, hypoxia, nutrients, circulation changes). TMSs have rich oil and gas deposits, and there is increasing exploration for resources such as manganese, cobalt, and methane hydrates. Climate-related threats to deep-sea systems include changes in ocean circulation, changes in the extent of the oxygen minimum layer (Stramma et al. 2008), and productivity-related changes to the supply of particulate matter from the euphotic zone.

Deep-sea areas are often recognized as having vulnerable and fragile biota and as potentially being spawning areas for a number of fish species, characteristics that they share with tropical coral reefs. Dunstan et al. (2011) used a formalized process of applying data on seamounts to EBSA criteria to identify a subset of southwest Pacific seamounts that best satisfied the criteria within a defined boundary. This worked example used the seamount map underlying the South Pacific area in conjunction with other published data sets to identify possible sites of unique or rare species (using seamount depth and predicted presence of vent communities as a surrogate), spawning sites of deepwater fishes (as an indicator for importance to life history stages), and habitat suitability for stony corals (as a surrogate for vulnerability) (Davies & Guinotte 2011). Naturalness could be estimated from overlays of bottom trawling effort on seamount locations, and biological productivity could be estimated from particulate organic carbon flux (Lutz et al. 2007). Similar analyses could be conducted for seamounts within TMSs and extended to other deep benthic systems.

Pelagic Biomes

Most of the TMSs reviewed here are located in Longhurst's (2007) Sunda-Arafura Shelves (SUND) province, in which there is a well-defined, nutrient-depleted mixed layer 30–90 m in depth (20–40 m in the Caribbean) and a nutricline coincident with the thermocline (**Figure 5**). Vertical profiles of phytoplankton biomass have low concentrations near the surface and a well-defined subsurface chlorophyll maximum layer embedded within the upper thermocline. Phytoplankton populations in TMSs are dominated by very small unicellular cyanobacteria [*Synechococcus* spp. (~1.5 μm) and *Prochlorococcus* spp. (~0.6 μm)] as well as eukaryotic algae in the picoplankton (<2 μm) size fraction (Vaulot et al. 2008). Populations of these groups are relatively stable in oceanic waters because mortality rates from protistan grazing (the microbial loop; Fenchel 2008) and viral infections (the viral shunt; Suttle 2005) are of similar magnitude to growth rates. There is also a highly diverse assemblage of microplankton >10 μm in size comprising diatoms,

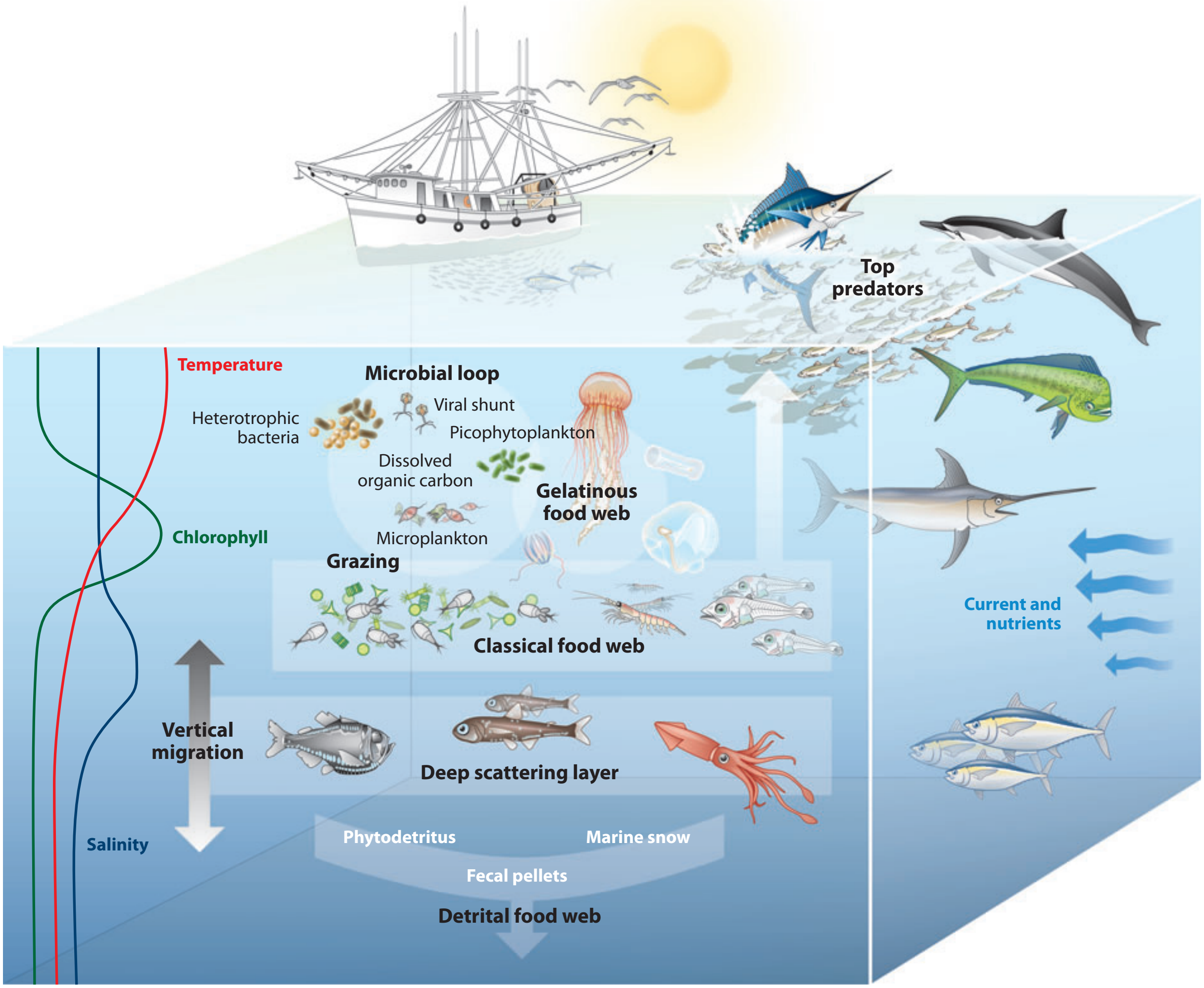

Figure 5

Biodiversity assets and ecosystem processes of pelagic biomes in tropical marginal seas. See **Figure 2** for spatial context.

dinoflagellates, and flagellates that can rapidly increase in abundance as a result of the introduction of new nutrients from upwelling around fronts and mesoscale eddies, as well as from the interaction of currents with topographic features (Young et al. 2011).

TMS pelagic ecosystems comprise a complex series of food webs that link phytoplankton, zooplankton, micronekton, and midtrophic species to top predators (**Figure 5**). Lower trophic levels are characterized by the microbial loop, the gelatinous (or jelly) food web, classical food webs based on microplankton, and detrital food webs. All operate in parallel, but the balance changes depending on the physical oceanographic regime and the occurrence of disturbance events. Under typical oligotrophic conditions, the microbial and gelatinous food webs predominate. Because picoplankton are responsible for most primary production (e.g., Furnas & Mitchell 1996), protistan grazers (e.g., ciliates) account for most grazing and nutrient recycling, but gelatinous grazers such as larvaceans, salps, doliolids, and pyrosomes also graze these small cells. Gelatinous predators such as ctenophores and narcomedusae recycle some of this energy within the gelatinous food web. When new nutrients are introduced via vertical mixing across the thermocline, the so-called classical food web can become important. In these conditions, photosynthetic microplankton can undergo pulses of growth that provide greater food availability for mesozooplankton such as copepods, which in turn are prey for visual predators such as fish larvae, resulting in increased transfer of energy to higher trophic levels. The classical food web is connected to the microbial and gelatinous food webs via the detrital food web, which has several components. First, in the epipelagic zone, organic aggregates are formed from coagulation of sticky diatoms, discarded larvacean houses, and other organics (Lampitt et al. 1993), providing a substrate for bacterial growth and trapping picoplankton (Richardson & Jackson 2007). These aggregates are of a size available to mesozooplankton grazers. Second, detrital particles raining out of the epipelagic zone are an important food source for mesopelagic zooplankton (Steinberg et al. 2008) and for vertebrate detritivores such as eel leptocephali that feed mainly on larvacean houses (Miller 2009).

These complex relationships in lower trophic levels support a range of macrozooplankton (<2 cm) and micronekton (2–20 cm) composed of fish, squid, crustacean, and gelatinous species recognizable in acoustic cross sections of the water column to approximately 500 m (Kloser et al. 2009). In TMS pelagic waters, these species form the main prey of larger midtrophic predators [e.g., albacore (*Thunnus alalunga*), dolphinfish (*Coryphaena hippurus*)] and top predators (e.g., larger tunas, sharks, and billfish; see Young et al. 2010). Competition is avoided through niche separation. For example, small albacore feed on crustacea, and large albacore and swordfish (*Xiphias gladius*) feed mainly on squid, whereas other tuna species, dolphinfish, and striped marlin (*Kajikia audax*) feed mainly on fish (Young et al. 2010). Where prey overlaps exist between predators, they feed either at different times or at different depths. In some TMSs, marine mammals such as pilot and beaked whales are the apex predators in pelagic food webs (McPherson & Nishida 2010). Where the transfer of energy from lower trophic levels occurs through only a few key midtrophic species, a bottleneck known as wasp-waist control can occur (Bakun 2003). In the Coral Sea, top predators represent only 1% of total pelagic biomass, with midtrophic "waist" species accounting for much of this biomass (Griffiths et al. 2010). At seamounts, seasonal pulses of myctophid aggregations contribute to the diets of a range of tuna and billfish (Flynn & Paxton 2012). As much as 10% of tuna species' annual consumption can occur closer to shore, particularly around reefs, and juvenile tuna take as much as a third of their prey from reef-associated organisms (Griffiths et al. 2007, Allain et al. 2012).

Top oceanic predators such as tunas and billfish are spawned in oligotrophic seas (Farley & Davis 1998, Kopf et al. 2012), apparently to avoid predation (Bakun 2003). Accordingly, it comes as no surprise that a major component of the diets of larval tuna consists of larvaceans (Young & Davis 1990, Sampey et al. 2007, Llopiz et al. 2010), which are capable of feeding on picoplankton. Density-dependent growth in these larvae underlines the close relationship between available prey and their survival (Jenkins et al. 1991), and their low abundance in the oligotrophic regions of TMS renders them less susceptible to predation (Bakun 2006).

The largest issue for the management of TMS pelagic ecosystems concerns fishery resources, particularly those relating to pelagic species in transboundary areas, though plastic pollution is an emerging problem (Andrady 2011). Even in the productive seas of Southeast Asia (including the SCS), offshore fishery resources are threatened by the competitive rather than cooperative fishing practices used by countries sharing the resources, and greatly improved regional cooperation will be necessary if fisheries are to survive (Kang 2006). This problem is exacerbated by the migration of fishing effort from the industrialized countries to the developing world

(Worm et al. 2009), threatening local food security and biodiversity. The pressure on fisheries for large pelagic species is well known (Worm et al. 2009), but most fishery collapses have in fact been for small, low-trophic-level species (Pinsky et al. 2011). Improving knowledge of the ecosystem processes supporting high-value pelagic fisheries in TMSs is critical, but these are driven largely by oceanographic processes, for which climate change may be the greatest threat (Brown et al. 2010). Where key oceanographic processes are associated with specific areas, spatial management based on time-series data can be applied to identify areas of interest (Grantham et al. 2011), but otherwise the only management action possible is through climate change mitigation. For higher trophic levels, the identification of "fisheries-conservation hotspots" (Worm & Branch 2012) is a priority to ensure fishery sustainability, an example of which is the black marlin spawning area in the Coral Sea (Domeier & Speare 2012). Nevertheless, recognition of EBSAs and the subsequent development of spatial management is challenged by the mobility of key organisms and the dynamic nature of the pelagic environment (Game et al. 2009, Trebilco et al. 2011). In the pelagic ecosystems of TMSs, therefore, fishery management strategies such as those applied to tuna may be more appropriate (e.g., Williams & Terawasi 2008), and binding management actions involving more than just neighboring states will be necessary.

THE UTILITY OF AN EBSA APPROACH TO TROPICAL MARGINAL SEAS

EBSA criteria identify the key biological and ecological habitats that are most significant in terms of biodiversity, ecological processes, and naturalness. The identification of EBSAs within TMSs would provide a common framework for discussing the importance of these areas, the pressures that are impacting EBSAs, and the options for managing these areas. Within each EBSA, an ecosystem-based management approach could include a mix of spatial and nonspatial approaches and tools, including multiple use and zoning, the establishment of MPAs, and agreement on fishery closures, controls, and offsets. For MPAs to be effective, socioeconomic factors are critically important, and stakeholder communities must be actively involved and supportive (Russ & Alcala 1999). However, MPAs are not appropriate means for managing all threats to marine systems, such as invasive species or the effects of pollution (Kearney et al. 2012). We now have a reasonable understanding of the identity, if not the magnitude, of the major energy flows through representative ecosystems and can identify areas of high productivity (**Figures 3–5**; **Table 2**, criterion 5). The high biodiversity of TMSs is due mainly to the presence of coral reefs, which are therefore obvious candidates for EBSAs (**Table 2**, criterion 6). Similarly, seamounts, vents, and seeps are ideal candidates for EBSAs in the deep sea owing to their vulnerability and fragility (**Table 2**, criterion 4), though biodiversity hot spots such as vents and seeps can be ephemeral (Ramirez-Llodra et al. 2010). Apparently, productive resources such as the fish populations associated with seamounts are sensitive to exploitation because of their life history characteristics (Morato & Clark 2007). Further, all TMSs contain breeding grounds for threatened, endangered, and commercially important species, satisfying criteria on life history and threatened and endangered species (**Table 2**, criteria 2 and 3). The one criterion that all TMSs will struggle to meet, as a consequence of their proximity to human activity, is naturalness (**Table 2**, criterion 7).

The large populations of nations bordering TMSs, their dependence on the ocean for food security and livelihoods, and often depleted fisheries make the management of TMSs a challenge for future generations. The Indonesian Sea large marine ecosystem (LME) is managed by only one country, yet the same conflicts and management failures have occurred there as in other LMEs managed by multiple countries, e.g., the Caribbean Sea LME (Sherman & Hempel 2008). The governance system emerging in the Coral Triangle provides a template for regional collaboration

LME: large marine ecosystem

Table 2 Template for identifying ecologically and biologically significant areas within the three representative ecosystems of tropical marginal seas

Criterion	Coral reefs and emergent atolls	Deep benthic systems	Pelagic biomes
1. Uniqueness or rarity	Coral reefs with unusual biodiversity Habitats for threatened species	Isolated seamounts or seamount chains Hydrothermal vents and cold seeps	Areas visited on a recurrent basis by charismatic megafauna such as manta rays, whale sharks, and beaked whales
2. Special importance for life history stages of species	Sea turtle nesting sites Seabird rookeries Areas of recurrent spawning or feeding aggregations	Spawning on seamounts of many otherwise widespread demersal species	Feeding grounds Nursery grounds Sites of spawning aggregations
3. Importance for threatened, endangered, or declining species and/or habitats	Areas likely to be resilient to climate change Refugia for overfished species	Waypoints for migrating species Locations for threatened, endangered, and protected species	Migration corridors Areas important for seabird feeding
4. Vulnerability, fragility, sensitivity, or slow recovery	Areas prone to bleaching Areas with high exposure to storm damage	Locations with high proportions of fragile, benthic species (e.g., corals and sponges)	Locations that may be vulnerable to rapid changes in sea-surface temperature and ocean acidification
5. Biological productivity	High-productivity areas arising from topographically forced intrusion of nutrient-rich deep water	Areas of high species biomass Areas of high productivity (e.g., over seamounts, vents, and seeps)	Areas of localized upwelling or mixing responsible for increased productivity
6. Biological diversity	Regions with extensive interconnected reefs Isolated oceanic atolls with lower diversity	Areas of high geomorphic complexity (e.g., canyons and seamounts)	Large-scale ecoregions that have high diversity
7. Naturalness	Relict unimpacted areas in heavily impacted tropical marginal seas	Relict unimpacted areas in heavily impacted tropical marginal seas	Relict unimpacted areas in heavily impacted tropical marginal seas

in TMSs with joint jurisdictions, but also points to the many cultural and political differences of the peoples sharing responsibility for the region (Fidelman & Ekstrom 2012). The effective management of TMSs in the future would be improved by the recognition of EBSAs by all stakeholders.

SUMMARY POINTS

1. Tropical marginal seas (TMSs) have the highest biodiversity of any marine region. They are surrounded by rapidly developing countries with increasing human populations and demands for ecosystem services. Their effective management is challenged by major knowledge gaps and the need for multicountry management.
2. Most nations with marine jurisdictions have agreed to cooperate to develop management strategies for the conservation and sustainable use of marine biodiversity.
3. Key TMS ecosystems face threats from direct anthropogenic and climate-related impacts, yet the inventory of biodiversity is incomplete and the major processes determining ecosystem function are poorly understood.

4. Ecologically and biologically significant areas (EBSAs) provide an ideal framework for focusing management efforts both within national jurisdictions and in transboundary areas.

FUTURE ISSUES

1. A better understanding of biodiversity and of the drivers of productivity and ecosystem function is needed to underpin management of TMSs.
2. Improved recognition of EBSAs from each major ecosystem within TMSs will help achieve Convention on Biological Diversity goals. New approaches to EBSAs are needed to embrace oligotrophic seas, including the ocean "deserts" critical for the early life history stages of economically important species.
3. It will be important to effectively recognize resources in transboundary areas and mechanisms to overcome socioeconomic issues and differing cultural perspectives on the sustainable use of biodiversity.
4. The development of integrated observational and modeling tools reflecting environmental, social, and economic values will enable evaluation of alternative management strategies in TMSs.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank the Australian Institute of Marine Science and the Commonwealth Scientific and Industrial Research Organisation Wealth from Oceans Flagship for providing funding for two workshops on biodiversity and ecosystem function in the Coral Sea. Fisheries data were provided by the Sea Around Us project at the University of British Columbia, which is supported by Pew Charities. We also thank Franzis Althaus for geographic information system analysis. P.D. and D.G. were supported by the Australian government's National Environmental Research Program (NERP) through the Marine Biodiversity Hub. A.J.R. was supported by Australian Research Council Future Fellowship FT0991722.

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Annual Review of Marine Science

Volume 6, 2014

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Errata

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