NEW ZEALAND MARINE ECOSYSTEM SERVICES

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ABSTRACT: New Zealand's marine realm, including the Territorial Sea, Exclusive Economic Zone (EEZ), and Extended Continental Shelf, totals 5.7 M km^2, an area about 21 times larger than New Zealand's land mass and almost 1.7% of the world's oceans. This enormous area is not uniform, and New Zealand has one of the most diverse ranges of marine habitats on the planet, with a rich and mostly endemic marine flora and fauna that provide at least 12 regulatory services, 5 provisioning services, and 9 non-consumptive services. Based on global estimates, marine ecosystems may provide about two-thirds of the value of services provided by New Zealand ecosystems annually. For instance, provisional estimates based on mapping of surface dissolved CO_2 indicate that the New Zealand EEZ CO_2 sink may be equivalent to about 5% of global ocean CO_2 uptake, and is larger than that of New Zealand forests. In coastal regions terrestrial and marine ecosystems are closely linked. For example, in the Firth of Thames, local rivers contribute about 70% of the nitrogen supply that supports fisheries and aquaculture, with the remainder supplied by upwelling of slope-associated deep water, rich in nutrients, onto the shelf and into the coast. Denitrification processes can remove about 70% of the new nitrogen loaded to the system from land. Wild food support and provision is the ecosystem service that provides species targeted by humans for food. In New Zealand, human utilisation of marine living resources began with the arrival of Māori, increased during European settlement, and continues as one of New Zealand's most significant primary industries with an annual catch of about 480 000 tonnes of fish and invertebrates worth over NZ$1.4 billion. One species, hoki (*Macruronus novaezelandiae*), comprises about 30% of the wild catch. It is very difficult to judge whether New Zealand marine ecosystem services are growing, stable, or declining. In part this is because we know little about the extent of marine habitats, and in part because the more remote and deeper marine ecosystems are difficult and expensive to monitor. Thus, for many habitats we have at best only a short time-series of information with which to judge trends in ecosystem services. Scaling for the size of New Zealand's marine area of responsibility suggests that US$357 billion worth of services may be contributed each year by New Zealand's marine ecosystems. Even if this estimate is out by one or two orders of magnitude it nevertheless suggests that it would be worthwhile to improve measurement and understanding, to safeguard this substantial natural contribution to our well-being.

Key words: aquaculture support and provision, carbon sequestration, climate regulation, non-consumptive services, nutrient cycling, provisioning services, regulatory services, wild food provision and support.

INTRODUCTION

New Zealand's vast marine realm includes ecosystems within the Territorial Sea to 12 nautical miles offshore, the Exclusive Economic Zone (EEZ) that extends to 200 nautical miles offshore, and the extended continental shelf (ECS) that in places stretches well beyond the EEZ (Figure 1). Together they cover a total area of 5.7 million square kilometres, about 21 times larger than New Zealand's land area and almost 1.7% of the world's oceans. They extend from the sea surface to over 10 km depth giving a volume of about 11.4 million cubic kilometres. This enormous area and volume contains one of the most diverse ranges of marine habitats on the planet, and includes a rich and mostly endemic marine flora and fauna – a consequence of New Zealand's geophysical setting, geographical isolation, and history (Gordon et al. 2010). Accordingly, the services provided to New Zealand by this wide variety of ecosystems over an enormous area are both varied and important.

This chapter describes the range of New Zealand marine ecosystems and outlines the services they provide. We provide examples of ecosystems where these services are maximal and also where they operate at minimal levels or do not exist. We also describe in more detail the contribution of five ecosystem services (climate regulation, carbon sequestration, nutrient cycling, wild food provision, and aquaculture support and provision). Finally, we comment on conditions and trends in the levels of marine ecosystem services provided to New Zealand and on interactions between terrestrial and marine ecosystems, and we suggest where more research effort is required to document present levels of service.

NEW ZEALAND MARINE ECOSYSTEMS

Ecosystem services provided across the New Zealand marine realm vary considerably depending on the type of ecosystem – different habitats, species and communities combine to provide different types of ecosystem service. So, before examining the services they provide, we consider the diversity and extent of New Zealand marine ecosystems and highlight how much remains to be understood about these varied ecosystems.

There is no single agreed list of New Zealand's marine ecosystems as they can be defined in a variety of ways to meet different needs. Over a decade ago, as part of the Environmental Performance Indicator programme, the Ministry for the Environment (MfE) identified the need to develop a classification of marine ecosystems as a means to organise and stratify environmental data and help its interpretation and reporting. MfE commissioned NIWA to advise how ecosystem classification could help marine environmental management and to develop different approaches to classification, including identifying their strengths and weaknesses. The report by Snelder et al. (2001) focused on the classification of marine ecosystems in general, and was not specific to an ecosystem type; instead, its purpose was to provide background information to help environmental managers evaluate ecosystem classification systems for specific applications.

An outcome of this initial report was the New Zealand Marine Environment Classification (MEC). This was defined by Snelder et al. (2005) using multivariate clustering of several spatially explicit data layers (including depth, slope, orbital velocity at the sea floor, mean solar radiation, SST amplitude, SST gradient,

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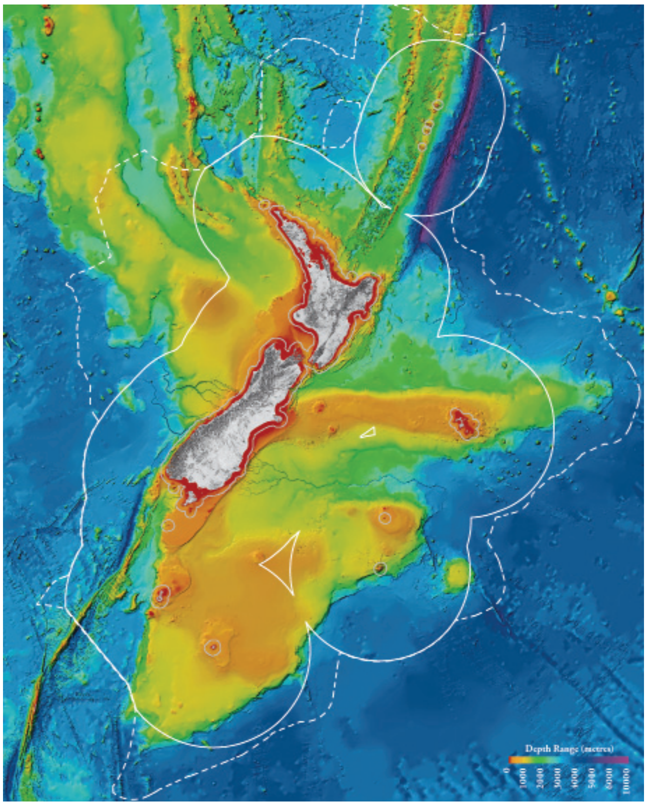

FIGURE 1 The New Zealand region continental mass, seafloor, and areas of responsibility. The solid grey line indicates the outer edge of the territorial sea, the solid white line shows the boundary of the New Zealand Exclusive Economic Zone, the dashed white line indicates the proposed extension to New Zealand's legal continental shelf (ECS). Map adapted from Mitchell et al. (2012).

winter SST, mean tidal current velocity) that described the physical environment. The resulting classification was hierarchical, enabling the user to delineate environmental variation at different levels of detail and a range of associated spatial scales. Snelder et al. (2005) chose a physically based classification because data (or modelled data) were available across the whole New Zealand marine realm and because environmental pattern can be a reasonable surrogate for biological pattern, particularly at larger spatial scales. Large but patchy biological datasets were used to tune the physically-based classes; the resulting 20-level classification maximised discrimination of variation in biological composition at various levels of classification detail from 3 to 290 classes. The classification was not optimised for a specific ecosystem component (e.g. fish communities or individual species) but sought to provide a general classification relevant to a broad range of biological groups (Figure 2a).

Advances in analysing the distribution of organisms and communities opened up new avenues for integrating biological and environmental data to better understand the patterns of occurrence of marine species. Leathwick et al. (2006) demonstrated how spatial analysis using boosted regression trees could provide distribution maps of demersal fish. Fish were chosen because good quality distributional data were available from a series of scientific trawl surveys in deep waters. The overall approach used statistical models to relate the distributions of 122 fish species to a set of environmental variables chosen for their functional relevance. They then combined the statistical models at a resolution of one square kilometre to predict distributions of self-similar assemblages of species (see Figure 2c).

Subsequently, Leathwick et al. (2012) developed a benthic optimised marine environment classification (BOMEC) specifically to identify New Zealand 'bioregions' that can be considered ecologically distinct to some degree (Figure 2b). BOMEC was developed by combining data on the benthic community (over 100 demersal fish species and 7 groups of invertebrates: asteroids, bryozoan, foraminifera, octocorals, polychaetes, scleractinian corals, sponges), and environmental data including sediment type. A multivariate technique for fitting community compositions to environmental data – generalised dissimilarity analysis – was used (Leathwick et al. 2012). BOMEC is restricted to depths less than 3000 metres where reasonable amounts of scientific sampling have been conducted (Leathwick et al. 2012). BOMEC is displayed at the level of 15 bioregions because this provides a broad-scale classification of the EEZ and does not imply any level of statistical differences between regions (Leathwick et al. 2012).

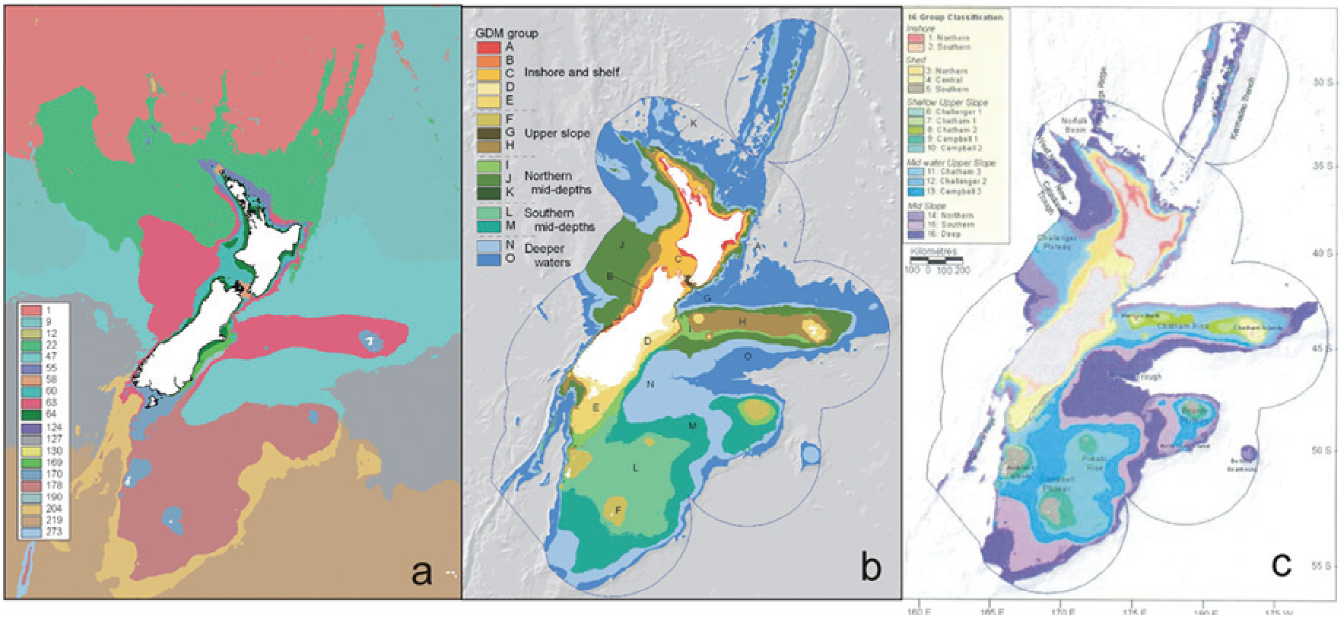

FIGURE 2 Marine environment classifications. **a**, Marine Environment Classification (MEC) at the 20-class level (from Snelder at al. 2005). **b**, Benthic optimised MEC (BOMEC) for 15 groups (from Leathwick et al. 2012). **c**, Demersal fish classification (from Leathwick et al. 2006).

In an assessment of anthropogenic threats to New Zealand marine habitats, MacDiarmid et al. (2012) identified 62 distinct marine habitats within New Zealand's territorial seas and EEZ. They used as a starting point the list of marine habitats developed by Halpern et al. (2007) in a global assessment of anthropogenic impacts on the marine environment, modifying this list by eliminating marine habitats not relevant to New Zealand (e.g. coral reefs and sea ice), adding others particular to New Zealand (e.g. fiord rock walls), and subdividing some habitats into finer categories. For example, rocky intertidal reef was divided into sheltered coasts, exposed coasts, and rocky reefs bordering harbours, because a different suite of threats would affect similar habitats in different areas. The marine habitats MacDiarmid et al. (2012) used were defined by the type of benthic substrate (rock, sand, mud, calcareous rubble, etc.), the dominant biological structural element (saltmarsh, mangrove forest, seagrass, cockle bed, pipi bed, kelp forest, turfing algae, biogenic calcareous reef), or by depth and degree of exposure (harbour, sheltered coast, exposed coast, slope habitats, deepwater habitats).

New Zealand's Department of Conservation and the Ministry of Fisheries used a marine habitat classification system to define 58 habitats in the territorial sea alone. This habitat classification was designed to meet the needs of biodiversity conservation and was based on four depth intervals (intertidal, 0<30 m, 30–200 m, >200 m), seven substrate classes (mud, sand, gravel, undefined substrate, mixed sediment and rock, rock, and biogenic), and three exposure categories (exposed, moderate, sheltered) (DOC and MFish 2011).

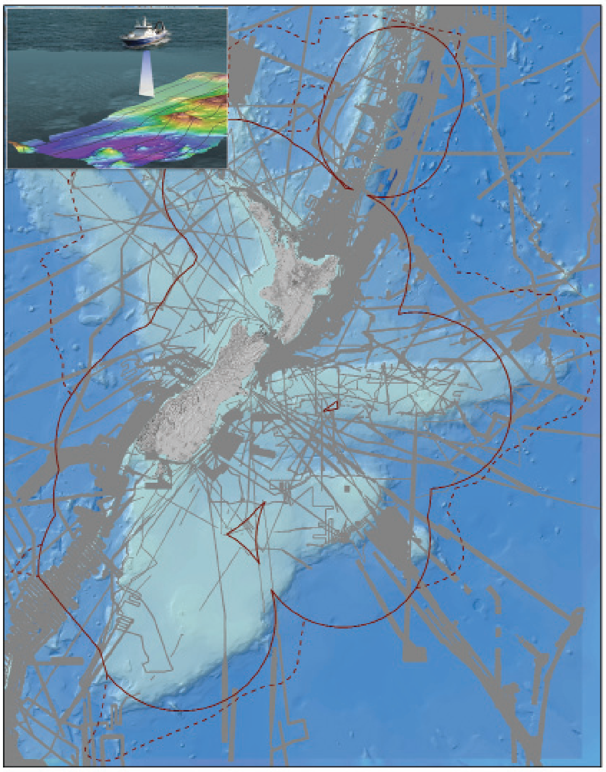

FIGURE 4 Map of the New Zealand Exclusive Economic Zone and Extended Continental Shelf showing the extent of swath mapping coverage. Inset is a cartoon of swath mapping being carried out by the R.V. *Tangaroa*. The swath width is up to seven times the depth of water below the survey vessel, thus swath mapping in deep water is generally faster and less expensive than mapping the same area of seafloor in shallow water.

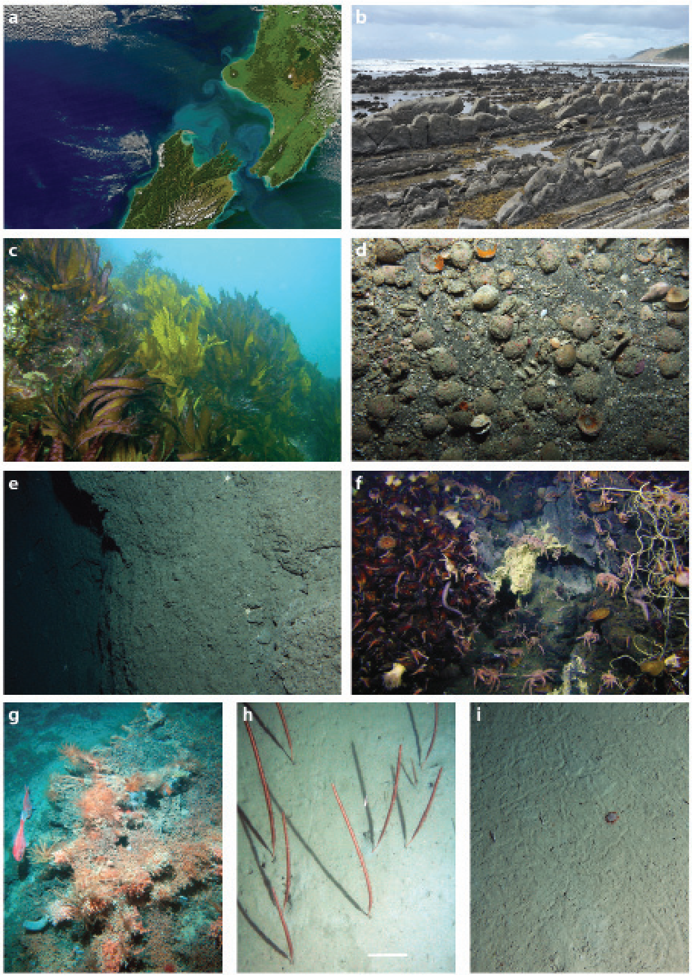

FIGURE 3 Some New Zealand marine ecosystems. **a**, pelagic ecosystems in central New Zealand (Aqua MODIS). **b**, coastal rocky reefs at Mataikona (H. Nelson). **c**, subtidal kelp forest (S. Schiaparelli). **d**, dog cockle beds at 50 m (Trans-Tasman Resources Ltd). **e**, canyon wall (NIWA). **f**, hydrothermal vent and associated bacterial mat, vent mussels, crabs and tube worms on Monowai Seamount – Ring of Fire Expedition 2005 (NOAA-GNS-NIWA). **g**, deep-sea coral bed (NIWA). **h**, sea pen field (NIWA). **i**, abyssal ooze (NIWA).

In summary, in New Zealand's extraordinarily diverse marine environment at least 60 distinct ecosystems can be identified. While physical factors such as depth, temperature, salinity, substrate type, and water movement due to currents and wave action are important in defining ecosystems, biological features can also be critical; examples include levels of primary productivity and the presence of key organisms like kelps and sponges that provide three-dimensional structure for other organisms. Benthic ecosystems (those on the seafloor) include the saltmarsh and mangrove forests that fringe harbours and estuaries, the beaches and rocky reefs that border the coast, steep-sided canyons that notch the edge of the continental shelf, seamounts, and deep-sea abyssal plains and trenches (Figure 3). Pelagic ecosystems (those occupying the water column) are strongly three-dimensional and range from the productive, sunlit photic zone of the upper water column to the dark ocean interior. Some marine ecosystems, such as cold methane seeps and hot hydrothermal vents, though distinct with specialised fauna, cover just a few hectares; others, such as the pelagic ecosystems, cover thousands of square kilometres (Figure 3).

Discovery and mapping of New Zealand's marine habitats is still underway and much of the marine environment and its diverse communities remain poorly charted. We do not have a clear idea of the location and full extent of many common inshore habitats such as subtidal rocky reefs, let alone sea floor habitats in deeper waters. Nevertheless, swath mapping using a multi-beam acoustic system (see inset in Figure 4) offers the opportunity to define seafloor habitats over wide areas, although this must be carried out at the required frequencies to provide finely detailed bathymetry and must collect backscatter data so that surface texture can be defined. To date only about 855 000 square kilometres or 15% of the total area has been swath-mapped to a standard necessary to map benthic habitats (Figure 4). At current rates, full swath mapping of the seafloor in the Territorial Sea, EEZ and ECS will take another 50 years.

MARINE ECOSYSTEM SERVICES

Ecosystem services are defined as 'the direct and indirect benefits that humans receive or value from natural or semi-natural habitats' (Costanza et al. 1997; Daily 1997; Boyd and Banzhaf 2007). A classification of ecosystem services adapted from Townsend and Thrush (2010) recognises three broad groups. Regulatory services represent the capacity of ecological systems to provide favourable conditions for humans by processing material (e.g. climate regulation). Provisioning services represent the tangible resources that humans can extract and utilise (e.g. food and raw materials); these resources are often labelled ecosystem goods. Finally, non-consumptive services represent the capacity of ecological systems to provide humans with intrinsic benefits ranging from recreational opportunities to visual amenity values like landscape and seascape. New Zealand marine ecosystems provide at least 12 regulatory services, 5 provisioning services and 9 non-consumptive services (Tables 1–3, adapted from MacDiarmid et al. 2011).

The 12 widely recognised regulatory services (Table 1) comprise climate regulation, biophysically mediated sediment capture and stabilisation, biologically mediated sediment capture and stabilisation, carbon capture and sequestration, pollutant capture and sequestration, pollutant detoxification, storm surge amelioration, erosion dampening, storage of nutrients, cycling of nutrients, net annual oxygen production, and provision of biogenic habitat material (Costanza et al. 1997; Daily 1997; Boyd and Banzhaf 2007; Armstrong et al. 2012). This classification does not include physical aspects of processes that would continue even if all ecosystem functioning were absent; for example, climate regulation does not include the physical capacity of seawater to absorb and transport heat. We have not included ecosystem resilience or biodiversity here as separate regulatory services because both can be considered to support other services.

The five provisioning services (Table 2) comprise wild food provision, aquaculture support and provision, presently used biological compounds, bacterially enhanced gas and mineral deposits, and biodiversity. The first three of these services include a strong human cultural component. Consequently, what we currently recognise as suitable for exploitation as a provision depends on cultural norms, and these can change. For example, 100 years ago we generally considered whales as providers of high quality oil, but New Zealand now values the non-consumptive services they provide. We have included biodiversity here as a future-proofing service, because this enormous diversity may provide new food, molecules and genes.

Table 3 lists nine non-consumptive services provided by marine ecosystems. Visual amenity values, including the coastal landscape and the broader seascape, are important components of New Zealand's identity as a maritime nation. Important spiritual and inspirational values are provided by the coast and the sea, sometimes to considerable distances offshore (Verschuuren 2007) – in New Zealand, this is particularly true for Māori. The knowledge that marine ecosystems or the biota they support continue to exist and function has value for humans, even if some of these ecosystems are difficult or impossible to visit by most of society. Marine ecosystems also provide places where humans undertake a range of non-consumptive activities; we have divided these into areas supporting coastal non-water recreation such as beach walking and horse riding, and areas supporting water recreation such as surfing and swimming. 'Watchable wildlife' is identified as a separate ecosystem service to people. This includes everything from whales to small fish and invertebrates, watched from land, air, boats, and/or underwater. Increased accessibility to deeper marine habitats via new technology may strongly influence the future definition of this service. Marine ecosystems also support considerable human cognitive activities including educational and scientific research – an ecosystem service close to the authors' hearts! Lastly, marine ecosystems provide marine managers and policymakers with biological indicators of the health or state of marine environments. We have not included tourism as an ecosystem service because it is a socio-cultural activity that draws on the whole range of ecosystem services listed in Tables 1–3.

In defining these 26 ecosystem services we followed the advice of Boyd and Banzhaf (2007) that ecosystem services should be viewed strictly as the ecosystem's contribution, not the human contribution, towards an activity. For example, wild fisheries result from several elements: the ecosystem's sustaining of a range of edible species; the technology that humans develop and use to capture the fish; and the economic resources that society invests to build the boats, the fishing gear and the transport system to take the fish to market. Clearly the marine ecosystem provides only the first of these elements and this, not the technology or enterprise, is the ecosystem service.

The magnitude of the services provided by marine ecosystems is in many cases poorly known. For example, a recent review of the valuation of deep-sea (below 200 m) ecosystem goods and services concluded that for 65% of the services provided by deep-sea habitats little or nothing was currently known about the magnitude of the service (Armstrong et al. 2012). The best understood services tended to be the provisioning services for wild food species and the non-consumptive or cultural services for education and scientific research, and the best understood ecosystems were water column or pelagic habitats.

To help overcome this lack of direct knowledge, we used a general principles approach that links the provision of ecosystem services to the underlying ecosystem processes (Townsend et al. 2011). Using this approach, for each service we provide examples of New Zealand marine ecosystems that lie at the upper and lower end of service provision, and frequently the intermediate levels of service as well (see Tables 1–3). The magnitude of service is assessed per unit area over a year rather than as total area of habitat because the extent of these habitats is poorly known.

CLIMATE REGULATION AND CARBON SEQUESTRATION

The ocean influences climate via a variety of pathways and processes (Figure 5). Large-scale regulation of global temperature occurs through the absorption and transport of heat by thermohaline circulation; as a result, the ocean contains more than 90% of the additional energy retained in the global system between 1961 and 2003 (Bindof et al. 2007). Furthermore, 93% of the earth's carbon dioxide (CO_2) is stored in the oceans, with the deep ocean

TABLE 1 Regulatory services provided by New Zealand marine ecosystems. The magnitude of the provided service is based on per unit area of habitat over a year. Adapted from MacDiarmid et al. (2011)

Regulatory services	**Magnitude**	**Descriptive notes**	**Example ecosystem**
Climate regulation			
This includes contribution to dimethlysulphide production, biological contribution to evapotranspiration, and heat absorbance or reflectance but not carbon sequestration, which is assessed separately. We have not included the physical capacity of seawater to absorb heat.	Trace	Minimal climate regulatory role	Deep benthic habitats
	Low	Very limited climate regulatory role	Offshore, oligotrophic surface waters; pelagic habitats below photic zone
	Medium	Minor though persistent role	Shallow subtidal reefs
	High	Important role	Intertidal reefs
	Extreme	Critical climate regulatory role	Highly productive inshore surface waters and frontal regions in the open ocean. Mangrove forest
Biophysically mediated sediment capture, stabilisation			
Capture of sediment by virtue of shape or density of organisms. Every habitat is likely to have at least a trace of such activity.	Trace	Almost no role in sediment capture	Deep ocean below photic zone
	Low	Very limited role in trapping and stabilising sediments	Hard canyons
	Medium	Minor though persistent role	Cobble beaches
	High	Important role	Mussel beds on sediments
	Extreme	Very active role in trapping and stabilising sediments	Mangrove forest, intertidal mud flats
Biologically mediated sediment capture and stabilisation			
Capture and stabilisation of sediments by virtue of active biological processes. Every habitat is likely to have at least a trace of such activity.	Trace	Almost no role in sediment capture	Surface shelf pelagic waters
	Low	Very limited role in trapping and stabilising sediments	Cobble beaches
	Medium	Minor though persistent role	Biogenic calcareous reefs
	High	Important role	Shallow coastal waters
	Extreme	Very active role in trapping and stabilising sediments	Dense mangrove forest, saltmarsh
Carbon capture and sequestration			
The capture and/or sequestration of carbon. Every habitat is likely to have at least a trace of such activity.	Trace	Trace carbon sequestration role	
	Low	Limited capture and sequestration of carbon	Offshore, oligotrophic surface waters
	Medium	Minor though persistent role. May capture carbon but limited role in sequestration	Productive shelf waters (e.g. Hauraki Gulf); ocean waters below photic zone
	High	Important role in capture and sequestration	Dense, long-lived mangrove forest; salt marshes and seagrass beds; oceanic frontal regions (e.g. Subtropical Front along Chatham Rise)
	Extreme	Very active fixation of carbon by oceanic algae and carbonate animals and eventual deposition in shell banks or in deep water	Dense shellfish beds, dense vent mussel and tube worm beds around hot vents and cold seeps
Pollutant capture and sequestration			
Biological and physical capture. Every habitat is likely to have at least a trace of such activity.	Trace	Trace role in pollution capture	Cobble beaches
	Low	Very limited uptake and storage of pollutants	Habitats with impoverished fauna and flora
	Medium	Minor though persistent role	Subtidal reefs
	High	Important role	Shelf muds
	Extreme	Very active uptake and storage of pollutants	Dense populations of filter and deposit feeders
Pollutant detoxification			
Biochemical change in toxicity. No habitat is likely to be at zero level.	Trace	Trace levels of detoxification	Deoxygenated and/or highly toxic environments
	Low	Limited or intermittent role	Deep-shelf habitats
	Medium	Medium persistent role	Mid-shelf habitats
	High	Important role in processing and degrading of pollutants	Saltmarsh, mangrove forest
	Extreme	Very high, rapid processing & detoxification of pollutants	Diverse high biomass habitats or high density of filter feeders
Storm surge amelioration			
Slows or dampens effects of occasional storm surge.	None	No impact on storm surge	No biological buffer zone present
	Low	Very limited impact on storm surge	All habitats deeper than 30 m
	Medium	Minor though persistent role	Thick beds of giant kelp
	High	Important role	Inshore sand habitats
	Extreme	Presence eliminates or drastically ameliorates the effects of storm surge	Wide, intact, mature mangrove forests

Erosion dampening			
Generic dampening effect on erosion. May occur along shoreline or deeper part of habitat.	None	No impact on waves or erosion	No biological buffer zone present
	Low	Very limited impact on waves or erosion	Habitats 10–30 m depth
	Medium	Minor though persistent role	Thick beds of giant kelp
	High	Important role	Shellfish beds lining channels
	Extreme	Presence eliminates or drastically ameliorates the effects of waves and erosion	Wide, intact, mature mangrove forests
Storage of nutrients			
Storage of nutrients for short to longer time periods.	Trace	No known or only trace amounts of storage capacity	Cobble beaches
	Low	Habitats with low levels of biological activity	Offshore, oligotrophic surface waters
	Medium		Shelf muds
	High		Shallow shelf reefs, kelp forest
	Extreme	Habitats with very high levels of biological activity and capacity to store nutrients	Very dense cockle or oyster beds
Cycling of nutrients			
Uptake and release of nutrients often in modified form	Trace	Trace amounts of nutrient cycling	Cobble beaches
	Low		Saltmarsh, mangrove forest
	Medium		Seagrass, shellfish beds, kelp forest
	High		Shelf mud habitats
	Extreme	Rapid and extensive recycling of nutrients	Shallow sandy habitats
Net annual oxygen production per unit area			
Scale ranges from high net oxygen consumer to high net producer	None	Anoxic habitats. Permanent large consumer of oxygen per unit area	Benthic ‘dead zones’
	Low	Habitats with a small or intermittent oxygen deficit	Habitats deeper than the photic zone
	Medium	No net surplus or consumption of oxygen	Shellfish beds
	High	Small net producer of oxygen	Offshore oligotrophic surface waters
	Extreme	Habitats that are large net annual oxygen producers per unit area	Surface waters (Frontal regions) with very high levels of primary production; coastal seagrass and salt marsh beds, mangroves
Provision of biogenic habitat materials to same and/or other habitats			
Includes both living and dead organic materials. Every habitat is likely to have at least a trace of such activity.	Trace	No known or only trace amounts of biogenic habitat material produced for any habitat	Trenches
	Low	Very limited production of biogenic material	Pelagic habitat below the photic zone in deep-ocean low productivity zones; deep-ocean surface waters
	Medium	Moderate production of biogenic materials	
	High	High production	Inshore pelagic waters
	Extreme	Very active production of biogenic material that builds or maintains same or different habitat	Dense cockle beds, horse mussels beds, kelp forest, shallow and deep-sea coral thickets, bryozoan reefs, vent communities; salt marshes, seagrass beds, mangroves

containing the largest pool of carbon on the planet, of more than 38 000 gigatonnes. Approximately 48% of all anthropogenic CO_2 released into the atmosphere now resides in the ocean (Sabine et al. 2004), largely as a result of two processes. The solubility pump operates at higher latitudes with CO_2 dissolved in colder surface water being subducted into the deep ocean, whereas the biological pump uses phytoplankton photosynthesis in the surface ocean to convert dissolved CO_2 into particulate matter, of which about 10% sinks into deeper water. The two pumps result in a net transfer of about 2 gigatonnes of carbon per year from the atmosphere to the deep ocean (Wanninkhof et al. 2012). Photosynthetic uptake of CO_2 is also associated with the production of oxygen, a critical ecosystem service that provides more than 50% of the atmospheric oxygen pool upon which all aerobes, including humans, rely.

Phytoplankton photosynthesis plays a critical role; if the ocean's biological pump were absent, atmospheric CO_2 would be 70% higher than at present (Siegenthaler and Sarmiento 1993). The amount of carbon sequestered is determined by nutrient availability; thus, elevated nutrient supply in coastal and oceanic frontal regions, such as on the Chatham Rise (Murphy et al. 2001), supports high phytoplankton production and associated carbon fixation, whereas the oligotrophic subtropical waters north of New Zealand support lower phytoplankton production and carbon fixation. Carbon sequestration is further influenced by ecosystem structure; pelagic plankton communities dominated by mesozooplankton and larger phytoplankton such as diatoms export more carbon to deeper waters, whereas more efficient grazing and regeneration by microzooplankton and bacteria in oligotrophic subtropical waters minimises carbon sequestration

TABLE 2 Provisioning services provided by New Zealand marine ecosystems. The magnitude of the provided service is based on per unit area of habitat over a year. Adapted from MacDiarmid et al. (2011)

Provisioning services	Magnitude	Descriptive notes	Example
Wild food support and provision			
Includes the provision and support of commercial, recreational, customary and illegally fished species. Also includes nursery roles played by some habitats. Definitions of what sea food is acceptable to eat vary among cultures and change over time.	None	No presently exploited marine species	Saltmarsh, hot vents
	Low	Habitats presently supporting only 1 or 2 food species	Shallow subtidal sediment flats supporting limited fisheries
	Medium	Habitats presently supporting up to 5–6 food species	Flatfish and mullet in harbour subtidal habitats
	High	Habitats presently supporting up to 10–12 food species	Intertidal reefs
	Extreme	Habitats supporting or providing 15 or more fished species	Demersal species on sand and mud habitats in Hauraki Gulf, subtidal reefs; mangroves, seagrasses?
Aquaculture support and provision			
Includes spat or seed and brood-stock sourced from the wild as well as the sustenance of cultured species. The range of species changes over time with technological innovation and cultural definitions of which species are acceptable to eat or use.	None	No source species, does not support any cultured species	Saltmarsh, hot vents
	Low	Source of 1 aquaculturable species and/or supports 1–5% of a cultured species	Harbour intertidal reefs; mangroves
	Medium	Source of 2 species and/or supports 5–20% of a cultured species	Snapper and kingfish from Hauraki Gulf habitats
	High	Source of 3 species and/or supports 21–49% of a cultured species	Pacific oysters, cockles, pipis on intertidal flats
	Extreme	Source of 4 or more species and/or supports >50% of a cultured species	Subtidal rocky reefs – blue cod, mussels, sea cucumber, groper, butterfish, lobsters; Pelorus Sound – sustains >65% of NZ green mussel harvest
Presently used biological compounds (number)			
This service includes all compounds extracted from living organisms for use as medicines or pharmaceuticals but not those used directly for food. The range of compounds extracted is likely to grow and may soon include wild genes.	None	No compounds presently utilised	Most habitats
	1	One compound	Anti-cancer compound from yellow-slimy sponge from Kaikoura Canyon lip
	2	Two compounds	Types of collagen used from hoki fished from deep slope habitats
	3	Three compounds	Shallow subtidal reefs
	4+	Four or more compounds	Numerous compounds from shallow reef red algae
Bacterially enhanced gas and mineral deposits			
Few, if any, habitats with intermediate levels.	None	No role in formation of gas or mineral deposits	Most habitats
	Low		None known
	Medium		None known
	High		None known
	Extreme	Habitats with concentrated bacterial activity	Cold seeps and hot vents (deep ocean)
Biodiversity (future proofing service)			
Future use options for provisioning services. Assumes high biodiversity equals high option use.	None		None known
	Low	Low diversity habitats	Cobble beaches, trenches
	Medium		Ocean waters in photic zone; cold seeps and hot vents (deep ocean)
	High		Harbour sediment habitats
	Extreme	Very species diverse habitats	Coastal habitats 10–30 m water depth

TABLE 3 Non-consumptive services provided by New Zealand marine ecosystems. The magnitude of the provided service is based on per unit area of habitat over a year. Adapted from MacDiarmid et al. (2011)

Non-consumptive services	Magnitude	Descriptive notes	Example
Visual amenity value (landscape/ seascape)			
Regional councils must make provision for these values in their territorial waters	None	Habitats invisible to the general public	All deep-water sea-floor habitats
	Low	Habitats usually unseen by the general public	
	Medium	Seascapes that require use of specialised equipment	Underwater ecosystems at diveable depths
	High	Seascapes that can be appreciated without specialised equipment	Coastal fringe ecosystems
	Exceptional	Marine habitats with the strongest physical and visual characteristics	Seascapes comprising alternating sandy beaches and rocky headland reefs with clear waters
Spiritual and inspirational value			
Culturally defined value and belief systems that affect the way humans perceive the marine environment	None	Marine habitats	All deep-water sea-floor habitats
	Low		
	Medium		
	High		
	Exceptional	Marine habitats with the strongest cultural values	Surface waters off North Cape
Existence value			
Value placed by society on an ecosystem because it exists in a wild state. An ecosystem may have considerable existence value even though it may be rarely, if ever, seen and has no current use.	None		
	Low	Habitats supporting high abundances of species rated by society as of low value	
	Medium		
	High		
	Exceptional	Habitats supporting high abundances of species rated highly by society such as charismatic megafauna.	Kaikoura canyon with its sperm whales, dolphins and sea birds
Areas supporting coastal non-water recreation			
Includes beach walking, horse riding, sand yachting, etc.	None	No activities known	All non-coastal habitats
	Low		
	Medium		
	High		
	Exceptional	Very high non-water recreational use	Specific coastal locations
Areas supporting water recreation			
Includes surfing, swimming, canoeing, water skiing, sailing, boating, etc.	None	No water recreation activities	All deep-water benthic habitats.
	Low		
	Medium		
	High		
	Exceptional	Very high water recreational use	Specific inshore coastal habitats
Current foci for education			
Ecosystems utilised for educational purposes by the range of educational institutions from preschools to universities	None	No current educational focus	All deep benthic habitats
	Low		
	Medium		
	High		
	Exceptional	Persistent very high focus for educational activities	Rocky reefs along Wellington's south coast
Current focus for scientific research			
Ecosystems that are the focus for current New Zealand and international research activities. Few if any ecosystems have no research activity.	None	Remote ecosystems too difficult and expensive to access	Deepest parts of the Kermadec and Macquarie trenches
	Low	Remote ecosystems accessed rarely	Abyssal plains
	Medium		
	High		
	Exceptional	Easily accessible habitats that act as test beds for more widely applicable theory	Rocky reefs in the Leigh Marine Reserve and at Kaikoura Peninsula

Currently watchable wildlife			
Includes everything from whales to worms watched from land, air, boats and underwater. Increased accessibility to deeper habitats via new technology may strongly influence the definition of this service.	None	No species watched	Trenches
	Low	Very occasional, rare wildlife watching activities	Offshore, oligotrophic surface waters
	Medium	Minor though persistent role	Mangrove forest
	High	Important site for watching one type of wildlife	Harbour intertidal sand and mud flats
	Exceptional	Abundant and varied marine wildlife to watch	Shallow subtidal reefs on exposed coasts. Surface waters of Kaikoura Canyon
Biological indicators of ecosystem health			
Usefulness of present biological indicators to regional councils.	None	No currently used indicators	Trenches
	Low	Infrequently used indicators available	Cold seeps, hot vents
	Medium	Some highly specific indicators available but not generalisable	Seagrass beds, pipi and cockle beds
	High	Several indicators available and generalisable, but not readily accessible	Subtidal reefs
	Exceptional	Several indicators, frequently used, readily accessible and generalisable	Intertidal reefs, mud and sand

in these regions. In a study of marine ecosystem services in Spanish waters (Murillas-Maza et al. 2011), carbon uptake by primary producers exceeded the total value of all other marine ecosystem services. Provisional estimates based on mapping of surface-dissolved CO_2 indicate the New Zealand EEZ CO_2 sink is equivalent to about 5% of CO_2 uptake by the world's oceans (K. Currie, pers. comm.), and is an order of magnitude greater than that of New Zealand forests (Ministry for the Environment 2012). An alternative approach to estimating the New Zealand EEZ CO_2 sink uses net primary production estimated from satellite ocean colour data (0.5 Gt C yr^{-1}; Pinkerton 2007), and an export efficiency of 10%; this suggests an annual net carbon sink of c. 0.05 gigatonnes, which is similar to New Zealand's total annual anthropogenic CO_2 emissions. This estimate does not include carbon sequestration by coastal macrophyte communities.

The marine ecosystem also influences climate in other ways. For example, of the 85 teragrams of methane produced in the ocean each year, 75 teragrams are consumed by methane-oxidising bacteria (Reeburgh 2007), and this restricts marine methane emissions to 2% of the global budget. New Zealand waters are characterised by significant methane concentrations in coastal regions and also in deeper waters near methane seeps on the North Island continental shelf (Law et al. 2010), yet marine methane emissions are insignificant in relation to terrestrial emissions, in part due to methane oxidation. A similar ecosystem service exists to a lesser extent for another greenhouse gas, nitrous oxide. Although the global ocean is a source of nitrous oxide to the atmosphere, denitrification in anoxic sediments (e.g. in the Firth of Thames; see coastal nutrient dynamics section) represents a potential sink that reduces nitrous oxide emissions.

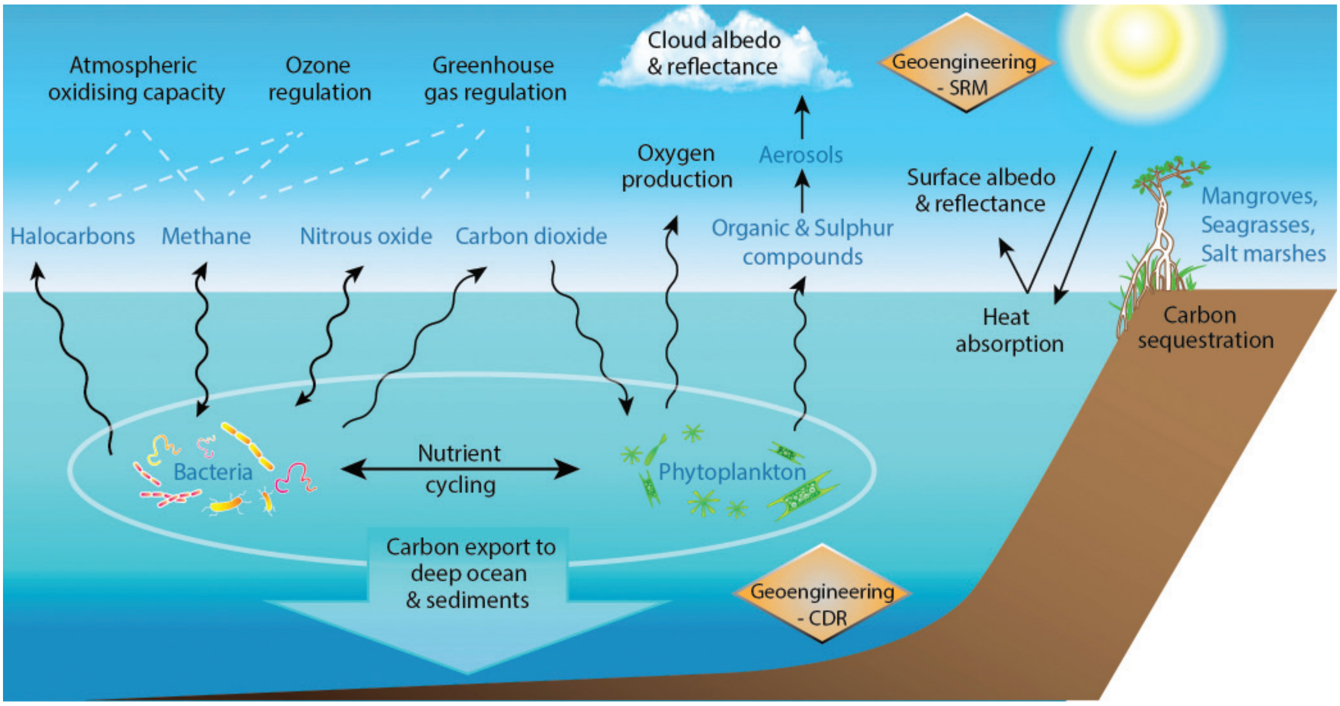

FIGURE 5 A conceptual diagram of climate-regulating marine ecosystem services, with ecosystem services identified in black font and the key chemical species and biotic groups in blue font. The geoengineering options are identified in the diamonds, as SRM – solar radiation management and CDR – carbon dioxide removal.

Phytoplankton also produces other compounds that influence atmospheric chemistry with feedbacks to climate. For example, phytoplankton-derived halocarbons and volatile organic compounds (Meskhidze and Nenes 2006; Carpenter et al. 2009) influence oxidising capacity and ozone production in the troposphere, and thus the residence time of trace gases such as methane. Charlson et al. (1987) suggested that dimethlysulphide (DMS), a trace gas derived from certain phytoplankton groups, was a potential precursor of aerosol particles that stimulate cloud formation. Recent measurements along the subtropical front on the Chatham Rise have identified elevated levels of dissolved and atmospheric DMS (C. Walker, T. Bell pers. comm.), suggesting potential for marine biota to influence aerosols and atmospheric reflectance in the New Zealand region. Volatile organic compounds and microgels released by phytoplankton may also play an important role in cloud formation once transferred into the atmosphere (Meskhidze and Nenes 2006; Orellana et al. 2011). Furthermore, phytoplankton directly influence the albedo or reflectance, and hence heat retention, of the surface ocean (Jolliff et al. 2012). Thus, all these processes suggest the high phytoplankton productivity in frontal regions around New Zealand may contribute to a broad range of climate regulation ecosystem services.

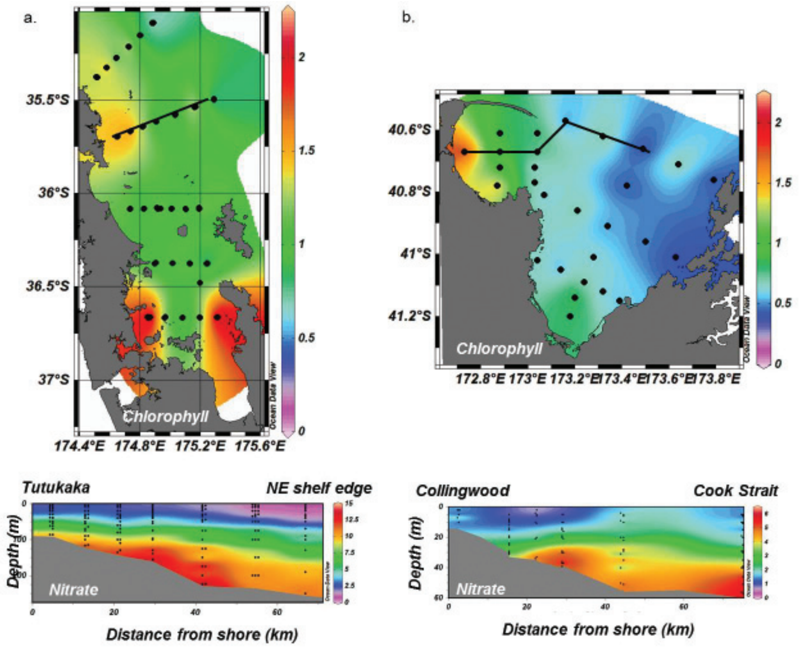

FIGURE 6 Responses of phytoplankton and nutrient concentrations to upwelling dynamics: **a**, Hauraki Gulf / NE shelf. **b**, Nelson Bays. Upper panels show annually-averaged chlorophyll-a (micrograms L^{-1}) and lower panels show nitrate concentrations (micromoles L^{-1}) through the water column, on the indicated transects. The data are from Zeldis et al. (2004) and Zeldis (2008a).

Various mechanisms have been proposed for utilising marine ecosystems to control climate. Although none has yet been employed, there are two main types of geoengineering approaches: solar radiation management (SRM), which would reduce incident solar radiation by increasing the albedo of the surface ocean, and carbon dioxide removal (CDR), which would increase the transfer of CO_2 to long-term reservoirs (Lenton and Vaughan 2009). SRM approaches are relatively limited in the ocean, with one proposed option being to increase the production of cloud precursor compounds such as DMS by fertilisation (Wingenter et al. 2007). In contrast, a variety of CDR approaches have been proposed, chief among which is ocean iron fertilisation. Low availability of iron limits phytoplankton growth in areas such as the Southern Ocean and Sub-Antarctic waters of the southern New Zealand EEZ, and so adding iron to surface waters may increase phytoplankton growth and therefore carbon fixation and sequestration (Boyd et al. 2007). Other approaches, such as enhancement of nitrogen fertilisation and macrophyte growth, have also been suggested. The relative merits of these approaches are discussed elsewhere (Williamson et al. 2012), but the interest in such approaches reflects the significance of marine ecosystems as natural regulators of climate.

ECOSYSTEM SERVICES PROVIDED BY COASTAL NUTRIENT DYNAMICS

Nutrient supply and cycling provide vital ecosystem services on our coasts by fuelling productivity. Dissolved macronutrients (nitrogen, phosphorus, silica) fertilise phytoplankton (the base of the food chain) and thereby support biological production in natural ecosystems, wild fisheries, and aquaculture (Nixon and Buckley 2002). In New Zealand, the dynamics of nutrient supply have been described in two well-studied regions: Hauraki Gulf and Nelson (Golden and Tasman) Bays. Production in both regions is strongly driven by upwelling of slope-associated deep water, rich in nutrients, onto the shelf and into the coast, where nutrients are utilised within the photic zone to generate primary production (via photosynthesis) and secondary production (zooplankton, fish, and so on) (Shirtcliff et al. 1990; Zeldis 2004, 2008a; Zeldis et al. 2004, 2013; Bradford-Grieve et al. 2006; MacDiarmid et al. 2009; Bury et al. 2011; Gall and Zeldis 2011) (Figure 6). Both the north-east shelf and Northwest Nelson upwelling zones are stimulated by winds from the west, which promote upwelling during the El Niño phase of the Southern Oscillation (MacDiarmid et al. 2009; Zeldis et al. 2013). Rivers are also critical sources of nutrients for coastal production. For example, rivers contribute on average about 70% of the nitrogen supply to the Firth of Thames, although, in contrast, the Nelson Bays receive only about 15% of nutrient supply from their rivers (Zeldis 2008b). Across New Zealand, the production supported by upwelling and river dynamics underpins wild fisheries and aquaculture worth hundreds of millions of dollars annually to the New Zealand economy, as well as huge recreational and cultural fisheries and natural amenities on our coastlines.

Coastal waters also provide critical ecosystem services by assimilating runoff of dissolved inorganic nutrients, organic matter, and sediment from land. Delivery of these materials has increased dramatically in post-colonial New Zealand, exacerbated by erosion, deforestation, and land development (Zeldis et al. 2010b). Excessive input of land-derived organic matter loading can be hazardous because it stimulates net respiration and hypoxia in deeper (near-seabed) coastal waters (Caffrey 2003; Vaquer-Sunyer and Duarte 2008). In extreme cases this causes 'dead zones' to form (Rabalais et al. 1996). Countering this is the capability of the system to mineralise the organic matter without causing hypoxia, through physical mixing and adequate oxygen supply. Nitrogen is particularly important in these coastal marine waters because it is typically the limiting nutrient there (Pearl 2009; Larned et al. 2011) and in excess can cause eutrophication (NRC 2000; Bricker et al. 2003; Hughes et al. 2011) by promoting excessive organic matter fixation. In healthy coastal

TABLE 4 Results from New Zealand nutrient and carbon budgets for Hauraki Gulf, Firth of Thames and Nelson Bays systems. Shown are system sizes and inorganic and organic dissolved and particulate nitrogen (N) fluxes (DIN, DON and PON, respectively) entering the Bays from rivers and the ocean (tonnes N yr^{-1}). The last two columns show net dissolved inorganic carbon (DIC) fluxes (tonnes C yr^{-1}) and net N denitrification (tonnes N yr^{-1}). Positive values indicate inflows to the systems, negative values indicate outflows. River organic N was not split for DON and PON in the hydrometric data. Ocean PON was estimated by difference with respect to the other fluxes. Results revised from Zeldis (2006) and Zeldis (2008a, b)

System	Area (km^2)	Volume (km^3)	River DIN	River DON+PON	Ocean DIN	Ocean DON	Ocean PON	DIC flux	Denitrification
Hauraki Gulf	2700	82	800	150	8200	−10 400	2000	8500	−700
Firth of Thames	1100	16	3700	900	600	−3200	6100	−75 000	−8100
Golden Bay	800	13	900	200	6300	−3700	−400	7700	−3400
Tasman Bay	1300	31	500	100	5000	−2100	−600	8200	−2900

ecosystems, eutrophication is mitigated by the loss of nitrogen through denitrification; that is, the release of gaseous nitrogen to the atmosphere via microbial processes operating at the oxic/suboxic boundary in sediments (Seitzinger 1988). Deleterious synergistic effects may occur if near-seabed waters become hypoxic, because this removes the sediment conditions needed for denitrification. This leaves more nitrogen in the system, leading to further organic fixation in overlying waters and to sedimentation. Hence, both oxidation and denitrification should be considered valuable ecosystem services of our coastal waters for the maintenance of water quality.

New Zealand research has demonstrated the scales of these processes in the Hauraki Gulf / Firth of Thames and Nelson Bays (Table 4; Zeldis 2008a, b). In the Firth of Thames, denitrification removes about 70% of the new nitrogen loaded to the system, and so is a crucial ecosystem component, especially because farming in the Waikato Region delivers some of the heaviest nutrient loading to any New Zealand coastal water body (Unwin et al. 2010). The Firth is also highly net-respiratory, generating large amounts of dissolved inorganic carbon (DIC), driven by the heavy organic and inorganic loading it receives. In contrast, Nelson Bays receive relatively little nutrient loading from their catchments and, as described above, are dominated by oceanic inorganic nutrient loading from Cook Strait. Denitrification there is only moderate (c. 50% of N load) and is net-productive (i.e. consumes inorganic nutrients and DIC). In these ways, Nelson Bays resemble the Greater Hauraki Gulf, seaward of the Firth of Thames (Table 4). Significantly, high rates of organic respiration in coastal waters can amount to an 'ecosystem disservice' because they generate DIC, which causes ocean acidification (Sunda and Cai 2012). This is occurring in the Firth of Thames (J. Zeldis, K. Currie, NIWA, unpubl. data), with the overall implication that high loadings of nutrients and organic matter significantly stress coastal ecosystem services.

At the national scale, the importance of continental shelf oxidation and burial of organic matter was described by Zeldis et al. (2010b). Based on a New Zealand sediment flux budget, it was calculated that about 4 Mt carbon yr^{-1} is delivered to the coastal sea (Page and Trustrum 1997; Carey et al. 2005; Scott et al. 2006). This carbon loss is similar in magnitude to the New Zealand plantation forest annual carbon sink (Scott et al 2006), and to about 50% of New Zealand fossil fuel emissions (Ministry for the Environment 2001). It is likely that most of this material is trapped on our continental shelves, rather than exported to deep water (Zeldis et al. 2010b). The extent to which it is oxidized or permanently buried there is not well known, but it nevertheless represents a massive sink for New Zealand's terrestrial carbon.

MARINE AQUACULTURE SUPPORT AND PROVISION

Marine aquaculture is supported by ecosystem services that sustain the growth and process the wastes of the cultured organism. In New Zealand the endemic green shell mussel (*Perna canaliculus*) provides most of the aquacultural activity, with 75 000 tonnes' annual production worth over NZ$200 million in revenue (New Zealand Marine Farming Association 2009). A case study illustrates how coastal ecosystems provision this industry. Pelorus Sound sustains 68% of the national mussel harvest across hundreds of farms. To describe the drivers of mussel production in Pelorus Sound, Zeldis et al. (2008) correlated physical, chemical and biological data collected over 9 years by NIWA and the mussel industry. Starting in early 1999, farm production (meat yield per mussel) in the sound declined by c. 25% then recovered through 2002 (Figure 7). This resulted in substantial economic impacts within the industry. Over-grazing by mussels (i.e. 'top-down' effects) did not explain the yield minimum; instead, 'bottom-up' effects of nitrogen supply from oceanic and river sources drove the variation by affecting the abundance of mussel food ('seston'). A subsequent study (Zeldis et al. 2013) provided quantitative models for Pelorus Sound mussel yield and elucidated the underlying oceanographic mechanisms. Yield was best predicted using biological variables, including seston, collected near the farms (Figure 7a), but it was also predictable using only physical variables that index large-scale environmental processes (Southern Oscillation Index, along-shelf winds, sea surface temperature, and river flow; Figure 7b). These large-scale predictors are available in New Zealand national databases, and the study described the seasonally-dependent mechanisms by which they drive the supply of nitrogen to the sound from the ocean (upwelling in north-west Cook Strait) and the Pelorus River. This case study illustrates how the Pelorus Sound ecosystem provisions New Zealand's most valuable aquaculture industry, and also how it imposes environmental limits and variability.

Because the mussel farming industry is large, an important

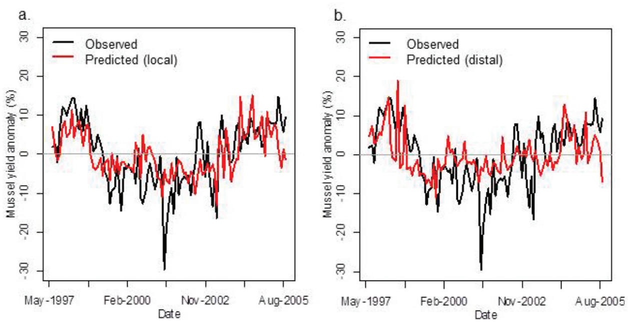

FIGURE 7 a, Time-series of Pelorus Sound mussel yield anomalies predicted by 'local' biological predictors (seston, phytoplankton), plotted with actual yield anomalies observed by the mussel industry from 1997 to 2005. **b**, same as (**a**) but for yield anomalies predicted using only 'distal' physical predictors (Southern Oscillation Index, winds, sea temperatures, river flow).

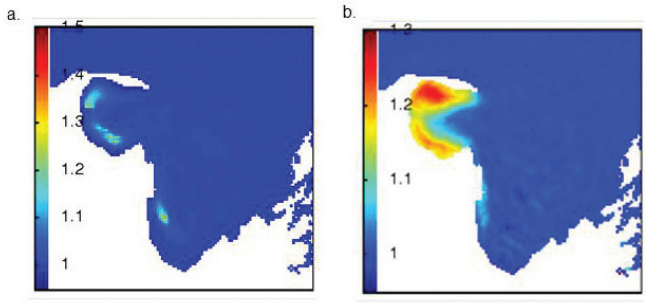

FIGURE 8 Computer-modelled projections of increased nitrogen and phytoplankton in Nelson Bays under a medium fish farm development scenario (Zeldis et al. 2011). **a**, inorganic nitrogen ($\log_{10}$ [mg m^{-3} N]). b, diatom phytoplankton (mg m^{-3} C).

resource management issue is whether farming significantly depletes coastal phytoplankton and thereby prevents it from provisioning the rest of the ecosystem. This has been studied through environmental monitoring at Wilson Bay, Firth of Thames, for the Group A mussel farming consortium. This bay sustains an annual harvest of 15 000 tonnes from the largest single block of farms in New Zealand. Consents monitoring and modelling conducted since 2001 (Stenton Dozey et al. 2005; Zeldis 2005; Broekhuizen and Zeldis 2006) demonstrated the sustainability of this activity relative to 'Limits of Acceptable Change' in phytoplankton abundance (Turner and Felsing 2005), thus confirming that this coastal ecosystem can sustain large mussel farms while provisioning the remainder of the food web.

Marine fish farming in New Zealand is already established for introduced Chinook salmon (*Oncorhynchus tshawytscha*), and is set to develop for two native species: kingfish (*Seriola lalandi*) and hāpuku (*Polyprion oxygeneios*). In contrast to mussel aquaculture, which is sustained by local production of phytoplankton, marine fish farming requires the addition of industrially-produced food. This externally supplied organic matter is a potential threat to coastal systems from eutrophication (see nutrient cycling section). This threat is most acute at the sea bottom directly below and adjacent to the fish pens, where fish waste and unconsumed food may fall in large amounts. Such benthic effects occur beneath New Zealand salmon farms in the Marlborough Sounds (Forrest et al. 2007) and elsewhere. Impacts are also possible in the water column, where large amounts of nitrogen are dispersed via fish excretion and the breakdown of organic matter (Figure 8). The capacity of inner Hauraki Gulf and Nelson Bays coastal zones to assimilate pollution from prospective fish farms was investigated in reports to regional and national resource managers (Zeldis et al. 2010a, 2011). Critical ecosystem variables are the muddiness of underlying substrates, which correlates inversely with their ability to absorb organic loading, and water depth and current speed, which correlate directly with dispersal of wastes (Findlay and Watling 1997; Hargrave 2010). The reports suggested contrasting prospects for siting of future marine fish farms in inner Hauraki Gulf and Nelson Bays (see: http://www.ew.govt.nz/ Publications/Technical-Reports/TR200816/).

To summarise, coastal ecosystems contribute provisioning services for aquaculture: namely, the cultured species themselves and, in the case of mussels and oysters, the food that that sustains them. They also provide regulating services by assimilating waste (especially for fish farms), recycling nutrients, and providing oxygen. All the examples show how environmental time-series and modelling are important for explaining how these services support our expanding aquaculture industry and for assessing its sustainability.

WILD FOOD SUPPORT AND PROVISION

Humans have used the oceans as a source of food for millennia. In New Zealand, human harvesting of marine living resources began with the arrival of Māori, increased during settlement of New Zealand by Europeans, and continues as one of New Zealand's most significant primary industries with an annual turnover in excess of NZ$1.4 billion (SeaFIC 2009). "Wild food support and provision" is the ecosystem service that provides and sustains species that are targeted by humans for food.

Between 2005 and 2007 New Zealanders obtained about 6% of their protein intake from seafood (Ministry of Health 2012). New Zealand's commercial seafood catch varies from year to year, but typically comprises about 400 000 tonnes per year of finfish, 77 000 tonnes of invertebrates (>80% squid), 56 000 tonnes (meat weight) of mussels and oysters by aquaculture, and 14 000 tonnes of cultured salmon (Aquaculture NZ 2012; Ministry for Primary Industries 2012). The total seafood catch of about 550 000 tonnes per year is equivalent to about 110 000 tonnes of protein. This total does not include the recreational catch (by non-commercial fishers), which is still unknown, nor the Māori cultural catch. Nor does this figure include 'by-catch' – fish that are caught but discarded or converted to fishmeal on board fishing vessels. Nevertheless, enough seafood is caught or cultured commercially in New Zealand to provide the New Zealand population of 4.46 million (Statistics New Zealand 2013) with their entire recommended intake of 52 grams of protein per person per day (WHO 1985) with 20% to spare.

Of the wild commercial New Zealand catch of 400 000 tonnes per year, about 60% is finfish caught offshore in waters deeper than about 250 metres (Ministry for Primary Industries 2012). About 20% of the annual wild catch is inshore fish, and 20% is invertebrates (mainly offshore squid). The wild catch is dominated by hoki (*Macruronus novaezelandiae*), which comprises about 30% of the total wild catch. Key fishing areas in New Zealand waters include the Chatham Rise and Subantarctic Plateau, although there are important seasonal fisheries for hoki during spawning in Cook Strait and off the west coast of the South Island. We now trace the trophic processes that enable this harvest, with a focus on wild-caught finfish.

The provisioning ecosystem services begin with the photosynthetic microbes that generate new organic matter in the surface ocean (Figure 9). Photosynthesis by phytoplankton is the dominant source of energy in the marine realm, although near the coast, and in localised areas such as around deep-sea vents, organic matter is formed by other primary producers including macroalgae, seagrass, mangroves, epiphytes, autotrophic periphytes, microphytobenthos, and chemosynthesisers. Phytoplankton production takes place in the upper ocean within a complex microbial system including archaea, viruses, heterotrophic bacteria, and a range of small heterotrophic zooplankton (Kirchman 2008). Some phytoplankton are grazed by protists (single-celled eukaryotes) and some are broken down by viral lysis. The resulting complex soup of dissolved organic matter fuels bacteria and archaea, which are themselves consumed by other protists. Energy from this lower food web follows two main pathways, the first via mesozooplankton (typically mainly copepods) and the second via detritus sinking to the seabed. We are only just beginning to appreciate the complex processes taking place in the ecosystem that underpin provisioning services for wild-caught seafood in New Zealand's open ocean and coastal regions.

'Trophic level' measures the number of feeding steps between an organism and the base of the food web; thus, primary producers

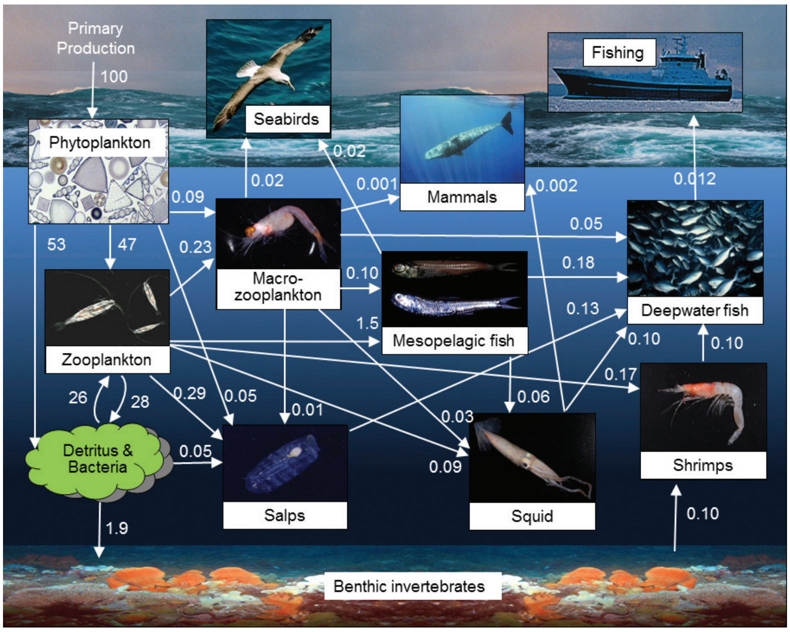

FIGURE 9 Schematic food web of New Zealand's offshore waters (approximately 300–1300 m depth). The white arrows and numbers indicate the magnitude of flows of energy through the system, scaled so that net primary production is represented as 100. Flows are based on trophic modelling of Pinkerton (2013) and Bradford-Grieve et al. (2003). The central importance of middle-trophic level groups (meso- and macro-zooplankton, squid and mesopelagic fishes) is highlighted.

have a trophic level of 1, herbivores have a trophic level of 2, and carnivores in marine systems have trophic levels of between 3 and about 5. Commercially caught finfish and squid are almost exclusively carnivorous, and in New Zealand waters trophic levels of finfish typically range from 3.3 to 4.5. The efficiency with which energy passes between trophic levels is often considered to be about 10% (Pauly and Christensen 1995), although this varies with trophic level, type of ecosystem, and which organisms are functionally important. This means that only about one-tenth of the energy consumed by marine organisms is used to build new body mass; the rest is used for metabolic processes or activity. Consequently, a transfer efficiency of 10% means each tonne of predatory fish caught by humans has been supported by over 1000 tonnes of microbial primary production that has been moved through at least two intermediate levels in the marine food web before being consumed by fish and squid.

The diet of commercially-targeted fish in the New Zealand EEZ has been studied over the last 25 years using extensive examination of stomach contents (e.g. Clark 1985; Rosecchi et al. 1988; Clark et al. 1989). More recent studies have improved the sampling designs, the quantitative analysis methods, and the statistical analysis tools, thereby helping understand the factors separating the ecological niches of key species (e.g. Dunn et al. 2009, 2010a, b; Connell et al. 2010; Stevens and Dunn 2011). An analysis of feeding guilds (groups of species with similar diets) in the Chatham Rise region of New Zealand identified nine predator guilds (Dunn et al. unpublished data). As found previously (e.g. Ross 1986), for marine fishes trophic separation tends to be more important than habitat separation. The Chatham Rise guilds included salp specialists (oreos, warehous), pelagic foragers (small to medium hoki, large javelinfish), benthopelagic invertebrate feeders (small javelinfish), benthopelagic predators (hake, large hoki), benthic invertebrate feeders (rattails and ghost-sharks), and benthic predators (ling).

Five groups of prey organisms form the key linkages between the lower marine food web and finfish: small mesopelagic fish, pelagic squids, hard-bodied (crustacean) macrozooplankton, gelatinous or soft-bodied macrozooplankton, and benthic or hyperbenthic crustaceans. Mesopelagic fish around New Zealand are predominantly myctophid lanternfishes (McClatchie and Dunford 2003; O'Driscoll et al. 2009). These species of mesopelagic fish are typically 5 cm long and weigh only a few grams. Arrow squid (*Nototodarus sloani*) is common in New Zealand waters, but other squid such as warty squid (*Moroteuthis ingens*, *M. robsoni*) and red squid (*Ommastrephes bartrami*) are likely to be relatively common (Livingston et al. 2003). Hard-bodied macrozooplankton (longer than 20 mm) tend to be mainly euphausiids by weight, although decapoda and amphipoda are also abundant (e.g. Robertson et al. 1978; Nodder 2011). Soft-bodied macrozooplankton include jellyfish, salps, siphonophores, and chaetognaths. Decapods often eaten by commercially important fish species include squat lobsters, scampi, prawns, and shrimps (e.g. Dunn et al. 2009; Connell et al. 2010). These key 'middle-trophic level' groups are crucial to the ecosystem services that lead to the wild-caught seafood harvest in New Zealand. However, scientific understanding of the ecology of these groups is at a relatively early stage, partly because these organisms have several characteristics that make them hard to study. They are hard to catch and can often move faster than research vessels can tow the fine-mesh nets required to retain them. The assemblages are taxonomically and functionally complex and many species of middle-trophic level biota in New Zealand waters remain poorly described. For example, Dunn et al. (2009) identified about 400 categories of prey from the stomach contents of 25 demersal fish species on the Chatham Rise and was forced to use prey categories ranging in taxonomic detail from phylum to species. Middle-trophic-level animals are relatively short-lived (typically 1–5 years) and tend to have highly opportunistic feeding behaviour, and consumption and growth rates that can vary greatly according to food availability. This ecological flexibility enables them to respond rapidly to changing conditions, meaning their biomass can change substantially with the seasons and between years (Brodeur et al. 2008).

A crucial component of an ecosystem approach to fisheries is the recognition that species in an ecosystem are linked (Francis et al. 2007). New Zealand is moving towards a more holistic view of fisheries that recognises the interconnectedness of organisms in marine ecosystems and appreciates the complexity of the provisioning ecosystem services underpinning the New Zealand wild-caught seafood industry.

DISCUSSION

The above examples identify the large scope and range of services provided by New Zealand marine ecosystems. It is very difficult to judge whether these services are growing, holding steady over periods of years, or declining. In part this is because we know little about the extent of marine habitats, and in part because the more remote and deeper marine ecosystems are difficult and expensive to monitor. Thus, for many habitats, the information with which to judge trends in levels of ecosystem services is either missing or is based on short time-series. There is inherent climate-driven variability in the capacity of specific ecosystems to sustain aquaculture and no long-term trend is apparent at this stage; similarly, the productivity of most species of wild-caught finfish also varies from year to year, but the environmental and ecosystem drivers of these variations are not understood. In contrast, for some (mainly coastal) ecosystems there is sufficient archaeological, historical, and contemporary data available to indicate trends in services; for example, Thrush et al. (2013) document declining trends in services for some New Zealand harbours and estuaries where humans have compromised ecosystem functioning. In more open seas, there is generally no scientific consensus on trends in ecosystem services. One clear exception is the decline in marine mammals that followed the well-documented onset of Māori sealing soon after initial settlement, and European whaling in the early 19th century. Both cultures viewed many species of marine mammals as valuable commodities to be harvested, so the numbers of these mammals declined precipitously (Smith 2005; Carroll 2006). Now, these species are protected and their value to New Zealand as a provisioning service has declined to zero. Instead, we currently prize marine mammals for their spiritual and existence value; we enjoy directly viewing them from land, sea, and air; and we appreciate them as subjects for research and educational activities. Moreover, whales have recently been recognised as possibly having important roles in ecosystem regulation (e.g. Nicol et al. 2010).

There is no doubt that marine ecosystems and the services they provide are affected by interactions with terrestrial ecosystems. This is clearly seen in harbour and estuarine systems but also occurs along open coasts and in deeper waters. Evidence for land-based effects on coastal fisheries and biodiversity in New Zealand has been reviewed by Morrison et al. (2009), while an assessment of anthropogenic threats to New Zealand marine ecosystems concluded that many of the top threats, fully or in part, stemmed from human activities external to the marine environment itself (MacDiarmid et al. 2012). Some of these external threats, such as sedimentation of coastal habitats, arose from activities in New Zealand catchments, while other, mainly land-based, threats such as ocean acidification arose from human activities on a global scale. Not surprisingly, coastal ecosystems were particularly vulnerable to catchment-based threats. Conflicting uses of New Zealand's marine environment are increasing (fishing, gas and mineral extraction, aquaculture, tourism), so the oceans require a comprehensive and effective framework for evaluating and managing resources.

New Zealand research into the services provided by marine ecosystems is at a very early stage. Although determining service production may be reasonably straightforward for some ecosystems and some services, so far little funding has been directed to determining their magnitude or value, or to characterising variability and trends. For example, while the national magnitude and value of wild and cultured foods is well described, the contribution of particular ecosystems remains poorly understood and demands further effort. Similarly, further effort should firm up the existing provisional estimates of the marine contribution to New Zealand's carbon dioxide sink. A recent comprehensive assessment of marine ecosystem services in the Spanish EEZ (Murillas-Maza et al. 2011) could serve as a model for New Zealand research efforts.

Ecosystems produce at least US$33 trillion worth of services globally each year (in comparison, global GNP is US$25 trillion per year) (Costanza et al. 1997). The oceans contribute about US$21 trillion per year, with 60% of this from coastal and shelf systems and the other 40% from the open ocean (Costanza et al. 1997). Scaling for the size of New Zealand's marine area of responsibility suggests our marine ecosystems may contribute US$357 billion worth of services each year. Even if this estimate is out by one or two orders of magnitude, it nevertheless leaves no doubt about the imperative to measure, understand, and safeguard New Zealand's marine ecosystem services over the coming decades.

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