

The relationships between macroalgae and New Zealand's wild fisheries, key vulnerabilities and monitoring approaches

New Zealand Aquatic Environment and Biodiversity Report No.362

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PLAIN LANGUAGE SUMMARY

This report reviews key national and international research on the ecological importance of macroalgae, such as kelp, in supporting fisheries in Aotearoa New Zealand. This research shows that macroalgae are important in providing habitat and contributing to coastal food webs, as well as playing a significant role in global carbon cycles. These ecological services contribute to macroalgal habitats that are integral to a number of important fishery species, such as kōura papatea (red rock lobster), pāua, and various finfish and bivalves, resulting in substantial economic contributions. For example, the thirteen fisheries that are associated with kelp had a combined asset value of \$NZD 5.2 billion in 2019.

But macroalgae are vulnerable to a number of significant stressors including rising temperatures, sedimentation, and kina grazing. To better understand the impacts of these large-scale environmental pressures and support effective monitoring and management, a range of methods can be applied. For example satellite remote sensing has been identified as a valuable tool because it enables the generation of updateable maps showing the extent of large canopy forming kelps. When combined with other monitoring methods, it can aid our understanding of macroalgal dynamics and further contribute to more informed ecosystem-based management of New Zealand's coastal marine resources.

EXECUTIVE SUMMARY

Mangan, S.¹; Tait, L.W.¹; Wing, S.R.²; D'Archino, R.¹; Neill, K.F.¹; Battershill, C.N.³; Schiel, D.R.⁴ (2025). The relationships between macroalgae and New Zealand's wild fisheries, key vulnerabilities and monitoring approaches.

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A review of the key literature was conducted on the ecological significance of macroalgae to wild fisheries in Aotearoa New Zealand, emphasising their crucial roles in marine ecosystems and their vulnerability to various stressors. Large habitat-forming macroalgae play vital ecological roles by providing biogenic habitat that enhance habitat complexity, significantly contribute to coastal food webs and modify local environmental conditions. Their high productivity also influences global carbon cycles through detritus export and carbon sequestration.

Macroalgal habitats are integral to several important fishery species, including kōura papatea (red rock lobster), pāua, and various finfish and bivalves. These fisheries are supported through multiple pathways including habitat provision, grazing by key fishery species (e.g., pāua), support of epifauna biomass which provides food for fish and their prey, and the production of suspended particulate organic matter and detrital production which are assimilated by filter feeders and benthic invertebrates, thereby enhancing secondary productivity and energy transfer through food webs. The combination of these direct and indirect pathways underpins the economic value of macroalgae to New Zealand's wild fisheries. It is estimated that the ecosystem services provided by macroalgae, including their support for fisheries, contributes approximately \$NZ 4 billion to the asset value of 13 kelp-associated fishery species.

Macroalgae are, however, vulnerable to number of local and global stressors. Rising sea temperatures, including marine heatwaves, have been shown to negatively impact macroalgal health and distribution. Additionally, sediment deposition reduces light availability and ultimately affects the settlement and growth of macroalgae, reducing their productivity and altering community structures. Overgrazing by sea urchins is a significant stressor in northern New Zealand and can lead to the formation of urchin barrens which can significantly reduce kelp forest cover and its associated biodiversity.

This report additionally highlights some of the main methods for monitoring macroalgae across multiple scales, including *in situ* diver surveys, camera surveys, acoustic surveys, and aerial imagery. Utilising methods across varying scales can be useful to track the distribution, abundance and health of kelp in response to varying stressors, which is essential to understand the impacts to the associated fisheries.

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1. REVIEW CONTEXT

Large habitat-forming macroalgae are important components of Aotearoa New Zealand's inshore marine ecosystems. The importance of macroalgae ranges from amenity values to ecological and ecosystem services, to intrinsic values (Bennett et al. 2015; Eger et al. 2023; Hynes et al. 2021). This includes their crucial role in supporting commercial and recreational fisheries by providing habitat and food to a multitude of species. When large areas of kelp are removed, biodiversity can decrease dramatically, affecting coastal fishes that rely on kelp for nursery habitat, as well as small invertebrates like isopods, amphipods, sponges, and gastropods that live and feed on and among kelp, and which can provide an important food source (Teagle et al. 2017).

The objective of this report is to summarise the key literature around the role of large habitat-forming macroalgae within Aotearoa New Zealand (hereafter New Zealand) and examine the direct and indirect relationships between macroalgae and New Zealand's wild fisheries. This report was funded by Fisheries New Zealand research project ZBD2023-05 which includes the development of a tool to map trends in macroalgal distribution over time, and assess changes in extent relative to a number of environmental stressors. Overall, this project aims to inform advice on ecosystem-based management of relevant fisheries and provide context for policy related to marine biodiversity and critical fish habitats.

This report focuses on two dominant Orders of large habitat-forming macroalgae which have distinct life-histories: Laminariales and Fucales. Laminarian algae, commonly known as kelp, represent the largest brown alga and exhibit an alternation of generations, a microscopic haploid gametophyte and a conspicuous diploid sporophyte each with distinct environmental requirements. Although large brown algae of the Order Fucales are increasingly referred to as kelps (Fraser 2012), they differ by having a direct life cycle, that is without an alternation of generations. Further details of the life histories of these taxa, their biological, physical, chemical and ecological requirements can be found in Schiel & Foster (2006).

Within this report we consider the impact of harvesting on macroalgal stocks, the influence of broad stressors on macroalgae, and the techniques and tools for monitoring macroalgae in order to understand the effects on the respective fisheries. This review does not consider specific distributions of kelp and macroalgae or assess the relative health of macroalgae in specific regions. For this review we have recruited national experts in macroalgae and its contribution to fisheries, and we utilise national and international literature.

2. DISTRIBUTION OF MACROALGAE IN AOTEAROA NEW ZEALAND

Macroalgal distribution is limited by a combination of light, temperature and nutrients which have differing effects on the various life stages (e.g., Graham 2002; Graham et al. 2007; Lüning 1991). New Zealand sits mainly in the warm – cold temperate zone and kelp occurs from the subtropical waters of the Rangitāhua/Kermadec Islands (29° to 31.5°S) to the subantarctic islands (47° to 53°S) (Kingsford et al. 1989; Nelson 1994; Schiel 1990; Shears & Babcock 2007).

Kelp stands around New Zealand are typically found in waters less than 20–30 m deep. The exception is the nearshore areas of the Rangitāhua/Kermadec Islands where shallower waters are dominated by the fucoid *Sargassum* (Cole et al. 1992; Schiel et al. 1986), and stands of the New Zealand common/golden kelp *Ecklonia radiata* have only been identified at approximately 72–90 m depth (Nelson et al. 2018). Such deep kelp assemblages have been found elsewhere on mesophotic reefs in subtropical areas (e.g., Graham et al. 2007) but little is known about them and we will not consider them further in this review.

New Zealand does not have a high diversity of kelp species (Order Laminariales) with only three native genera, *Lessonia*, *Ecklonia*, and *Macrocystis* and the introduced *Undaria* (Nelson et al. 2023). There are eight species in the Family Lessoniaceae, seven of which are in the genus *Lessonia*, three of which were recently described (Zuccarello & D'Archino 2024). Within the genus *Ecklonia*, *Ecklonia* radiata occurs around the coast of mainland New Zealand and the nearshore islands, including Rakiura/Stewart Island. *Ecklonia* beds can occur from the immediate subtidal zone to depths of more than 20 m, depending on the light environment. It does not occur at the Wharekauri/Chatham Islands or the subantarctic islands, where shallow reefs to around 8 m are dominated by *Lessonia* species and deeper areas by rimurimu/ giant kelp, *Macrocystis pyrifera* (Family Laminariaceae) (Schiel 1990; Schiel et al. 1995).

Macrocystis pyrifera is distributed from the southern North Island to the subantarctic islands (Adams 1994). Within New Zealand, it inhabits the upper subtidal zone down to about 20 m but is predominantly found at less than 10 m depth (Schiel & Foster 2015). Macrocystis is not uniformly abundant along rocky coastlines, but can form large colonies within calmer bays, harbours and offshore reefs. Macrocystis is one of the fastest growing photosynthetic organisms globally. Thalli are perennial and grow to 20 m in length with maximum biomass occurring in late winter through spring months.

The invasive kelp *Undaria pinnatifida* (Family Alariaceae) has been in New Zealand since at least 1987 (Hay & Luckens 1987) and is now widespread from Northern New Zealand to the Snares Islands including the Chatham Islands (Nelson et al. 2021). *Undaria* predominately occurs in waters less than 5 m deep, except in some areas with clear coastal waters such as in Fiordland and the Marlborough Sounds where it has been found at more than 10 m depth (Nelson et al. 2021). *Undaria* is the only kelp in New Zealand with an annual life history. It can form extensive stands and plants can reach over 2 m in length. Because of the quick turnover of its populations, *Undaria* fills gaps in canopies of other algae (Thompson & Schiel 2012; Valentine & Johnson 2004).

Most fucoids in New Zealand have a very shallow depth distribution. For example, the greatest abundance of *Carpophyllum* species (*C. maschalocarpum*, *C. plumosum*, *C. angustifolium*), *Cystophora* species and *Sargassum sinclairiii* were found within the immediate subtidal zone to approximately 8 m (Choat & Schiel 1982). Additionally, *Carpophyllum flexuosum* has been found to form extensive stands up to 10–15 m (Cole et al. 2001). The lower depth limit is most likely set by light limitation (Thoral et al. 2023) and in many places in northern New Zealand by urchin-dominated coralline habitats.

Durvillaea (rimurapa/ bull kelp) species occur at the intertidal – subtidal margin and down to approximately 3 m depth, mostly from Raukawa Moana/Cook Strait southwards (e.g., Fraser et al. 2020), although it can be found in wave-driven sites across coastal New Zealand. This group forms very dense stands inshore, and also forms intertwined rafts when individuals break free in storms which may float for long distances (Fraser et al. 2009). This not only increases dispersal potential for distant recruitment but also provides transport and a source of organic matter for rafting flora and fauna (Waters et al. 2018).

Another important factor of macroalgae presence around New Zealand is the need for suitable rocky substrata for settlement and growth. Typically, this requires rocky reef or boulder habitats that are elevated above sand and gravel areas to avoid frequent and intense scour. New Zealand has a very heterogenous coastline of approximately 15 000 km length. Estimates of how much of the coastline is rocky habitat suitable for kelp vary considerably, but it is likely in the order of 35% of waters out to 20 m depth (e.g., Schiel et al. 2021 for the earthquake-affected Kaikōura coastline). The rest of the coastline consists of bays, estuaries, gravel and sand.

3. THE IMPORTANCE OF MACROALGAE TO COASTAL AND OFFSHORE ECOSYSTEMS ON A GLOBAL SCALE

Kelps and fucoids that form multilayered forests or stands have long been recognised for their role in supporting a vast diversity of life. As far back as 1860, Darwin observed: "..if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp" (Darwin 1909). These early observations of the importance of kelp forests form a cornerstone for our current understanding of the role that macroalgae play in supporting coastal marine diversity and the ecosystem functions and services they provide.

Macroalgae have some of the highest per-area primary productivity of any of the world's ecosystems (Gerard 1982; Leigh et al. 1987; Mann 1972, 1973; Pessarrodona et al. 2022; Schiel & Foster 1986). Globally, kelp forests provide habitat for valuable fisheries, particularly abalone, lobsters, and finfish (Steneck et al. 2002). They also represent important fisheries in their own right (Schiel & Nelson 1990). Further, through their high productivity, kelp forests fix carbon from the atmosphere, release oxygen, and alter the physico-chemical environment they inhabit (Kosek & Kukliński 2023). The combined global annual financial value of kelps (including assessments of *Ecklonia*, *Lessonia*, and *Macrocystis*) ranges between \$465–562 billion per annum, primarily driven by fisheries and nitrogen, phosphorus, and carbon removal (Eger et al. 2023).

Through the combined provision of ecological services, and direct and indirect contributions to fisheries, kelps represent a vital component of global economics, biogeochemical cycling, and ecosystem health. Declining abundance and distribution of kelp forests (e.g., Tait et al. 2021) threaten to reduce the quantity and distribution of these global benefits with implications for carbon storage, ecosystem health, and fisheries (Durante et al. 2022).

4. KEY ECOSYSTEM SERVICES AND PATHWAYS WHERE MACROALGAE SUPPORT FISHERIES

For the purpose of this review, we define 'ecosystem function' as the provision and transport of energy, nutrients and organic matter through food webs within diverse, 'healthy' ecosystems, whereas 'ecosystem service' is used to highlight services, benefits or value derived from a healthy ecosystem to the benefit of people. Therefore, the provision of food is a valuable ecosystem service, while the maintenance of pathways and channels by which kelp-derived organic matter pass through food webs are a measure of ecosystem function. These distinctions are particularly important for management because without the maintenance of healthy function there will be no service.

4.1 Habitat provision

Kelp forests form some of the largest biogenic structures in coastal marine ecosystems (Dayton 1985), which provide essential habitat for a diverse array of flora and fauna. Extensive three-dimensional canopies offer shelter to species such as pāua, red rock lobsters, and various fish. The structural complexity of kelp forests, including holdfasts, stipes, and fronds, creates numerous microhabitats that serve as nursery and refuge grounds (Anderson et al. 2019; Morrison et al. 2014). The biomass and structural volume of habitat provided by kelps can vary significantly depending on the species, location, and region. These variations are further influenced by environmental factors such as wave exposure, substrate type, and light availability (Teagle et al. 2017). As a result, both the quantity and complexity of kelp-derived habitat differs across New Zealand.

It has been estimated that in northeastern New Zealand, approximately 130 fish species inhabit rocky reefs and their associated kelp forests (Jones 2013). Specific fish species, such as rarī/butterfish/greenbone (*Odax pullus*), utilise kelp forests throughout their juvenile and adult life stages, with the presence of giant kelp correlating with increased abundance and frequency of

occurrence (Pérez-Matus & Shima 2010a). *Ecklonia* forests have been identified as nursery habitats for leatherjackets, where kelp serves as principal settlement and initial growth areas (Kingsford & Milicich 1987). Additionally, it has been suggested that kelp beds provide habitat for grey mullet and john dory. In New Zealand, the critical role of kelp forests in habitat provision has led to their classification as foundation species under the Fisheries Management Act 1996, recognising their significance for fisheries management (Cryer et al. 2016). Consequently, the preservation of kelp beds is a key tenet of ecosystem-based management approaches to fisheries in New Zealand.

4.2 Kelp harvest

With the addition of *Macrocystis pyrifera* to the quota management system (1509.6 tonnes total allowable harvest in 2024–25), commercial kelp harvest has become a direct link between kelp forests and 'fisheries', with a range of other seaweeds also targeted or being considered for harvesting (e.g., Schiel & Nelson 1990; White & White 2020). In addition to direct harvest for commercial, recreational or customary use and the collection of drift kelp for natural fertilisers and animal feed supplements, there is considerable interest in the direct harvest of Phaeophyceae algae for a wide range of biomolecules. Alginate, which is a gelling polysaccharide, fucoidan a bioactive sulphated polysaccharide and phlorotannins are used extensively in a wide range of applications in food, cosmetics, pharmaceuticals and nutraceuticals (Kim & Bhatnagar 2011; Mak et al. 2013; Porse & Rudolph 2017) and comprise some of the key commodities obtained from the harvest of kelps. Within New Zealand, the invasive kelp *Undaria pinnatifida* is now able to be commercially harvested. Increasing interest, investment, and demand for algal products has the potential to lead to growing industries in the culturing and wild harvest of macroalgae (Bradly et al. 2021; Wheeler et al. 2021), although this has been done in the past with species other than kelps (Brasch et al. 1984).

4.3 Direct grazing

Direct macroalgal grazing by sea urchins (Echinoidea) and pāua (Gastropoda) supports two of the most accessible and valuable coastal fisheries in coastal rocky reef systems. Kina (*Evechinus chloroticus*) directly consume macroalgae and are the source of a local fishery. Kina comprise a localised fishery, but poor roe quality in the wild fishery restricted early expansion of the market internationally (Andrew 1988). Efforts to enhance roe quality within mariculture or natural restoration programmes persist (Miller et al. 2024). Nevertheless, as a customary and local commercial fishery managed under the Quota Management System (QMS), a majority of the sea urchins landed in New Zealand are sold on the domestic market (Miller & Abraham 2011). In contrast, the commercial, recreational and customary fisheries for pāua comprise a multi-million dollar enterprise with large cultural value and persist as one of the last wild caught abalone fisheries in the world (e.g., Gerrity & Schiel 2024; Schiel et al. 2023). These gastropods directly consume macroalgal-derived organic matter from a range of species and are reliant on healthy macroalgal communities for growth and reproduction. In addition to sea urchin and gastropod grazers, there are several herbivorous fishes that feed exclusively on kelps, most notable of these are butterfish which are subject to a commercial gillnet and recreational spear fishery (Paul et al. 2000).

4.4 Epifauna

One of the most important secondary channels for provision of kelp-derived organic matter into food webs supporting fisheries are epifaunal amphipods, isopods and annelids that graze and live on kelp (Taylor 1998; Taylor & Cole 1994). For example, Taylor (1998) estimated that epifauna comprise over 90% of the secondary biomass in many coastal macroalgal beds. These epifaunal species are important food for both juvenile and adult fishes many of which are subject to coastal fisheries (Newcombe & Taylor 2010). Epifaunal amphipods and isopods either directly consume macroalgae or graze on the eroding tips of thali. The functional group is ubiquitous within algal beds and dense concentrations of epifauna can be found on all of the native large brown algae, green algae as well as in turfing species (Taylor 1998). Additionally, the epifauna community structure on the invasive kelp *Undaria pinnatifida* has been shown to be similarly diverse and productive (e.g., Suárez-Jiménez et

al. 2017). Epifauna provide a direct channel for macroalgal-derived organic matter to support many coastal finfish and are found in the diets of a large number of species.

4.5 Production of suspended particulate organic matter

Through seasonal breakdown of thali or persistent erosion of the eroding ends of blades, kelps produce large amounts of suspended particulate organic matter (SPOM) that mix with phytoplankton, mixotrophs and bacteria to form the particulate organic matter pool in coastal regions. SPOM is directly taken up by suspension feeders and in many regions macroalgal-derived particulate matter can comprise a large fraction of the organic matter provision to suspension feeding invertebrates (Schlieman et al. 2022; Wing & Jack 2012). This important channel for kelp, and other macroalgalderived organic matter directly supports several important bivalve fisheries such as for wild kuku/green-lipped mussel (Perna canaliculus) and tipa/scallops (Pecten novazelandiae) (Schlieman et al. 2022). In addition, species such as the koura papatea/red rock lobster (Jasus edwardsii), rāwaru/pākirikiri/blue cod (Parapercis colias) and tāmure/snapper (Chrysophrys auratus) feed extensively on bivalves, thereby directly linking kelp-derived organic matter with production of key coastal fisheries species (Jack & Wing 2011; Jack et al. 2009; Kolodzev et al. 2023; Wing et al. 2012). For example, Jack & Wing (2011) found that among migrating rock lobsters, individuals were supported by an average of 73% macroalgal-derived organic matter, while reef-associated resident rock lobsters received a majority of their organic matter from macroalgal-derived sources (79%). While much of the labile SPOM produced by kelps is directly consumed in the food web, some enters the detrital food web channel and can then be recycled into the benthic food web for additional support for a range of coastal biodiversity including fished species.

4.6 Detrital production by kelps

Through their high productivity, kelp and other macroalgae are major producers of detritus for coastal food webs (Mann 1986) which can be detected using isotopic analysis (Duggins et al. 1989; Walton et al. 2022). Detritus is produced by kelps through constant erosion and loss of tissue from the distal portion of fronds, and the loss or removal of standing biomass. Production of macroalgal-derived detritus is vast with an estimated 80–90% of macroalgal based productivity entering detrital pathways either as SPOM or benthic detritus (Walton et al. 2022). Additionally, the estimated annual detrital production from the erosion of kelp blades ranged from 50–513 g C m⁻² across Nova Scotia, which exceeded the annual phytoplankton production and estimates of detrital production in seagrass beds in North America (Krumhansl & Scheibling 2011). The spatial distribution of kelp-derived organic matter is equivalently vast with evidence of kelp-derived production into the deep sea via submarine canyons (Harrold et al. 1998; Vetter & Dayton 1998).

Similarly, production of drift kelp and beach wrack represent wide ranging dispersal of kelp derived organic matter, both of which are consumed relatively quickly by amphipods and other grazers, thereby providing additional links to the food web. Through studies of kelp detritus it has been recognised that the nutritional quality and chemical composition of macroalgal-derived organic matter varied widely among species, according to concentrations of phenolic compounds and bacterial decomposition (e.g., Duggins & Eckman 1997). In New Zealand, concentrations of phenolic compounds in kelp derived detritus can vary over three orders of magnitude with some macroalgae containing halogenated forms that are natural toxins (McCarthy et al. 2024). Consequently, uptake of kelp derived organic matter in food webs can be very species specific (McCarthy et al. 2024). These findings highlight the importance of intact community structure of multilayered macroalgal forests in mediating the channels for macroalgal-derived organic matter into the coastal food webs that support fisheries.

4.7 Economic value of ecosystem services

Scientific advances since the seminal paper by Mann (1973) have resolved key pathways by which macroalgal-derived organic matter support coastal food webs and by extension coastal fisheries.

These studies have highlighted the scale of productivity in coastal systems supported by macroalgae, along with their key role in providing critical three-dimensional biogenic habitat, supporting biodiversity, secondary productivity and coastal fisheries. Through these studies, it is possible to estimate the direct and indirect economic contributions of macroalgae to coastal ecosystem services including fisheries. The research focus has shifted from studies of ecosystem function to economic estimates of the value of ecosystem goods and services provided by kelps and other macroalgae. In the southern hemisphere, for example, Vásquez et al. (2014) estimated that kelp beds in northern Chile had a total value of \$US540 million per annum of which \$82 million was direct support of associated fisheries and \$US409 million was direct harvest of kelps primarily for alginate. Similarly, Blamey & Bolton (2018) placed the economic value of South Africa's coastal kelp forests at \$US434 million per annum, with 59% of that value (\$US256 million per annum) attributed to fishing. The authors highlight severely overexploited abalone and rock lobster fisheries at less than 3% preexploitation values contributing to an underestimate of the economic potential of South Africa's kelp forest-based fisheries. Valuations focussed on Australia's Great Southern Reef place fisheries values for kelp-dependent rock lobster and abalone fisheries at approximately \$US350 million per annum (Bennett et al. 2015). Valuations such as these have been summarised and extended by Eger et al. (2023) who estimated that globally the ecosystem services derived from kelp forests are worth between \$US465 and 562 billion per annum of which approximately 28% (\$US144 billion) was attributed to direct kelp-derived fisheries production. These figures are likely to be underestimates as they only recognise direct commercial fisheries returns and not recreational fisheries or the indirect pathways of kelp-derived organic matter supporting fisheries in food webs. In the Australasian region (Australia and New Zealand) total ecosystem services of three species, Ecklonia radiata, Lessonia spp. and *Macrocystis pyrifera* have been estimated to be \$US3.7 billion per annum, with large percentages of the key fisheries for rock lobsters and abalone supported by kelp forest habitats (Eger et al. 2023). These estimates, both the existing and potential value of kelp-derived fisheries, highlight the need to quantitatively assess the contribution of kelp forests to biodiversity and fisheries in New Zealand.

5. QUANTITATIVE ASSESSMENT OF THE MACROALGAL CONTRIBUTION TO KEY FISHERIES

Kelps are globally recognised as foundation species supporting both abundance and diversity of associated fishes and invertebrates, many of which are exploited species (Dayton et al. 1998). These observations have been experimentally quantified in many kelp forest systems using kelp removal experiments at a variety of spatial and temporal scales (Carranza et al. 2024). For example, an experimental 9 year giant kelp removal study by Castorani et al. (2018) demonstrated a 30–60% decline in mobile invertebrate and fish biomass and a 40% decline in kelp-derived detrital availability in experimental plots cleared of giant kelp in California.

A complementary line of research has focussed on tracking the supply of kelp-derived organic matter to fish and invertebrates within kelp forest ecosystems. For example, a review by Elliott Smith & Fox (2022) demonstrated that among 43 studies using stable isotope analysis to trace the relative contribution of kelp-derived and phytoplankton-derived organic matter, average contributions of kelp-derived organic matter often exceeded 50% in coastal ecosystems. Resolving macroalgal-derived organic matter in food webs from organic matter produced by phytoplankton or terrestrial plants is facilitated by the fractionation of the stable carbon isotopes ¹³C and ¹²C between alternate inorganic carbon sources fixed by primary producers, CO₂, CO₂(aq) and bicarbonate. Because large brown algae can access carbon from the vastly abundant bicarbonate pool, the ratio of carbon isotopes tends to be more enriched in the heavy isotope ¹³C relative to phytoplankton or terrestrial plants which primarily access carbon from the CO₂ pools. This difference results in a reliable chemical tracer, the relative ratio of ¹³C and ¹²C relative to a standard or d¹³C, for broad resolution of the origin of organic matter between macroalgal-derived and phytoplankton-derived sources in coastal marine systems. Application of these tracers has resolved the contributions of kelp-derived organic matter to key

fisheries in New Zealand, including rock lobsters, bivalves and both coastal and shelf-based finfishes (Schlieman et al. 2022; Udy et al. 2019a; Udy et al. 2019b).

5.1 Kōura papatea/red rock lobster (Jasus edwardsii)

Kōura papatea/red rock lobsters (Jasus edwardsii) comprise the most valuable coastal fishery in New Zealand with landings that exceed \$300 million per annum in export value. They feed on a variety of invertebrates including sea urchins, sea stars, clams, mussels, pāua and other gastropods. All of their significant diet items have direct links to kelp-based organic matter through direct (sea urchins, gastropods), suspended particulates (clams and mussels) and detrital channels, therefore the food webs supporting red rock lobster populations are heavily dependent on healthy kelp forests. For example, Jack & Wing (2011) quantified the trophic position and contribution of kelp-derived organic matter to two distinct red rock lobsters populations in Fiordland: "run" lobsters migrating along the coast and "resident" lobsters directly associated with kelp forest habitats. The best descriptors/predictors of lobster abundance were the presence of kelp and mussels. The resident lobster population relied more heavily on macroalgal based organic matter with 79% of their biomass supported by macroalgal based production. In a related study in Fiordland, Jack et al. (2009) used stable isotopes to resolve food web position and use of macroalgal-based organic matter in lobsters from abundant kelp forest habitats compared to habitats in the inner fjord where macroalgal beds had been greatly reduced by freshwater outflows from the Manapouri Power Plant (Batham 1965; Jack et al. 2009). The inner fjord lobster population was very small and persisted on an alternative recycled source of benthic productivity linked to bacterial recycling, compared to the more abundant kelp forest-based population relying heavily on macroalgal-based organic matter. These results highlight the critical direct role that macroalgal based organic matter plays in supporting a valuable coastal fishery in New Zealand.

Kelp forest habitats also provide important ecological functions beyond food supply. They offer refuge and settlement cues for lobsters, particularly during vulnerable life stages (Shelamoff et al. 2022). For example, Hinojosa et al. (2014) found that both the settlement success and survival from predation of the early benthic phase of lobsters were significantly higher in natural *Macrocystis* habitat compared to artificial kelp or no habitat at all. Adult lobsters are also known to use kelp forests for shelter, food and foraging (MacDiarmid et al. 2013).

In addition, under some environmental conditions lobster can help to control the proliferation of kina, thereby contributing to kelp forest habitats by lessening overgrazing (Shears et al. 2008; Wing et al. 2022). This effect depends on environmental conditions, including low rates of coastal sedimentation and coastal warming, as well as recruitment and population dynamics of sea urchins, but represents a key positive feedback between a species dependent on kelp forest production, lobster, and healthy kelp forests (Schiel 2013).

5.2 Coastal and Continental Shelf Finfishes

Significant coastal finfish fisheries that utilise kelp forest habitats (but not necessarily exclusively) include blue cod, snapper, tarakihi (*Nemadactylus macropterus*), blue moki (*Latridopsis ciliaris*), kohikohi/trumpeter (*Latris lineata*), pūaihakarua/sea perch (*Helicolenus percoides*), kōkiri/leatherjacket (*Parika scaber*) and butterfish. These fisheries support recreational, customary and commercial usages. Each of these species, with the exception of butterfish, are broad spectrum omnivorous species feeding on a variety of marine invertebrates and small fishes. Butterfish is a herbivorous species directly consuming macroalgae throughout its life history but becoming fully dependent on a macroalgal-based diet following maturation (Curtis et al. in prep).

To quantify the contribution of a macroalgal-based diet to some of these species, Udy et al. (2019a) carried out a comparative study of the whole community contribution of macroalgal-based organic matter to fish biomass per unit area in the Fiordland region, where kelp forest habitats were abundant,

and in the Marlborough Sounds, where large areas of kelp forest habitats have been lost to sedimentation, urchin grazing, and coastal warming. Subtidal surveys were used in both regions to quantify the abundance and average biomass per unit area of 19 common coastal fish species, including many of the fisheries species cited above. Stable isotope analysis was then used to quantify the contribution of macroalgal-based organic matter to the fished species group and compare it between regions. In Fiordland, 77% of the biomass of fished species was supported by macroalgal-based organic matter. In the Marlborough Sounds, which had both depressed finfish populations and declining kelp forest habitats, only 31% of the biomass of fished species was supported by macroalgal-based productivity. These results provide a strong direct link between healthy kelp forest habitats and productive coastal finfish fisheries.

Further evidence for direct linkages between finfish fisheries and macroalgal based productivity comes from isotopic analysis of museum wet-fish collections and modern collections from coastal and shelf-based fisheries species (Durante et al. 2022; Sabadel et al. 2020). In a study using isotopic analysis of 16 species of New Zealand inner shelf, outer shelf, mid slope and outer slope fisheries species, significant amounts and changes in the use of macroalgal-based organic matter between modern and historic fisheries time periods were detected (Durante et al. 2022; Durante et al. 2020). Most exploited fish communities since the 2000s were found to have increased their reliance on pelagic production compared to the pre-2000s period when there was more coastal production supported by macroalgae. These data highlight the critical role that macroalgal-based organic matter has played in supporting fisheries production in New Zealand. Further, analysis of historical data has also highlighted the vulnerability of kelp forest production to land-based and climate-based stressors (Udy et al. 2019b).

5.3 Bivalves

New Zealand's coastal bivalve fisheries include valuable mussel (*Perna canaliculus*) and scallop (*Pecten novazelandiae*) fisheries. Both of these species rely on the coastal SPOM pool for food and actively filter large amounts of seston from the water column. Because macroalgae produce large amounts of particulate organic matter, their contribution to the SPOM pool can be significant, particularly in areas with abundant kelp forest habitats. For example, Schlieman et al. (2022) used stable isotope analysis to quantify the contribution of macroalgal-derived organic matter to five bivalve species, including scallops and mussels, in the Marlborough Sounds and Fiordland. The results indicated that large amounts of macroalgal-derived organic matter were used by both species and that the bivalve populations were particularly supported by macroalgal-based organic matter in areas where kelp forest habitats were abundant, and land-based stressors from runoff and sedimentation were low. These data provide a direct link between productive macroalgal communities and bivalve fisheries in New Zealand and also give an example of how important coastal management of stressors such as sedimentation can be to these valuable bivalve fisheries (Schlieman et al. 2022). The scallop fishery is, however, largely closed commercially because of multiple stressors leading to severely degraded habitats and poor recruitment.

5.4 Summary of the economic value of key macroalgal supported fisheries

It is difficult to provide accurate estimates of the total economic value of foundation species such as *Ecklonia radiata* or *Macrocystis pyrifera*, but estimating the contribution of fisheries asset value from bioenergetic contributions of macroalgae is slightly more straightforward. This can be a useful heuristic exercise for understanding the scale of bioenergetic contributions of macroalgae to fisheries based solely on their provision of organic matter. For example, as an estimate of relative value, we can add up the proportional contributions of macroalgal-based organic matter to the biomass of kelp forest-associated species from the studies cited above and apply these to the estimated fisheries asset value of each of these species (Stats NZ 2021). However, there are several important caveats that need to be considered. First, the current asset value represents, in many cases, devalued assets because many of the stocks are significantly below the biomass that delivers the maximum sustainable yield (e.g., Cryer et al. 2016). Therefore, the calculation does not represent the full potential value of

macroalgal contributions. Second, the list of species considered is not complete and there is ample evidence that contributions of macroalgal-based organic matter extend beyond species in this list. Furthermore, the direct asset values of *Macrocystis pyrifera* or other harvested macroalgae are as yet undefined in New Zealand, so this may be an underestimate of the total value (e.g., Durante et al. 2022). Third, the spatial resolution of macroalgal based contributions to fisheries is limited to only a few regions in New Zealand. Nevertheless, the data do resolve patterns across several regions and represent the best available information for New Zealand species. With these caveats in mind the calculation presents an order of magnitude estimate of the important contributions of healthy kelp forest habitats to the bioenergetics of a select group of kelp forest-associated fisheries assets of New Zealand. The contribution of macroalgae comprises approximately 72% of the asset value of these 13 kelp-associated fisheries species, whose total estimated asset value in 2019 was \$NZD5.24 billion, or approximately \$NZD4 billion of contributions of macroalgae to the asset value of these species alone (Table 1). Asset value is defined as the monetary value of a species derived from average values per tonne for quota transactions during the fishing year. It is a measure of the total combined tradable value of quota for a species. It is not a measure of annual value derived from the fisheries. This is a simplified calculation, but it does highlight the very large contribution of kelp in underpinning the full value of fisheries.

Table 1: Key fishery species supported by macroalgae and their associated annual asset value (from Stats NZ 2021).

| Species | Asset value (NZD millions) | Estimated proportion of biomass supported by macroalgae | Estimated asset value (NZD millions) of macroalgal contribution |
|----------------------|----------------------------|---|---|
| Red rock lobster | 3 482.5 | 0.77 | 2 667.6 |
| Pāua | 694.4 | 1.00 | 694.4 |
| Snapper | 650.7 | 0.54 | 351.4 |
| Blue cod | 168.8 | 0.61 | 102.6 |
| Tarakihi | 146.2 | 0.71 | 103.2 |
| Sea cucumber | 29.8 | 1.00 | 29.8 |
| Green-lipped mussel | 23.7 | 0.58 | 13.7 |
| Kina | 20.4 | 1.00 | 20.4 |
| Blue moki | 8.8 | 0.74 | 6.5 |
| Sea perch | 7.6 | 0.49 | 3.7 |
| Greenbone/Butterfish | 3.5 | 1.00 | 3.5 |
| Leatherjacket | 3.3 | 0.41 | 1.4 |
| Trumpeter | 1.4 | 0.50 | 0.7 |
| Giant kelp | | 1.00 | |
| Total | 5 241.1 | 0.72 | 3 998.9 |

6. LITERATURE ASSESSMENT OF THE IMPACTS OF MACROALGAE HARVESTING ON ECOSYSTEM HEALTH AND BIODIVERSITY

There is worldwide interest in the harvesting of kelps and other macroalgae. Buschmann & Camus (2019) provide an extensive list of globally harvested algae, and they estimated that the total wild harvest is approximately 526 000 t annually, which is likely to keep increasing from wild and cultivated populations. Within New Zealand, kelps, fucoids and other species have been harvested for decades, but currently only giant kelp is in the QMS. *Undaria* is permitted to be harvested from among the biofouling on mussel farms in select locations, and *E. radiata* and *L. variegata* are permitted to be collected from beach-cast material in some areas, but their commercial landings are estimated to be relatively small.

6.1 Macrocystis pyrifera harvesting

Macrocystis was harvested commercially for food, fertiliser and chemicals from the early 1900s for around a century along the coast of California (reviewed by Schiel & Foster 2015). Initial methods included removing whole plants (McPeak & Glantz 1984), but, this was soon replaced by cutting fronds, which was later restricted to an 8 m swath and a maximum depth of 1.2 m below the seasurface canopy. Kelp beds in southern and central California were numbered and harvested rotationally based on the state of the canopy and how much it had recovered from previous harvesting, storms and warm-water events.

Concerns about the ecological impacts of harvesting emerged in the 1950s, prompting investigations into potential effects on kelp forests and associated marine life. These concerns included the possible loss of kelp forests, reduction of canopy-dwelling fishes and invertebrates, reduction of fish populations due to loss of food and /or habitat, increased beach erosion due to less dampening of water motion, and an increase in the abundance of drift kelp on beaches from cut fronds and dislodged plants not captured by the harvester. Following investigations, North & Hubbs (1968) and Barilotti & Zertuche-González (1990) found no significant ecological effects of harvesting. While many organisms are removed with the cut fronds (e.g., North & Hubbs 1968), overall reductions within a forest were not reported. However, the possible changes in populations of consumers such as abalone and fishes in kelp forests, beaches, and offshore due to an indirect effect of removing the biomass and primary production of sea-surface kelp were not investigated. Within New Zealand, studies by Pirker (2002) also found minimal effects of *Macrocystis* canopy harvesting, however, they reported an overwhelming influence of land-sourced sedimentation on the standing crop of *Macrocystis* in Kāi Tahu/Akaroa Harbour, Waitaha/Canterbury.

The lack of detectable impacts from harvesting is at least partly due to the life history traits of *Macrocystis*. Individuals can have hundreds of fronds growing from a holdfast, although plants tend to have only several fronds in New Zealand (Kain 1982). Since reproductive fronds (sporophylls) are located just above the holdfast, surface harvesting primarily affects vegetative fronds. However, fecundity is a function of vegetative biomass (Neushul 1963) which can be reduced by storms, grazers (Graham 2002; Reed 1987), or artificial removal of the canopy (Geange 2014), and its recovery can lag behind vegetative recovery (Graham 2002). Other beneficial life history traits include high growth rates, where stipes can elongate 50 cm daily, which is among the fastest on record for any autotroph (Clendenning 1971). At least in California, the lifespan of an individual frond is about three to five months, and entire adult plants live an average of two to three years (North 1984). The large, year-round reproductive potential of *Macrocystis* and its ability to form floating rafts when whole plants are removed in storms greatly aids its recovery after a disturbance (Edwards & Estes 2006, Reed 2006). This differs from other kelps which usually do not have multiple fronds, have their reproductive structures in the laminae (blades) at the top of plants, and often have little or no ability to float and disperse (such as the New Zealand common kelp, *E. radiata* and *Lessonia* spp).

Differences in life history traits between kelp species led to restrictions on the harvesting of *Macrocystis* in California when it co-occurred with another kelp, *Nereocystis luetkeana*. In contrast to *Macrocystis*, *N. luetkeana* is an annual species that produces spores on surface fronds and therefore harvesting these fronds can reduce the abundance of future generations of sporophytes (Springer et al. 2006). This species has not been purposefully harvested, but it has undergone large die-offs in northern California due to a combination of repeated warm water events coupled with low nutrients and the significant expansion of sea urchin populations (Rogers-Bennett & Catton 2019). This highlights the variability of effects of biomass loss in different species, and the interactions with multiple environmental and ecological stressors that can differentially affect nominally similar species.

6.2 Removal and recovery of kelp

Kelp removal and recovery experiments and observations have been conducted for several decades in many areas of the world. One of the earliest examples of *Macrocystis* removal was by Pearse & Hines (1979) who cleared a 10×20 m plot in central California. They found that several species of kelp and red algae became established within a year, but that over time, *Macrocystis* dominated the areas due to shading by their canopy. More recent international examples include Castorani et al. (2021) who found that, over a decade, there was some compensation in net primary productivity by understory species following repeated removal of *Macrocystis*, but that the quality of the habitat was a significant factor mediating the effects of intensified disturbance on canopy and understory productivity.

Removal experiments using *Ecklonia* plants within New Zealand have dated back to the late 1970s. Studies by Schiel (1980) removed mature *Ecklonia* by cutting off individuals above the holdfast in replicate 1 m² plots inside and outside of the peak reproductive season. Plots cleared in early spring when *Ecklonia* was reproductive had four times as many recruits as control plots and soon formed a dominant canopy due to its faster growth rate compared to nearby fucoid species. However, plots cleared in summer when fucoids were reproductive had large numbers of fucoid recruits and eventually produced a mixed canopy of *Ecklonia* and fucoids. Overall, it was recommended that if any harvesting of *Ecklonia* were to be done, it should only be in small patches that are widely dispersed within a kelp bed so that short range dispersal from nearby reproductive plants is possible. This is especially important because *Ecklonia* adults do not float and effective spore dispersal is likely to be only a few metres (Gaylord et al. 2002).

The southern bull 'kelp' *Durvillaea*, which is the world's largest fucoid, has also been considered for potential harvest. Experimental clearances similar to those of *Ecklonia* showed that rocks cleared of *Durvillaea antarctica* during the reproductive season in winter had up to 7000 recruits of *Durvillaea* per square metre, whereas those cleared at other times had virtually no recruitment and other algae occupied the cleared area (Hay & South 1979). Larger scale removal where entire *Durvillaea* individuals are harvested is unlikely to be feasible. *Durvillaea poha/antarctica* reproduces for only about 6 weeks during winter, is dioecious (so male and female plants must be in close proximity for fertilisation to occur), the effective gamete settlement distance is mostly up to about 30 m, and the effective target area for sporefall and replenishment of populations is only a narrow band in the very low intertidal zone on exposed shores.

Futhermore, Schiel et al. (2021) showed that this species did not recruit in any significant numbers over the five years after the coastal uplift caused by the Kaikōura earthquake in November 2016. In addition, its loss had cascading effects on the nearshore ecosystem. One such effect was a large decrease in primary productivity as *Durvillaea* was replaced by smaller and far less productive fucoids, such as *C. mascahlocarpum* (Mangan et al. 2023). *Durvillaea* was also removed in many sites south of Kaikōura in the air and sea heatwaves of 2017–2018, and has not recovered (Thomsen et al. 2021). Previous considerations for the harvesting of *Durvillaea* were therefore deemed to be inadvisable (Hay & South 1979).

6.3 Kelp bed diversity

Diversity within kelp bed habitats is greater than diversity when kelps are removed, predominately because of the biogenic habitat and three-dimensional structure afforded by kelps (Graham et al. 2007). Within New Zealand, there are no known obligate species associated with *Macrocystis* (compared to California; Graham et al. 2007), but stipitate kelps such as *Ecklonia* can be present in the *Macrocystis* understory and are abundant on reefs in New Zealand. Studies internationally have shown that when *Macrocystis* canopies are removed, light increases to the understory and in some cases, there is productivity compensation by understory kelps (Castorani et al. 2021; Miller et al. 2011). With few exceptions (e.g., butterfish which feeds directly on kelp and fucoids, Clements & Bellwood 1988) these kelps in combination fuel the food web through detritus and particulate organic matter rather than direct feeding on attached tissue (Udy et al. 2019a).

There is an extensive literature on fish diversity in and around kelp forests (e.g., Jones 2013). For example, Williams et al. (2008) found that the diversity of fish assemblages decreased from kelp to sand habitats. In addition, Willis & Anderson (2003) found strong positive correlations between habitat complexity (*Ecklonia* forest versus urchin barrens) and the density and diversity of cryptic fish assemblages. A recent global meta-analysis highlights the increased abundance of reef fishes within kelp forest habitats and the enhanced recruitment of early life history stages (Pérez-Matus et al. 2025). Furthermore, increased fish diversity can positively influence kelp forest habitats via the consumption of macroalgal grazers (Pérez-Matus & Shima 2010b) and act as a potential zoospore disperser (Ruz et al. 2018).

6.4 Other potential community effects

Organic matter from kelps plays a crucial role in the coastal food web. As kelps grow, the older sections of their primary fronds move upwards and erode due to water motion, dispersing into the surrounding water. This dispersed organic matter is consumed by small invertebrates or bacteria, contributing significantly to the ecosystem. Additionally, large amounts of beach-cast seaweeds create fertile grounds for a diverse array of invertebrates and kelp flies (Inglis 1989). These seaweeds often break down within several days and return to nearshore waters during tidal surges. While these effects are generally diffuse, they can be detected chemically through isotopic studies within the food web, demonstrating that they enhance the productivity and food web of nearshore waters (Duggins et al. 1989; Walton et al. 2022).

7. NATIONAL AND INTERNATIONAL LEVEL ASSESSMENT OF THE TOP-DOWN INFLUENCE OF PREDATORS ON KELP FORESTS

One of the most pervasive issues relating to kelp forests is the role of herbivory, predation, and trophic cascades on kelp forest structure. In its simplest form, the idea is that the removal of top predators, usually large fish and lobsters, from kelp communities allows key grazers such as sea urchins to proliferate, which can decimate kelp beds. This change from kelp forest to urchindominated areas are often referred to as alternate stable states, which can last several decades (Elner & Vadas 1990; Filbee-Dexter & Scheibling 2014; Petraitis & Dudgeon 2004). Cessation of fishing, especially through marine protected areas (MPAs), has been proposed to restore ecological relationships, re-establish trophic control of grazers, and thereby allow kelp communities to flourish. This review aims to summarise some of the key arguments. Examples of more in-depth reviews include Doheny et al. (2023) for trophic cascades in kelp assemblages nationally and internationally, Steneck et al. (2002) for a global perspective and history of kelp forest deforestation, and Choat (1982) on the role of fishes in structuring benthic communities.

7.1 International examples of top-down influence

Top-down control mediated through trophic cascades has been observed in kelp forest communities globally (Estes et al. 1998; Ling et al. 2015; Steneck et al. 2002), and has been shown to explain 7–10 fold more variance in the abundance of bottom and mid-trophic levels than bottom-up control (Halpern et al. 2006). This effect has been shown to be particularly evident in mid-latitude regions where kelp communities can be less constrained by physical factors such as temperature and nutrients, resulting in herbivory being suggested as the most common and important agent of kelp forest declines (Steneck et al. 2002).

The conversion of kelp forests to urchin barrens has been documented worldwide, such as in Alaska, the Gulf of Maine, Japan, Chile, Australia and Norway (Ling et al. 2015; Steneck et al. 2002). Sea urchin barrens are defined as areas of rocky reef that would typically support kelp forest but are instead dominated by sea urchins and have little to no kelp due to overgrazing (Doheny et al. 2023). While many factors can influence sea urchin population dynamics (e.g., disease, storms, and warming

currents) the removal of predators has been frequently identified as the primary driver of urchin proliferation. Notable examples include the extirpation of sea otters in California (e.g., North & Pearse 1970), and the removal of predatory fish and lobsters in California and Nova Scotia (Chapman 1981; Dayton et al. 1998; Tegner & Dayton 2000). Predator traits, particularly size and foraging behaviour, have been shown to play a critical role in regulating urchin populations. For example, Hamilton & Caselle (2015) found that larger male sheephead wrasse exerted greater predation pressure on urchins, and their selective removal reduced top-down control. Similarly, Johnson et al. (2013) demonstrated that large lobsters were more effective at suppressing *Centrostephanus rodgersii* in Tasmania, with their distribution and foraging behaviour influencing the persistence of urchin barrens. These studies underscore the importance of predator traits and environmental variability in shaping kelp forest dynamics, and highlight the role of feedback mechanisms that can reinforce either kelp- or urchin-dominated states. Nevertheless, other mechanisms such as sea urchin population dynamics can also play a role, with significant kelp recovery occurring following disease outbreaks (Scheibling 1986, Williams et al. 2021).

7.2 National examples of top-down influence

Discussions and examples of the top-down influences on kelp forests within New Zealand often consist of the role of predation on sea urchins. Urchin overgrazing has been shown to be a significant driver of kelp forest loss, particularly where environmental conditions are favourable, such as in northeastern New Zealand (Kerr et al. 2024; Ling et al. 2015). Kina (*Evechinus chloroticus*) is the dominant barren-forming sea urchin in New Zealand (Shears & Babcock 2007), however, recently the sea urchin *C. rodgersii* has been increasing in parts of northeastern New Zealand (Balemi & Shears 2023). This species can co-occur with kina but can also form barrens in deeper water. An important morphological distinction between the two species is the longer spines of *C. rodgersii* when compared to kina which is likely to make it less vulnerable to predation.

In northeastern New Zealand, kina barrens are typically found in shallow waters from 2–10 m on open rocky coasts (Choat & Schiel 1982; Shears & Babcock 2004). These barrens are bordered by mixed algal forests dominated by wave-tolerant species such as *C. maschalocarpum* and *C. angustifolium*, and by largely monospecific beds of *Ecklonia* at greater depths (Blain et al. 2021). High densities of urchins can extend deeper than the limit of kelp beds, especially with increased wave exposure, reaching depths of up to 20 meters in highly exposed locations (Grace 1983; Shears & Babcock 2004). Urchin dominated areas have been observed across parts of the North Island and the Marlborough Sounds but have yet to be observed extensively further south.

Within New Zealand, the main predators of kina are considered to be snapper (predominantly in northern New Zealand (Marinovich et al. in press)), blue cod, and red rock lobster (Shears & Babcock 2002), but other predators are likely to include leatherjackets, large starfishes (Pātangaroa/Coscinasterias muricata and tangaroa wae whitu/Astrostole scabra), red moki (Cheilodactylus spectabilis), tāngahangaha/banded wrasse (Notolabrus fucicola) and hāpuku (Polyprion spp.) (Doheny et al. 2023). The presence of predators also indirectly alters behavioural interactions by modifying the movement and location of prey species (Doheny et al. 2023; Spyksma et al. 2017). In sea urchins, predator avoidance, escape responses and defence behaviours have been shown to reduce herbivory and grazing effects. Additional indirect effects include altering the supply of kelp-derived organic matter assimilated by filter feeders (Salomon et al. 2008).

In regions where kelp loss is linked to urchins and the harvest of their predators, rebuilding predator populations through MPAs has been shown to be a viable approach to restoring kelp forests and their associated ecosystem services (Babcock et al. 2010; Peleg et al. 2023). For example, the higher density of predators, mainly lobsters, within two marine reserves was estimated to increase the likelihood of kina predation by seven times (Shears & Babcock 2002), and there was a decrease in urchin-dominated regions in the Cape Rodney-Okakari Point Marine Reserve which was attributed to an increase in the number and size of snapper (Denny et al. 2004). Further, a review of long-term

studies within MPAs showed that recovery of predators can shift the balance from urchin to kelp dominance, with kelp and fucoids returning as urchin numbers decline (Shears & Babcock 2003).

While urchin overgrazing is a pervasive threat to kelp forests, the factors leading to barrens are context specific, varying across and within regions depending on biotic and abiotic factors (see review by Doheny et al. 2023). Additionally, it is important to understand the role of multiple stressors, including environmental factors, which can interact with species' life histories and demography and ultimately overwhelm ecological and trophic effects (Reed et al. 2011). For example, warming seas have had overwhelming effects on kelp, urchins and other key organisms in Tasmania where the onshore advection of warm water currents facilitated the transport of sea urchin larvae from the mainland (Johnson et al. 2013), and in New Zealand the range expansion and population explosion of *C. rodgersii* is rapidly impacting kelp in areas of the northeast exposed to warming currents (Balemi & Shears 2023).

8. THE VULNERABILITY OF KEY MACROALGAL GROUPS TO ENVIRONMENTAL STRESSORS

There is a vast literature on environmental influences on kelp, particularly temperature, light, nutrients, storm events – particularly those associated with basin-wide events such as El Nino – and the interaction of all of these on various life stages. Virtually all algal species are limited in distribution by a combination of these factors, but the specifics vary considerably by species and physiology. For example, giant kelp losses can be highly seasonal, localised or basin-wide, with considerable regional differences (Bell et al. 2015; Reed et al. 2011). In a global analysis of patterns of kelp forest change over the past 50 years, Krumhansl et al. (2016) identified kelp declines in 38% of ecoregions, no change in 35%, and increases in 27%. They concluded that while global drivers could be affecting kelp forests at multiple scales, local stressors and regional variability in the effects of these drivers dominate kelp dynamics. Notably, this study included data from northeastern New Zealand where it was inferred that relatively high magnitude increases could be expected, although there was some statistical uncertainty due to the limited data range from 1999 to 2011.

8.1 Rising temperatures

Temperature influences processes across all biological scales, and affects the growth, distribution and physiology of macroalgae. Species occupy defined thermal niches, partly because they are adapted to specific temperature ranges where cellular and physiological processes can occur close to their optima (Pörtner & Farrell 2008). As both atmospheric and oceanic temperatures increase, populations close to their upper thermal distributions can be disproportionately affected. Acute or chronic thermal stress to macroalgae can eventually lead to population changes such as decreased abundance, altered size structure, range shifts and regional extinctions (review by Smale 2020). Examples of these changes have been documented in a few places globally and include comparisons of macroalgal communities on both the Indian and Pacific Ocean sides of the Australian continent which showed poleward shifts between the periods of 1940–1960 and 1990–2009 (Wernberg et al. 2011), and a reduction in abundance, local extinction or range contractions for some kelp species across the North Atlantic (Smale 2020). However, it is less understood how permanent these shifts may be.

Superimposed on gradually increasing ocean temperatures, is the increase in marine heatwave events which are becoming progressively more frequent and intense (Frölicher et al. 2018; Montie et al. 2024; Oliver et al. 2018). Over a period of 30 years of satellite derived sea surface temperature estimates, there has been a 95% increase in coasts experiencing extremely hot conditions (Lima & Wethey 2012), and a >50% increase in the average number of days in the global ocean experiencing marine heatwave conditions over the last century (Oliver et al. 2018). In New Zealand from 1982–2021, there was an increase in marine heatwave metrics across 70% of all ecoregions (Montie et al. 2024). The consequences of these events have been shown to have severe deleterious effects on whole

populations of giant kelp in some places (Tait et al. 2021), including reducing the growth rate of juvenile sporophytes (Bunting et al. 2024), and on populations of bull kelp (Thomsen et al. 2019). In general, it is the relative deviation from the temperature variation normally experienced at a location that causes the greatest deleterious effects, rather than the absolute extent, duration or intensity of the event (Holbrook et al. 2019).

Marine heatwaves can cause local temperatures to exceed key physiological thresholds, which have already been shown to have deleterious ecological consequences in both temperate and subtropical regions. For example, several high-magnitude heatwaves have affected Western Australia in recent years, including in the summer of 2010–2011 when sea temperatures were up to 5°C above the climatological average (Wernberg et al. 2013). Within several months, there were significant declines of *Ecklonia* and a more than 100 km range contraction of the fucoid *Scytothalia dorycarpa*, both of which were ultimately replaced by weedy algal turfs which supported lower productivity and biodiversity (Filbee-Dexter & Wernberg 2018). After a succession of warm summers, it was estimated that 43% of kelp forests in southwest Australia had been lost or severely reduced (Wernberg et al. 2016). The duration of these reductions or whether they are very long lasting is, however, not well documented.

For intertidal macroalgae, ocean warming can occur concurrently with atmospheric temperature increases, desiccation and UV stress during emersion at low tide (Helmuth et al. 2006; Thomsen et al. 2019). In temperate zones, aerial thermal stress is greatest in summer, especially on calm and clear days when low tide occurs in the afternoon. If these conditions persist over consecutive days, the survival and physiology of intertidal macroalgae can be compromised (Fernández et al. 2015a; Ferreira et al. 2014; Hereward et al. 2020; Martínez et al. 2012).

Increases in ocean and atmospheric temperature can also indirectly affect kelp communities by introducing novel taxa (Cavole et al. 2016; Vergés et al. 2014) and altering habitat availability (Filbee-Dexter & Wernberg 2018; Kumagai et al. 2018), thereby affecting food web dynamics by changing the relative abundance of species and shifting trophic dynamics and competitive interactions between species (Harvell et al. 2019; Hawkins et al. 2009; Mieszkowska et al. 2006; von Biela et al. 2019). The latter is particularly evident in polar regions where decreased ice cover has led to changes in light and substrate availability in coastal regions which has resulted in an increase in suitable habitat and the expansion of kelp beds in some regions (Filbee-Dexter et al. 2019; Krause-Jensen & Duarte 2014).

8.2 Ocean acidification

Atmospheric carbon dioxide (CO₂) levels have risen by more than 150 ppm since the industrial revolution, and are continuing to rise at a current rate of 2.77 ppm per year (as at November 2024; Lan et al. 2024). The accompanying absorption of atmospheric CO₂ by the oceans has led to an average reduction of open ocean pH by 0.1 units and an alteration in carbonate chemistry, termed ocean acidification (OA) (Orr et al. 2005). These declines in global surface pH are expected to continue by a further 0.3–0.4 pH units by the end of the century. It is likely, however, that coastal environments may experience periods of these projected 2100 pH conditions sooner than open ocean environments because of their inherently large natural fluctuations of pH, along with temperature, salinity and oxygen which can occur on tidal, daily, seasonal and annual time scales (Baumann et al. 2015; Frieder et al. 2012; Hofmann et al. 2011; Saderne et al. 2013). The magnitude of pH fluctuations on these varying timescales is influenced by multiple factors such as, freshwater inputs, upwelling events, temperature, tidal cycles, photosynthesis and respiration.

While it is well documented that OA is likely to have negative consequences for many calcifying species (including some algae) such as reduced growth and calcification rates, it is currently unclear how OA will influence the physiology and ecology of large habitat-forming macroalgae (Cornwall et al. 2012; Falkenberg et al. 2013; Fernández et al. 2015b). Reductions in seawater pH may have minimal effects on photosynthesis and growth because kelps are able to actively uptake bicarbonate,

the most abundant source of dissolved inorganic carbon in seawater, using carbon concentrating mechanisms (CCM) (e.g., Fernández et al. 2015b). Alternatively, the projected increase in dissolved CO₂ may facilitate the diffusive uptake of CO₂, resulting in a down-regulation of CCM and potentially increasing growth and photosynthesis rates (Schlenger et al. 2021). However, reduced growth has also been observed in some species, such as *Fucus vesiculosus* (Gutow et al. 2014) and the kelp *Saccharina latissima*, with the latter attributed to the pH sensitivity of CCM (Swanson & Fox 2007), and reduced photosynthetic rates have been observed in juvenile *Ecklonia radiata* (Britton et al. 2016). To date, observations have been highly specific to species and location, with several environmental factors such as nutrient supply, light intensity, temperature and season reportedly influencing the response to reduced pH (elevated pCO₂) conditions (e.g., Ní- Longphuirt et al. 2013).

Kelp forests have been considered as a potential refugia from OA for associated calcifying species. Despite being transient and limited to daily and seasonal cycles, diel changes in pH occurring as a result of photosynthetic activity within kelp forests, have been observed to have positive effects in some marine species in highly retentive areas (Hurd 2015; Kapsenberg & Cyronak 2019). However, there is no uniformity in these effects because the scale of buffering depends on a multitude of interacting factors such as currents, wave climate, changes in flow attenuation within the kelp forest and other local physical characteristics (Bednaršek et al. 2024; Hoshijima & Hofmann 2019; Koweek et al. 2017; Traiger et al. 2022). In addition to direct effects, it has been suggested that OA alters competitive dynamics between calcareous species and fleshy seaweeds which has the potential to drive significant ecosystem shifts (Kroeker et al. 2013).

8.3 Sedimentation and a changing light climate

Sedimentation and increasing water column turbidity are pervasive issues in coastal ocean environments globally because they can alter physical, biological and biogeochemical properties and processes. Coastal erosion is amplified by land-based anthropogenic activities such as deforestation, agriculture, urbanisation and coastal development, which can be exacerbated by climatic changes such as increased precipitation, storm events and sea level rise (Neverman et al. 2023; Smith et al. 2023). New Zealand is no exception, with an estimated 192 million tonnes of soil lost each year equating to 1.7% of global sediment delivery (MfE and Stats NZ 2018).

Sedimentation has been shown to influence the distribution of macroalgae along rocky shore and soft sediment habitats (see review by Airoldi 2003), including within New Zealand (Morrison et al. 2009; Wing et al. 2022). Sediment can disrupt the settlement and attachment of kelps during their microscopic stages (Arakawa & Matsuike 1992; Chapman et al. 2002; Devinny & Volse 1978) and can lower the survival and germination rates of successfully attached spores through scouring and sediment burial (Arakawa & Matsuike 1992; Schiel et al. 2006). For adults, sedimentation has been found to decrease primary productivity (Alestra et al. 2014), reduce growth, and impair regeneration (Umar et al. 1998), which can ultimately influence species composition and distribution (Airoldi 2003). However, the persistence of some kelp forests in sediment-influenced habitats has been linked to specific morphological and life history traits, such as robust thali, apical growth and vegetative reproduction (Airoldi 2000; Airoldi & Cinelli 1997; Littler et al. 1983).

Often coupled with sedimentation is an increase in water column turbidity though suspended sediments which can greatly limit the light and therefore energy available for photosynthesis (Gattuso et al. 2006). Blain et al. (2021) showed that water column turbidity alone reduced light availability within *Ecklonia* forests by 63%, resulting in a 95% reduction in primary productivity. Considering that macroalgae can contribute up to 90% of total carbon to coastal food webs (Duggins et al. 1989; Gattuso et al. 2006), reduced primary productivity through light limitation can have direct implications for coastal food webs and carbon sequestration pathways (Blain et al. 2021). Gradients of increasing sediments have also been shown to severely compromise the health and resilience of giant kelp beds (Tait 2019).

Light availability within macroalgal forests is highly dynamic, and along with water column turbidity, can also depend on atmospheric conditions, tides and shading from canopy foliage (Tait 2019). Macroalgae employ a range of mechanisms to deal with this variability including dynamic photoinhibition under high light stress, acclimation through varying concentrations of specific pigments and adaption through changes to thallus morphology which can alter the efficiency of light absorption per unit of photosynthetic tissue (Blain et al. 2020; Colombo-Pallotta et al. 2006; Johansson & Snoeijs 2002). However, if turbidity persists, it can affect the density, biomass and depth distribution of kelp forests (Desmond et al. 2015; Kirkman 1989; Tait 2019), as well as affect the resilience of kelp beds to multiple stressors (Krumhansl et al. 2016).

8.4 Eutrophication

Coastal eutrophication is driven by elevated nutrient enrichment from increased anthropogenic inputs (which are often concomitant with sediment inputs). This stimulates the growth of phytoplankton which ultimately increases light attenuation within the water column (see Section 8.3 for implications of a changing light climate) and ephemeral, opportunistic macroalgae with high maximum intrinsic growth rates. Large, perennial algae with lower intrinsic growth rates are not stimulated to the same extent and therefore increased nutrient availability is not generally reported to have direct effects on kelp canopies. However, greater nutrient concentrations can create favourable conditions for turfing species to colonise rapidly and retain space if other stressors such as storm events cause losses of canopy cover (Andrew & Sean 2006). This is evidenced globally where turf-forming algae have formed extensive habitats within subtidal rocky reef environments adjacent to urbanised coastlines (Benedetti-Cecchi et al. 2001; Coleman et al. 2008; Eriksson et al. 2002; Gorgula & Connell 2004; Middelboe & Sand-Jensen 2000), which are anticipated to be more pronounced where there is a greater disparity between historical and current nutrient loads (Gorman et al. 2009).

Turf species generally have a limited capacity to store nitrogen (Pedersen & Borum 1996) but are often able to persist under continued elevated nutrient loading leading to enhanced competition for space. Over time, turf algae additionally accumulate sediment (Airoldi et al. 1995) which further acts to inhibit the recruitment of canopy-forming kelp (Kennelly 1987). The shift from perennial species that form structurally complex communities to opportunistic species that create simpler environments can lead to less diverse habitats, including changes to community dynamics such as reductions of grazing invertebrates and alteration of local physical properties (Benedetti-Cecchi et al. 2001; Graham 2004).

8.5 Changing wave climate

Waves and water motion influence many physical properties including light, oxygen, sediment movement and nutrient availability, and therefore strongly influences the composition of rocky shore communities (Burrows et al. 2008; Pedersen et al. 2012; Smale & Vance 2015; Wernberg & Connell 2008). Waves also indirectly influence canopy forming algal communities by altering the dispersal distance of propagules, with estimates up to several kilometres from the parent plants (Gaylord et al. 2002). Additionally, wave action influences the persistence of adult plants (Jonsson et al. 2006) and their depth distribution (Assis et al. 2024; Graham 1997). It also affects the vigour of canopy sweeping which in turn modifies sediment accumulation and light exposure (Kennelly 1989), as well as the abrasion from fronds which affects the recruitment, survival and growth of understory algae and invertebrates (Connell 2003). By modifying many ecological and physical processes that influence community dynamics, changes in wave exposure can have widespread implications for rocky shore communities.

As climate change progresses, coastal wave climates are predicted to change with higher wave heights, altered wave directions, and more intense and severe storm events which will increase the number and magnitude of physical disturbances these communities will experience (Meehl et al. 2000; Mori et al. 2013; Ummenhofer & Meehl 2017; Wang et al. 2014). While the implications of these changes are complicated and likely to be location and community specific, there is evidence of

reductions in the diversity and complexity of kelp forest food webs (Byrnes et al. 2011; Castorani et al. 2018) and modifications to kelp forest structure (Smale & Vance 2015). When combined with other stressors such as rising temperatures, canopy forming algae can reach lethal physiological and hydrodynamic stress, further decreasing population extent (Cavanaugh et al. 2011; Hawkins et al. 2009).

9. MONITORING METHODS, THEIR UTILITY, LIMITS, AND CAVEATS

9.1 In situ diver surveys

In situ diver surveys can provide accurate information on species' extent, distribution, abundance and biomass, and habitat characteristics. Additionally, experienced human divers are highly adaptable and can provide additional insights and detailed information on any unusual or significant observations. Divers are particularly useful in cases where thick macroalgal canopies are present. In these cases, towed or remote operated cameras can have difficulty observing key sub-canopy metrics, while divers are capable of moving canopies aside and collecting quantitative information.

Key methodology includes transect and quadrat surveys and timed searches which can be repeated by using fixed positions which can be revisited using GPS and on-surface location or fixed *in situ* marks. However, diver surveys require trained dive personnel with taxonomic skills if species identification is required. Because of this, spatial coverage is dependent on the size of the dive team, approach, depth and environmental conditions. Physiological limitations of divers underwater limit both the coverage and depth distribution of surveys.

9.2 Camera surveys

Camera surveys include drop cameras, towed video, or the use of robots either as autonomous underwater vehicles (AUVs) or remotely operated vehicles (ROVs). High accuracy of species identification, density and extent can be collected in good weather conditions, and these surveys are often faster and generally less expensive than diver surveys. In addition, these systems can ascend and descend repeatedly (unlike diver surveys), are typically rated well beyond standard diving depths, and therefore can complete more surveys within a day. However, overlap of the canopy can obscure understory species, all optical surveys require good visibility, and manoeuvrability is often limited.

Drop cameras are typically cheaper, quicker, easier to deploy and require less maintenance then AUVs or ROVs. They often require smaller teams to operate and can be used to rapidly image large areas of the seafloor. They can be towed to follow a transect line and have a relatively greater spatial resolution of up to 2 km²/day (Tillin et al. 2023), but there is little control over their exact position, and they are greatly affected by swell which can lead to a large proportion of photographs being unsuitable for quantitative analysis.

An AUV is a battery-powered, unmanned underwater robot that can operate independently of a surface vessel for durations ranging from a few hours to several days. AUVs can execute a fully preplanned survey mission or adapt their plan during the mission as more advanced control systems are developed. Once the AUV surfaces, the collected data are transferred via a WiFi link or data cable. In contrast, an ROV is connected to the surface by an umbilical cable. This cable transmits control signals to the ROV and sometimes supplies power to the ROV, while simultaneously sending video footage and telemetry data back to the operator at the surface.

Small AUVs and ROVs, typically less than 3 m long, can be manually deployed from the shore or small vessels making them particularly suited for macroalgae surveys. Both systems are adept at gathering geophysical, biological, and oceanographic data from both the seafloor and the water column. They can operate less than 5 m over the seabed as well as being equipped with high-definition camera systems. Combined with advancements in image processing, this enables the

creation of extensive imagery datasets. These datasets can be processed to produce continuous, georeferenced photographic coverage of the seabed, covering up to 1 km²/day (Tillin et al. 2023). However, AUVs and ROVs are more expensive to operate than towed systems, are more prone to equipment failure, and often require a highly skilled pilot or technical support. For smaller ROVs, there are power limitations at increased depths (due to increased drag) and challenging environmental conditions can also reduce performance, along with the risk of entanglement of the tether which can lead to the loss of the instrument.

9.3 Acoustic surveys

Acoustic surveys, although having been used in deepwater and pelagic fisheries for some time, are emerging as an efficient tool for marine benthic habitat assessments that can be automated and cover large spatial scales (Brown et al. 2011; Nau et al. 2025; Schimel et al. 2020). These types of surveys typically produce sonograms of reef sounds which, when identified, can lead to assessments of species present in an area. Macroalgal beds significantly influence the strength of acoustic backscatter by dampening the return echo signal. Sonar systems can be operated from boats with the sensor (transducer) mounted on the hull or towed. There are two main types of sonar: single beam echosounders (SBES) and swath sonars (sidescan and Multi Beam Echosounder (MBES)). Single beam echo-sounders emit a vertical cone of sound that ensonifies a specific area of the seabed (a circle in its simplest form) directly beneath the vessel. The sound reflects off the seafloor and returns to the transducer, which converts the sound energy back into an electrical signal. This signal is then analysed as a time-trace of the energy. SBES are the simplest of the SONAR systems, and their echo analysis is much less complex compared to swath systems like sidescan and multibeam sonars. Swath sonars, on the other hand, ensonify a strip of the seabed perpendicular to the vessel, with the range on either side depending on the sonar's frequency (Davies et al. 2001) and can provide a greater spatial coverage.

Acoustic surveys have the advantage that they are not limited by water column turbidity (Brown et al. 2011) and have been shown to distinguish between canopy-forming and filamentous macroalgae (Lubsch et al. 2020), such as different species of *Laminaria* (Blight et al. 2011). However, distinguishing between species with similar properties has been reported to be less feasible (Blight et al. 2011) and the detection of seaweeds without air-filled vesicles still remains difficult (Tillin et al. 2023). However, recent studies show that species such as *Ecklonia* with no pneumatocysts are able to be accurately identified over large areas (Nau et al. 2025). Additionally, the ability to detect species extent decreases with depth (McGonigle et al. 2011), overlapping fronds reduce abundance estimates, there is often a high acquisition cost of sonar equipment, and there is difficulty using the equipment from small boats. Despite the limitations of these methods (particularly the challenges of species-specificity), they are a useful tool for detecting kelp over large areas and at reasonable depths.

9.4 Aerial imagery

Aerial imagery can be used to increase spatial and temporal monitoring of coastal ecosystems. These range from satellites to manned aircraft to unmanned aerial vehicles (UAV; i.e., drones), which all vary in their spatial coverage, resolution and cost. Earth observation satellites have the greatest spatial and temporal coverage and are often freely available but are limited in their resolution and flexibility, particularly relating to when useful images are captured. In comparison, a drone provides high pixel resolution and flexibility in the timing of imagery capture but is more expensive (to acquire the imagery) than using satellite data and has less spatial coverage. The most suitable platform, therefore, depends on the requirements of the survey and typically involves a trade-off between spatial resolution (pixel size), spatial coverage, the skills of personnel and processing costs.

The spectral resolution of aerial imagery describes the number and width of spectral bands within the sensor, and dictates the level of detail that can be extrapolated. Visible light imagery, or red green blue (RGB), includes three bands of data representing the intensities of the red, green and blue wavelengths of each pixel. Multispectral imagery includes additional bands outside of the visible light

spectrum such as those in the ultra-blue, near infrared (NIR) and short-wave infrared wavelengths. This is particularly important when distinguishing vegetation because of the dissipation of infrared wavelengths during active photosynthesis. The reflection of electromagnetic radiation in specific wavelengths differs between species making it possible to distinguish species or higher functional groups in multispectral imaging. The combination of richer data (e.g., more bands) and specific spectral properties of different biogenic habitats in the NIR range provides a powerful tool for accurate identification of a greater range of species.

9.4.1 Drone imagery

UAVs or drones describe a range of aircraft than can be piloted from the ground. They are increasingly being used in various environmental and ecological monitoring campaigns (Chirayath & Earle 2016; Koh & Wich 2012; Tait & Mangan 2024; Ventura et al. 2023), across different ecosystem types such as intertidal rocky reefs, floating algal canopies and estuaries. UAVs can be fitted with a wide range of sensors including RGB cameras, multispectral cameras, hyperspectral cameras, thermal imagery, Light Detection and Ranging (LiDAR) imagery and high-resolution GPS positioning. For example, when fitted with multispectral cameras, drones are particularly effective for examining the spatio-temporal distribution of key biogenic features or functional groups, and within some functional groups of vegetation, it is possible to identify species or genus levels accurately (Tait et al. 2019). However, this also requires the integration of *in situ* sampling to both validate detections and provide estimates of uncertainty in analyses which are essential for accurately differentiating species.

UAV survey flights can be timed for alignment of optimal environmental conditions for the species of interest, such as during low spring tides. They can also be flown at differing altitudes to obtain the necessary pixel resolution to identify smaller features or patches which is particularly important within complex rocky reef communities. High pixel resolution also enables object-based recognition analyses compared to variations in spectral signatures of coarser imagery. Furthermore, UAV flight paths can be pre-programmed and repeated to generate multi-temporal datasets for change detection analysis. However, UAVs can only realistically cover relatively small areas (e.g., less than 10 km^2 for surveys within specific tide windows), and requires the field team to be deployed near study sites.

9.4.2 Manned fixed wing imagery

Manned fixed wing imagery has similar advantages of drone imagery but can typically be used for covering large areas by increasing flight durations. For example, they can stay airborne for periods from 20 minutes to several hours. However, they often need larger take-off and loading areas, assistance to launch or capture and can be costly to attain hardware and to deploy. In addition, the pixel resolution is often coarser when compared to drone captured imagery, a fixed flight speed is often necessary, there is a risk of smearing at low altitudes, and it is more difficult to be agile around optimal environmental conditions, such as cloud cover (Kvile et al. 2024). There can also be challenges in collecting high resolution overlapping imagery from fixed-wing aircraft, although some specialist craft and teams are specifically configured to acquire such data. While costs per unit area can be similar to UAV operations, the base cost for fixed-wing operations are much higher.

9.4.3 Satellite imagery

Satellite imagery can be used for passive remote monitoring using freely available satellites by providing imagery of high enough resolution for broad habitat classification (Bell et al. 2018). For example, earth observation satellites with a pixel size of 10–30 m have been used for remote imaging of *Macrocystis* providing data which relates well to *in situ* observations (Bell et al. 2018; Bell et al. 2015; Cavanaugh et al. 2011). Analyses can be run over very large scales and provide frequent observations through time. The spatio-temporal scale of these datasets provides a unique opportunity to assess how broad-scale variables and stressors impact kelp bed abundance and distribution (Hamilton et al. 2020).

A range of satellite products exist, but they vary in pixel resolution, the number of spectral bands they capture, and the frequency of passes. Readily available earth observation satellites regularly use broad

multispectral imaging, such as the Sentinel-2A constellation (European space Agency: 13 bands between 443–2190 nm) and Landsat-8 (U.S. Geological Survey: 9 bands between 430–1380 nm) where the pixel resolution varies between bands. Bands with resolution in the red-edge and NIR wavelengths enable accurate identification of surface canopies of kelp species (Timmer et al. 2022). Products incorporating these wavelengths are required to detect floating seaweed canopies.

In New Zealand, satellite remote sensing of *Macrocystis* has been successfully used to understand environmental effects on distribution, showing that water clarity and marine heatwaves were key drivers of kelp loss (Tait et al. 2021). The ability to freely and retrospectively assess changes in the distribution and abundance of kelp across its full range is only possible through satellite tools and represents a significant opportunity to provide near-real time information for use in management interventions. The suitability of satellite imagery to detect subtidal canopies of *Macrocystis* as well as other large macroalgal species is currently being investigated within New Zealand.

10. MONITORING KELP FOR BETTER FISHERIES MANAGEMENT

Kelp and macroalgae are a key component of all temperate marine ecosystems, and directly and indirectly support a range of fisheries. The value of macroalgal carbon is likely to be worth millions of dollars per annum, yet changes and variability of kelp beds are not incorporated into fisheries management in a meaningful way. Leveraging key datasets that provide evidence of the spatio-temporal variability of kelp and macroalgae may provide a novel and useful tool for better management of tightly linked fisheries. For example, giant kelp and other seaweeds have faced significant losses in years of severe marine heatwaves (Thomsen et al. 2019, Tait et al. 2021), and these events may be linked to year-class failure or reductions in dependent fisheries.

Here the utility of satellite remote sensing is considerable (Bell et al. 2018). Continuous passive monitoring of surface canopies by satellites provides a timely, cheap, and effective means of tracking the distribution, abundance and health of kelp (Cavanaugh et al. 2021), and can enable a more informed fisheries management approach. Given the scale, remoteness, accessibility, and variability of kelp in New Zealand, satellite remote sensing is one of the few methods able to be implemented across New Zealand immediately. This could be achieved through the creation and management of an updateable interface that ingests new satellite imagery and automatically processes it to produce layers of kelp distribution and abundance. As a separate objective of this wider project, we aim to collate existing datasets and produce a tool to map trends in *Macrocystis* distribution over time. These data can then be used to assess historical trends and model future scenarios of macroalgal distribution in response to the effects of climate change, and to discuss the implications this may have for fisheries.

10.1 Recommendations for updateable GIS database to store multi-scaled data

Two key long-term, freely available, earth observation satellite products exist, Sentinel-2 and Landsat. These products have been running for a decade or more, have good resolution, and have bands in the NIR wavelengths. The key difference between the two is currently the minimum pixel size, with 10×10 m pixels available for Sentinel-2, while Landsat 8 has 30×30 m pixels, and Landsat-9 (launched 2021) has 15×15 m pixels. Sentinel-2 has more spectral resolution in the red-edge wavelengths (i.e., 700-730 nm).

For these reasons we currently recommend Sentinel-2 imagery for the identification and delimitation of surface canopies of giant kelp. Access to these repositories can be achieved through freely available, open-access interfaces, such as Jupyter Notebooks. This Python coding interface allows various selection and processing algorithms to filter and prepare data for analysis and presentation.

11. DISCUSSION

This review synthesises current national and international literature on the ecological and economic relationships between large habitat-forming macroalgae and New Zealand's wild fisheries. The primary focus was to assess the direct and indirect pathways through which macroalgae support fisheries production, and to evaluate the vulnerability of these systems to environmental stressors.

Macroalgal habitats support fisheries through a range of ecological pathways. These include direct grazing by species such as pāua and kina, the provision of structurally complex habitat that enhances recruitment and survival of juvenile fish and invertebrates, and the support of epifaunal communities that serve as prey for higher trophic levels. Additionally, macroalgae contribute significantly to the production of SPOM and detritus, which are assimilated by filter feeders and benthic invertebrates, thereby enhancing secondary productivity and energy transfer through food webs. Stable isotope analyses have demonstrated that macroalgal-derived organic matter can comprise a significant proportion of the biomass of key fisheries species in regions with intact kelp forests. These findings underscore the importance of macroalgae in sustaining the productivity of high-value fisheries. The estimated asset value of 13 kelp-associated fisheries species in 2019 in New Zealand is approximately \$NZD5.24 billion, with macroalgal contributions accounting for around \$NZD4 billion of this total. While this valuation is based on quota asset values and does not capture the full range of ecosystem services or non-commercial benefits, it provides a useful heuristic for understanding the scale of macroalgal contributions to fisheries.

Despite these established linkages, several critical areas of uncertainty and information gaps remain. The cumulative impacts of multiple stressors, including rising sea temperatures, sedimentation, ocean acidification, and overgrazing by sea urchins, and their influence on macroalgal life histories, recruitment, and recovery dynamics pose complex challenges to the resilience of macroalgal ecosystems. This review additionally highlights the advantages of utilising satellite remote sensing to investigate the effects of large-scale environmental stressors. However, continued research, particularly into the potential to use satellite remote sensing to correlate to subtidal beds and other important macroalgal species, combined with other monitoring methods will improve our understanding of macroalgal dynamics and further contribute to more informed ecosystem-based management of New Zealand's coastal marine resources.

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REFERENCES

- Adams, N.M. (1994). Seaweeds of New Zealand: An illustrated guide. Cantnz.
- Airoldi, L. (2000). Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. *Marine Ecology Progress Series*, 195, 81–92. https://www.int-res.com/abstracts/meps/v195/p81-92/
- Airoldi, L. (2003). The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology*, 41, 169–171.
- Airoldi, L.; Cinelli, F. (1997). Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a mediterranean rocky shore. *Journal of Experimental Marine Biology and Ecology*, 215(2), 269–288. https://doi.org/10.1016/S0022-0981(96)02770-0
- Airoldi, L.; Rindi, F.; Cinelli, F. (1995). Structure, Seasonal Dynamics and Reproductive Phenology of a Filamentous Turf Assemblage on a Sediment Influenced, Rocky Subtidal Shore. *Botanica Marina*, *38*(1–6), 227–238. https://doi.org/10.1515/botm.1995.38.1-6.227
- Alestra, T.; Tait, L.W.; Schiel, D.R. (2014). Effects of algal turfs and sediment accumulation on replenishment and primary productivity of fucoid assemblages. *Marine Ecology Progress Series*, 5–11, 5970. https://doi.org/10.3354/meps10932
- Anderson, T.J.; Morrison, M.; MacDiarmid, A.; Clark, M.; D'Archino, R.; Nelson, W.; Tracey, D.; Gordon, D.; Read, G.; Kettles, H.; Morrisey, D.; Wood, A.; Anderson, O.; Smith, A.M.; Page, M.; Paul-Burke, K.; Schnabel, K.; Wadhwa, S. (2019). *Review of New Zealand's Key Biogenic Habitats* (NIWA Client Report no. 2018139WN. Prepared for the Ministry for the Environment)
- Andrew, D.I.; Sean, D.C. (2006). Physical disturbance by kelp abrades erect algae from the understorey. *Marine Ecology Progress Series*, *324*, 127–137. https://doi.org/10.3354/meps324127
- Andrew, N.L. (1988). Ecological aspects of the common sea urchin, *Evechinus chloroticus*, in northern New Zealand: A review. *New Zealand Journal of Marine and Freshwater Research*, 22(3), 415–426. https://doi.org/10.1080/00288330.1988.9516313
- Arakawa, H.; Matsuike, K. (1992). Influence on insertion of zoospores, germination, survival, and maturation of gametophytes of brown algae [*Undaria pinnatifida* and *Ecklonia*] exerted by sediments. *Bulletin of the Japanese Society of Scientific Fisheries*.
- Assis, J.; Fragkopoulou, E.; Gouvêa, L.; Araújo, M.B.; Serrão, E.A. (2024). Kelp forest diversity under projected end-of-century climate change. *Diversity and Distributions*, *30*(6), e13837. https://doi.org/10.1111/ddi.13837
- Babcock, R.C.; Shears, N.T.; Alcala, A.C.; Barrett, N.S.; Edgar, G.J.; Lafferty, K.D.; McClanahan, T.R.; Russ, G.R. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences*, 107(43), 18256–18261. https://doi.org/doi:10.1073/pnas.0908012107
- Balemi, C.A.; Shears, N.T. (2023). Emergence of the subtropical sea urchin *Centrostephanus* rodgersii as a threat to kelp forest ecosystems in northern New Zealand. Frontiers in Marine Science, 10. https://doi.org/10.3389/fmars.2023.1224067
- Barilotti, D.C.; Zertuche-González, J.A. (1990). Ecological effects of seaweed harvesting in the Gulf of California and Pacific Ocean off Baja California and California. *Hydrobiologia*, 204(1), 35–40. https://doi.org/10.1007/BF00040212
- Batham, E. (1965). Rocky shore ecology of a southern New Zealand fiord. *Transactions of the Royal Society of New Zealand Zoology*, *6*, 215–227.
- Baumann, H.; Wallace, R.B.; Tagliaferri, T.; Gobler, C.J. (2015). Large Natural pH, CO2 and O2 Fluctuations in a Temperate Tidal Salt Marsh on Diel, Seasonal, and Interannual Time Scales. *Estuaries and Coasts*, 38(1), 220–231. https://doi.org/10.1007/s12237-014-9800-y
- Bednaršek, N.; Pelletier, G.; Beck, M.W.; Feely, R.A.; Siegrist, Z.; Kiefer, D.; Davis, J.; Peabody, B. (2024). Predictable patterns within the kelp forest can indirectly create temporary refugia from ocean acidification. *Science of The Total Environment*, 945, 174065. https://doi.org/10.1016/j.scitotenv.2024.174065

- Bell, T.W.; Allen, J.G.; Cavanaugh, K.C.; Siegel, D.A. (2018). Three decades of variability in California's giant kelp forests from the Landsat satellites. *Remote Sensing of Environment*, 238, 110811. https://doi.org/https://doi.org/10.1016/j.rse.2018.06.039
- Bell, T.W.; Cavanaugh, K.C.; Reed, D.C.; Siegel, D.A. (2015). Geographical variability in the controls of giant kelp biomass dynamics. *Journal of Biogeography*, 42(10), 2010–2021. https://doi.org/https://doi.org/10.1111/jbi.12550
- Benedetti-Cecchi, L.; Pannacciulli, F.; Bulleri, F.; Moschella, P.S.; Airoldi, L.; Relini, G.; Cinelli, F. (2001). Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Marine Ecology Progress Series*, 214, 137–150. https://doi.org/10.3354/meps214137
- Bennett, S.; Wernberg, T.; Connell, S.D.; Hobday, A.J.; Johnson, C.R.; Poloczanska, E.S. (2015). The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. *Marine and Freshwater Research*, 67(1), 47–56. https://doi.org/10.1071/MF15232
- Blain, C.O.; Hansen, S.C.; Shears, N.T. (2021). Coastal darkening substantially limits the contribution of kelp to coastal carbon cycles. *Global Change Biology*, 27(21), 5547–5563. https://doi.org/10.1111/gcb.15837
- Blain, C.O.; Rees, T.A.V.; Hansen, C.S.; Shears, N.T. (2020). Morphology and photosynthetic response of the kelp *Ecklonia radiata* across a turbidity gradient. *Limnology and Oceanography*, 65(3), 529–544. https://doi.org/10.1002/lno.11321
- Blamey, L.K.; Bolton, J.J. (2018). The economic value of South African kelp forests and temperate reefs: Past, present and future. *Journal of Marine Systems*, *188*, 172–181. https://doi.org/10.1016/j.jmarsys.2017.06.003
- Blight, A.; Foster-Smith, R.; Sotheran, I.; Egerton, J.; McAllen, R.; Savidge, G. (2011). Development of a Methodology for the Quantitative Assessment of Ireland's Inshore Kelp Resource. Marine Institute 2011.
- Bradly, N.; Syddall, V.; Ingram, C.; Clarkson, R.; Elliot, A.; Major, R.; Adams, S. (2021). Stocktake and characterisation of Aotearoa New Zealand's seaweed sector: Market and regulatory focus (Sustainable Seas, Ko ngā moana whakauka Issue).
- Brasch, D.; Chuah, C.; Melton, L. (1984). The commercial agar from New Zealand *Pterocladia* species. *Australian Journal of Chemistry*, *37*(1), 183–190. https://doi.org/10.1071/CH9840183
- Britton, D.; Cornwall, C.E.; Revill, A.T.; Hurd, C.L.; Johnson, C.R. (2016). Ocean acidification reverses the positive effects of seawater pH fluctuations on growth and photosynthesis of the habitat-forming kelp, *Ecklonia radiata*. *Scientific Reports*, *6*(1), 26036. https://doi.org/10.1038/srep26036
- Brown, C.J.; Smith, S.J.; Lawton, P.; Anderson, J.T. (2011). Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuarine, Coastal and Shelf Science*, 92(3), 502–520. https://doi.org/10.1016/j.ecss.2011.02.007
- Bunting, I.; Kok, Y.Y.; Krieger, E.C.; Bury, S.J.; D'Archino, R.; Cornwall, C.E. (2024). Marine heatwave intensity and duration negatively affect growth in young sporophytes of the giant kelp *Macrocystis pyrifera*. Frontiers in Marine Science, 11. https://doi.org/10.3389/fmars.2024.1423595
- Burrows, M; Harvey, R.; Robb, L. (2008). Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Marine Ecology Progress Series*, *353*, 1–12. https://doi.org/10.3354/meps07284
- Buschmann, A.H.; Camus, C. (2019). An introduction to farming and biomass utilisation of marine macroalgae. *Phycologia*, 58(5), 443–445. https://doi.org/10.1080/00318884.2019.1638149
- Byrnes, J.E.; Reed, D.C.; Cardinale, B.J.; Cavanaugh, K.C.; Holbrook, S.J.; Schmitt, R.J. (2011). Climate-driven increases in storm frequency simplify kelp forest food webs. *Global Change Biology*, *17*(8), 2513–2524. https://doi.org/10.1111/j.1365-2486.2011.02409.x
- Carranza, D.M.; Wieters, E.A.; Vásquez, J.A.; Stotz, W.B. (2024). Exploring the consequences of kelp removal: a review shows we are missing a broader perspective. *Biodiversity and Conservation*, 33(2), 401–437. https://doi.org/10.1007/s10531-023-02769-7

- Castorani, M.C.N.; Harrer, S.L.; Miller, R.J.; Reed, D.C. (2021). Disturbance structures canopy and understory productivity along an environmental gradient. *Ecology Letters*, 24(10), 2192–2206. https://doi.org/10.1111/ele.13849
- Castorani, M.C.N.; Reed, D.C.; Miller, R.J. (2018). Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities. *Ecology*, 99(11), 2442–2454. https://doi.org/10.1002/ecy.2485
- Cavanaugh, K.C.; Bell, T.; Costa, M.; Eddy, N.E.; Gendall, L.; Gleason, M.G.; Hessing-Lewis, M.; Martone, R.; McPherson, M.; Pontier, O.; Reshitnyk, L.; Beas-Luna, R.; Carr, M.; Caselle, J. E.; Cavanaugh, K.C.; Flores Miller, R.; Hamilton, S.; Heady, W.N.; Hirsh, H.K.; Hohman, R.; Lee, L.C.; Lorda, J.; Ray, J.; Reed, D.C.; Saccomanno, V.R.; Schroeder, S.B. (2021). A Review of the Opportunities and Challenges for Using Remote Sensing for Management of Surface-Canopy Forming Kelps. *Frontiers in Marine Science*, 8. https://doi.org/10.3389/fmars.2021.753531
- Cavanaugh, K.C.; Siegel, D.A.; Reed, D.C.; Dennison, P.E. (2011). Environmental controls of giant-kelp biomass in the Santa Barbara Channel, California. *Marine Ecology Progress Series*, 429, 1–17. https://doi.org/10.3354/meps09141
- Cavole, L.M.; Demko, A.M.; Diner, R.E.; Giddings, A.; Koester, I.; Pagniello, C.M.; Paulsen, M.-L.; Ramirez-Valdez, A.; Schwenck, S.M.; Yen, N.K. (2016). Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. *Oceanography*, 29(2), 273–285. https://doi.org/10.5670/oceanog.2016.32
- Chapman, A.R.O. (1981). Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. *Marine Biology*, 62(4), 307–311. https://doi.org/10.1007/BF00397697
- Chapman, A.S.; Albrecht, A.S.; Fletcher, R.L. (2002). Differential effects of sediments on survival and growth of fucus serratus embryos (fucales, phaeophyceae). *Journal of Phycology*, *38*(5), 894–903. https://doi.org/10.1046/j.1529-8817.2002.t01-1-02025.x
- Chirayath, V.; Earle, S.A. (2016). Drones that see through waves preliminary results from airborne fluid lensing for centimetre-scale aquatic conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26(S2), 237–250. https://doi.org/https://doi.org/10.1002/aqc.2654
- Choat, J.H. (1982). Fish Feeding and the Structure of Benthic Communities in Temperate Waters. *Annual Review of Ecology and Systematics*, *13*, 423–449. http://www.jstor.org/stable/2097075
- Choat, J.H.; Schiel, D.R. (1982). Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *Journal of Experimental Marine Biology and Ecology*, 60(2), 129–162. https://doi.org/10.1016/0022-0981(82)90155-1
- Clements, K.; Bellwood, D. (1988). A comparison of the feeding mechanisms of two herbivorous labroid fishes, the temperate *Odax pullus* and the tropical *Scarus rubroviolaceus*. *Marine and Freshwater Research*, 39(1), 87–107. https://doi.org/10.1071/MF9880087
- Clendenning, K.A. (1971). Photosynthesis and general development in Macrocystis. In W. J. North (Ed.), *The biology of Giant Kelp beds (Macrocystis) in California* (pp. 169–190). Lehre, Germany, J. Cramer.
- Cole, R.G.; Babcock, R.C.; Travers, V.; Creese, R.G. (2001). Distributional expansion of *Carpophyllum flexuosum* onto wave-exposed reefs in north-eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *35*(1), 17–32. https://doi.org/10.1080/00288330.2001.9516976
- Cole, R.G.; Creese, R.G.; Grace, R.V.; Irving, P.; Jackson, B.R. (1992). Abundance patterns of subtidal benthic invertebrates and fishes at the Kermadec Islands. *Marine Ecology Progress Series*, 82, 207–218. https://doi.org/10.3354/meps082207
- Coleman, M.A.; Kelaher, B.P.; Steinberg, P.D.; Millar, A.J.K. (2008). Absence of a large brown macroalga on urbanized rocky reefs around sydney, australia, and evidence for historical decline. *Journal of Phycology*, 44(4), 897–901. https://doi.org/10.1111/j.1529-8817.2008.00541.x
- Colombo-Pallotta, M.F.; García-Mendoza, E.; Ladah, L.B. (2006). Photosynthetic performance, light absorption, and pigment composition of *Macrocystis pyrifera* (laminariales, phaeophyceae)

- blades from different depths. *Journal of Phycology*, *42*(6), 1225–1234. https://doi.org/10.1111/j.1529-8817.2006.00287.x
- Connell, S.D. (2003). Negative effects overpower the positive of kelp to exclude invertebrates from the understorey community. *Oecologia*, *137*, 97–103. https://doi.org/10.1007/s00442-003-1312-6
- Cornwall, C.E.; Hepburn, C.D.; Pritchard, D.; Currie, K.I.; McGraw, C.M.; Hunter, K.A.; Hurd, C.L. (2012). Carbon-use strategies in macroalgae: differential responses to lowered ph and implications for ocean acidification. *Journal of Phycology*, *48*(1), 137–144. https://doi.org/https://doi.org/10.1111/j.1529-8817.2011.01085.x
- Cryer, M.; Mace, P.M.; Sullivan, K.J. (2016). New Zealand's ecosystem approach to fisheries management. *Fisheries Oceanography*, 25(S1), 57–70. https://doi.org/10.1111/fog.12088
- Curtis, J.S.; McCarthy, G.J.; Durante, L.M.; Chapple T.M.; Whittall, S.F.; Dillingham, P.W.; Wing, S.R. (in prep.) Stable isotopes in fish eye lenses record patterns and variation in resource-use ontogeny of three New Zealand kelp forest species. Submitted to Ecology and Evolution
- Darwin, C. (1909). The Voyage of the Beagle (Vol. 29). The Harvard Classics.
- Davies, J.; Baxter, J.; Bradley, M.; Connor, D.; Khan, J.; Murray, E.; Sanderson, W.; Turnbull, C.; Vincent, M. (2001). *Marine Monitoring Handbook*. Joint Nature Conservation Committee.
- Dayton, P.K. (1985). Ecology of Kelp Communities. *Annual Review of Ecology, Evolution, and Systematics*, 16(Volume 16), 215–245. https://doi.org/10.1146/annurev.es.16.110185.001243
- Dayton, P.K.; Tegner, M.J.; Edwards, P.B.; Riser, K.L. (1998). Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications*, 8(2), 309–322. https://doi.org/10.1890/1051-0761(1998)008[0309:SBGARE]2.0.CO;2
- Denny, C.M.; Willis, T.J.; Babcock, R.C. (2004). Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Marine Ecology Progress Series*, 272, 183–190. https://doi.org/10.3354/meps272183
- Desmond, M.J.; Pritchard, D.W.; Hepburn, C.D. (2015). Light Limitation within Southern New Zealand Kelp Forest Communities. *PLOS ONE*, *10*(4), e0123676. https://doi.org/10.1371/journal.pone.0123676
- Devinny, J.S.; Volse, L.A. (1978). Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Marine Biology*, 48(4), 343–348. https://doi.org/10.1007/BF00391638
- Doheny, B.; Davis J.P.; Miller, B. (2023). Fishery-induced trophic cascades and sea urchin barrens in New Zealand: a review and discussion for management. *New Zealand Aquatic Environment and Biodiversity Report No. 324*. 110 p.
- Duggins, D.O.; Eckman, J.E. (1997). Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. *Marine Biology*, *128*(3), 489–495. https://doi.org/10.1007/s002270050115
- Duggins, D.O.; Simenstad, C.A.; Estes, J.A. (1989). Magnification of Secondary Production by Kelp Detritus in Coastal Marine Ecosystems. *Science*, 245(4914), 170–173. https://doi.org/10.1126/science.245.4914.170
- Durante, L.; Wing, S.; Ingram, T.; Sabadel, A.; Shima, J. (2022). Changes in trophic structure of an exploited fish community at the centennial scale are linked to fisheries and climate forces. *Scientific Reports*, *12*(1), 4309. https://doi.org/10.1038/s41598-022-08391-x
- Durante, L.M.; Beentjes, M.P.; Wing, S.R. (2020). Shifting trophic architecture of marine fisheries in New Zealand: Implications for guiding effective ecosystem-based management. *Fish and Fisheries*, 21(4), 813–830. https://doi.org/10.1111/faf.12463
- Edwards M.S.; Estes J.A. (2006). Catastrophe, Recovery, and Range Limitation in NE Pacific Kelp Forests: A Large-Scale Perspective. *Marine Ecology Progress Series*, 320, 79–87. doi: 10.3354/meps320079
- Eger, A.M.; Marzinelli, E.M.; Beas-Luna, R.; Blain, C.O.; Blamey, L.K.; Byrnes, J.E.K.; Carnell, P.E.; Choi, C.G.; Hessing-Lewis, M.; Kim, K.Y.; Kumagai, N.H.; Lorda, J.; Moore, P.; Nakamura, Y.; Pérez-Matus, A.; Pontier, O.; Smale, D.; Steinberg, P.D.; Vergés, A. (2023). The value of ecosystem services in global marine kelp forests. *Nature Communications*, 14(1), 1894. https://doi.org/10.1038/s41467-023-37385-0

- Elliott Smith, E.A.; Fox, M.D. (2022). Characterizing energy flow in kelp forest food webs: a geochemical review and call for additional research. *Ecography*, 2022(6), e05566. https://doi.org/10.1111/ecog.05566
- Elner, R.W. Vadas, R.L. (1990). Inference in Ecology: The Sea Urchin Phenomenon in the Northwestern Atlantic. *The American Naturalist*, *136*(1), 108–125. http://www.jstor.org/stable/2556348
- Eriksson, B.K.; Johansson, G.; Snoeijs, P. (2002). Long-term changes in the macroalgal vegetation of the inner gullmar fjord, swedish skagerrak coast. *Journal of Phycology*, *38*(2), 284–296. https://doi.org/10.1046/j.1529-8817.2002.00170.x
- Estes, J.A.; Tinker, M.T.; Williams, T.M.; Doak, D.F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, *282*(5388), 473–476. https://doi.org/10.1126/science.282.5388.473
- Falkenberg, L.J.; Russell, B.D.; Connell, S.D. (2013). Contrasting resource limitations of marine primary producers: implications for competitive interactions under enriched CO2 and nutrient regimes. *Oecologia*, 172(2), 575–583. https://doi.org/10.1007/s00442-012-2507-5
- Fernández, Á.; Arenas, F.; Trilla, A.; Rodríguez, S.; Rueda, L.; Martínez, B. (2015). Additive effects of emersion stressors on the ecophysiological performance of two intertidal seaweeds. *Marine Ecology Progress Series*, *536*, 135–147. https://www.int-res.com/abstracts/meps/v536/p135-147
- Fernández, P.A.; Roleda, M.Y.; Hurd, C.L. (2015). Effects of ocean acidification on the photosynthetic performance, carbonic anhydrase activity and growth of the giant kelp *Macrocystis pyrifera*. *Photosynth Res*, *124*(3), 293–304. https://doi.org/10.1007/s11120-015-0138-5
- Ferreira, J.G.; Arenas, F.; Martínez, B.; Hawkins, S.J.; Jenkins, S.R. (2014). Physiological response of fucoid algae to environmental stress: comparing range centre and southern populations. *New Phytologist*, 202(4), 1157–1172. https://doi.org/10.1111/nph.12749
- Filbee-Dexter, K.; Scheibling, R. (2014). Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*, 495, 1–25. https://doi.org/10.3354/meps10573
- Filbee-Dexter, K.; Wernberg, T. (2018). Rise of Turfs: A New Battlefront for Globally Declining Kelp Forests. *BioScience*, 68(2), 64–76. https://doi.org/10.1093/biosci/bix147
- Filbee-Dexter, K.; Wernberg, T.; Fredriksen, S.; Norderhaug, K.M.; Pedersen, M.F. (2019). Arctic kelp forests: Diversity, resilience and future. *Global and Planetary Change*, *172*, 1–14. https://doi.org/10.1016/j.gloplacha.2018.09.005
- Fraser, C.I. (2012). Is bull-kelp kelp? The role of common names in science. *New Zealand Journal of Marine and Freshwater Research*, 46(2), 279–284. https://doi.org/10.1080/00288330.2011.621130
- Fraser, C.I.; Nikula, R.; Spencer, H.G.; Waters, J.M. (2009). Kelp genes reveal effects of subantarctic sea ice during the Last Glacial Maximum. *Proceedings of the National Academy of Sciences*, 106(9), 3249–3253. https://doi.org/10.1073/pnas.0810635106
- Frieder, C.A.; Nam, S.H.; Martz, T.R.; Levin, L.A. (2012). High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences*, *9*(10), 3917–3930. https://doi.org/10.5194/bg-9-3917-2012
- Frölicher, T.L.; Fischer, E.M.; Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, 560(7718), 360–364. https://doi.org/10.1038/s41586-018-0383-9
- Gattuso, J.P.; Gentili, B.; Duarte, C.M.; Kleypas, J.A.; Middelburg, J.J.; Antoine, D. (2006). Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. *Biogeosciences*, *3*(4), 489–513. https://doi.org/10.5194/bg-3-489-2006
- Gaylord, B.; Reed, D.C.; Raimondi, P.T.; Washburn, L.; McLean, S.R. (2002). A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. *Ecology*, 83(5), 1239–1251. https://doi.org/10.1890/0012-9658(2002)083[1239:APBMOM]2.0.CO;2
- Geange, S. (2014). Growth and reproductive consequences of photosynthetic tissue loss in the surface canopies of *Macrocystis pyrifera* (L.) C. Agardh. *Journal of Experimental Marine Biology and Ecology*, 453, 70–75. https://doi.org/10.1016/j.jembe.2014.01.004

- Gerard, V.A. (1982). Growth and utilization of internal nitrogen reserves by the giant kelp *Macrocystis pyrifera* in a low-nitrogen environment. *Marine Biology*, 66(1), 27–35. https://doi.org/10.1007/BF00397251
- Gerrity, S.; Schiel, D.R. (2024). Assessing methods of enhancement for New Zealand blackfoot abalone (*Haliotis iris*) populations affected by mass mortality. *New Zealand Journal of Marine and Freshwater Research*, 1–28. https://doi.org/10.1080/00288330.2024.2362719
- Gorgula, S.K.; Connell, S.D. (2004). Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Marine Biology*, *145*(3), 613–619. https://doi.org/10.1007/s00227-004-1335-5
- Gorman, D.; Russell, B.D.; Connell, S.D. (2009). Land-to-sea connectivity: linking human-derived terrestrial subsidies to subtidal habitat change on open rocky coasts. *Ecological Applications*, 19(5), 1114–1126. https://doi.org/10.1890/08-0831.1
- Grace, R.V. (1983). Zonation of sublittoral rocky bottom marine life and its changes from the outer to the inner Hauraki Gulf, northeastern New Zealand. *Tane*, *29*, 97–108.
- Graham, M. (2002). Prolonged reproductive consequences of short-term biomass loss in seaweeds. *Marine Biology*, *140*(5), 901–911. https://doi.org/10.1007/s00227-001-0761-x
- Graham, M.H. (1997). Factors determining the upper limit of giant kelp, Macrocystis pyrifera Agardh, along the Monterey Peninsula, central California, USA. *Journal of Experimental Marine Biology and Ecology*, 218(1), 127–149. https://doi.org/10.1016/S0022-0981(97)00072-5
- Graham, M.H. (2004). Effects of Local Deforestation on the Diversity and Structure of Southern California Giant Kelp Forest Food Webs. *Ecosystems*, 7(4), 341–357. https://doi.org/10.1007/s10021-003-0245-6
- Graham, M.H.; Kinlan, B.P.; Druehl, L.D.; Garske, L.E.; Banks, S. (2007). Deep-water kelp refugia as potential hotspots of tropical marine diversity and productivity. *Proceedings of the National Academy of Sciences*, 104(42), 16576–16580. https://doi.org/10.1073/pnas.0704778104
- Gutow, L.; Rahman, M.M.; Bartl, K.; Saborowski, R.; Bartsch, I.; Wiencke, C. (2014). Ocean acidification affects growth but not nutritional quality of the seaweed *Fucus vesiculosus* (Phaeophyceae, Fucales). *Journal of Experimental Marine Biology and Ecology*, 453, 84–90. https://doi.org/10.1016/j.jembe.2014.01.005
- Halpern, B.S.; Cottenie, K.; Broitman, B.R. (2006). Strong Top-Down Control in Southern California Kelp Forest Ecosystems. *Science*, *312*(5777), 1230–1232. https://doi.org/10.1126/science.1128613
- Hamilton, S.L.; Bell, T.W.; Watson, J.R.; Grorud-Colvert, K.A.; Menge, B.A. (2020). Remote sensing: generation of long-term kelp bed data sets for evaluation of impacts of climatic variation. *Ecology*, *101*(7), e03031. https://doi.org/10.1002/ecy.3031
- Hamilton, S.L.; Caselle, J.E. (2015). Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proceedings of the Royal Society B: Biological Sciences*, 282(1799), 20141817. https://doi.org/10.1098/rspb.2014.1817
- Harrold, C.; Light, K.; Lisin, S. (1998). Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. *Limnology and Oceanography*, 43(4), 669–678. https://doi.org/10.4319/lo.1998.43.4.0669
- Harvell, C.D.; Montecino-Latorre, D.; Caldwell, J.M.; Burt, J.M.; Bosley, K.; Keller, A.; Heron, S.F.; Salomon, A.K.; Lee, L.; Pontier, O.; Pattengill-Semmens, C.; Gaydos, J.K. (2019). Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). *Science Advances*, *5*(1), eaau7042. https://doi.org/10.1126/sciadv.aau7042
- Hawkins, S.J.; Sugden, H.E.; Mieszkowska, N.; Moore, P.J.; Poloczanska, E.; Leaper, R.; Herbert, R.J.H.; Genner, M.J.; Moschella, P.S.; Thompson, R.C.; Jenkins, S.R.; Southward, A.J.; Burrows, M.T. (2009). Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series*, *396*, 245–259. https://doi.org/10.3354/meps08378
- Hay, C.H.; Luckens, P.A. (1987) The Asian kelp *Undaria pinnatifida* (Phaeophyta: Laminariales) found in a New Zealand harbour. *New Zealand Journal of Botany 25*: 329-332

- Hay, C.H.; South, G.R. (1979). Experimental Ecology with Particular Reference to Proposed Commercial Harvesting of Durvillaea (Phaeophyta, Durvilleales) in New Zealand. *Botanica Marina*, 22(7), 431–436. https://doi.org/10.1515/botm.1979.22.7.431
- Helmuth, B.; Mieszkowska, N.; Moore, P.; Hawkins, S.J. (2006). Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(Volume 37, 2006), 373–404. https://doi.org/10.1146/annurev.ecolsys.37.091305.110149
- Hereward, H.F.R.; King, N.G.; Smale, D.A. (2020). Intra-Annual Variability in Responses of a Canopy Forming Kelp to Cumulative Low Tide Heat Stress: Implications for Populations at the Trailing Range Edge. *Journal of Phycology*, *56*(1), 146–158. https://doi.org/10.1111/jpy.12927
- Hinojosa, I.A.; Green, B.S.; Gardner, C.; Jeffs, A. (2014). Settlement and early survival of southern rock lobster, *Jasus edwardsii*, under climate-driven decline of kelp habitats. *ICES Journal of Marine Science*, 72(suppl 1), i59-i68. https://doi.org/10.1093/icesjms/fsu199
- Hofmann, G.E.; Smith, J.E.; Johnson, K.S.; Send, U.; Levin, L.A.; Micheli, F.; Paytan, A.; Price, N.N.; Peterson, B.; Takeshita, Y.; Matson, P.G.; Crook, E.D.; Kroeker, K.J.; Gambi, M.C.; Rivest, E.B.; Frieder, C.A.; Yu, P.C.; Martz, T.R. (2011). High-Frequency Dynamics of Ocean pH: A Multi-Ecosystem Comparison. *PLOS ONE*, 6(12), e28983. https://doi.org/10.1371/journal.pone.0028983
- Holbrook, N.J.; Scannell, H.A.; Sen Gupta, A.; Benthuysen, J.A.; Feng, M.; Oliver, E.C.J.; Alexander, L.V.; Burrows, M.T.; Donat, M.G.; Hobday, A.J.; Moore, P.J.; Perkins-Kirkpatrick, S.E.; Smale, D.A.; Straub, S.C.; Wernberg, T. (2019). A global assessment of marine heatwaves and their drivers. *Nature Communications*, *10*(1), 2624. https://doi.org/10.1038/s41467-019-10206-z
- Hoshijima, U.; Hofmann, G.E. (2019). Variability of Seawater Chemistry in a Kelp Forest Environment Is Linked to in situ Transgenerational Effects in the Purple Sea Urchin, *Strongylocentrotus purpuratus. Frontiers in Marine Science*, 6. https://doi.org/10.3389/fmars.2019.00062
- Hurd, C.L. (2015). Slow-flow habitats as refugia for coastal calcifiers from ocean acidification. *Journal of Phycology*, 51(4), 599–605. https://doi.org/10.1111/jpy.12307
- Hynes, S.; Chen, W.; Vondolia, K.; Armstrong, C.; O'Connor, E. (2021). Valuing the ecosystem service benefits from kelp forest restoration: A choice experiment from Norway. *Ecological Economics*, 179, 106833. https://doi.org/10.1016/j.ecolecon.2020.106833
- Inglis, G. (1989). The colonisation and degradation of stranded *Macrocystis pyrifera* (L.) C. Ag. by the macrofauna of a New Zealand sandy beach. *Journal of Experimental Marine Biology and Ecology*, 125(3), 203–217. https://doi.org/10.1016/0022-0981(89)90097-X
- Jack, L.; Wing, S.R. (2011). Individual variability in trophic position and diet of a marine omnivore is linked to kelp bed habitat. *Marine Ecology Progress Series*, 443, 129–139. https://doi.org/10.3354/meps09468
- Jack, L.; Wing, S.R.; McLeod, R.J. (2009). Prey base shifts in red rock lobster *Jasus edwardsii* in response to habitat conversion in Fiordland marine reserves: implications for effective spatial management. *Marine Ecology Progress Series*, 381, 213–222. https://doi.org/10.3354/meps07971
- Johansson, G.; Snoeijs, P. (2002). Macroalgal photosynthetic responses to light in relation to thallus morphology and depth zonation. *Marine Ecology Progress Series*, 244, 63–72. https://doi.org/10.3354/meps244063
- Johnson, C.; Ling, S.; Sanderson, J.; Dominguez, J.; Flukes, E.; Frusher, S.; Gardner, C.; Hartmann, K.; Jarman, S.; Little, R.; Marzloff, M.; Soulie, J.-C.; Melbourne-Thomas, J.; Redd, K. (2013). Rebuilding ecosystem resilience: assessment of management options to minimise formation of 'barrens' habitat by the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania. FRDC Project 2007/045, 356 p.
- Jones, G.P. (2013). Ecology of rocky reef fish of northeastern New Zealand: 50 years on. *New Zealand Journal of Marine and Freshwater Research*, 47(3), 334–359. https://doi.org/10.1080/00288330.2013.812569

- Jonsson, P.R.; Granhag, L.; Moschella, P.S.; Aberg, P.; Hawkins, S.J.; Thompson, R.C. (2006). Interactions between wave action and grazing control the distribution of intertidal macroalgae. *Ecology*, 87(5), 1169–1178. https://doi.org/10.1890/0012-9658(2006)87[1169:ibwaag]2.0.co;2
- Kain, J.M. (1982) Morphology and growth of the giant kelp Macrocystis pyrifera in New Zealand and California. *Marine Biology*, 67, 143–157. https://doi.org/10.1007/BF00401280
- Kapsenberg, L.; Cyronak, T. (2019). Ocean acidification refugia in variable environments. *Global Change Biology*, 25(10), 3201–3214. https://doi.org/10.1111/gcb.14730
- Kennelly, S.J. (1987). Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. *Journal of Experimental Marine Biology and Ecology*, 112(1), 49–60.
- Kennelly, S.J. (1989). Effects of kelp canopies on understory species due to shade and scour. *Marine ecology progress series*. *Oldendorf*, 50(3), 215–224.
- Kerr, V.C.; Grace, R.V.; Shears, N.T. (2024). Estimating the extent of urchin barrens and kelp forest loss in northeastern Aotearoa, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 1–22. https://doi.org/10.1080/00288330.2024.2336081
- Kim, S.K.; Bhatnagar, I. (2011). Physical, chemical, and biological properties of wonder kelp-Laminaria. *Advances in Food and Nutrition Research*, *64*, 85–96. https://doi.org/10.1016/b978-0-12-387669-0.00007-7
- Kingsford, M.J.; Milicich, M.J. (1987). Presettlement phase of *Parika scaber* (Pisces: Monacanthidae): a temperate reef fish. *Marine Ecology Progress Series*, *36*(1), 65–79. http://www.jstor.org/stable/24821253
- Kingsford, M.J.; Schiel, D.R.; Battershill, C.N. (1989). Distribution and abundance of fish in a rocky reef environment at the subantarctic Auckland Islands, New Zealand. *Polar Biology*, *9*(3), 179–186. https://doi.org/10.1007/BF00297173
- Kirkman, H. (1989). Growth, density and biomass of *Ecklonia radiata* at different depths and growth under artifical shading off Perth, Western Australia. *Marine and Freshwater Research*, 40(2), 169–177. https://doi.org/10.1071/MF9890169
- Koh, L.P.; Wich, S.A. (2012). Dawn of Drone Ecology: Low-Cost Autonomous Aerial Vehicles for Conservation. *Tropical Conservation Science*, *5*(2), 121–132. https://doi.org/10.1177/194008291200500202
- Kolodzey, S.; Stroh, A.K.; Wing, S.R. (2023). Small-scale differences in blue cod length distribution, growth, and trophic ecology in New Zealand. *Marine Ecology Progress Series*, 708, 125–142. https://doi.org/10.3354/meps14275
- Kosek, K.; Kukliński, P. (2023). Impact of kelp forest on seawater chemistry A review. *Marine Pollution Bulletin*, 196, 115655. https://doi.org/10.1016/j.marpolbul.2023.115655
- Koweek, D.A.; Nickols, K.J.; Leary, P.R.; Litvin, S.Y.; Bell, T.W.; Luthin, T.; Lummis, S.; Mucciarone, D.A.; Dunbar, R.B. (2017). A year in the life of a central California kelp forest: physical and biological insights into biogeochemical variability. *Biogeosciences*, *14*(1), 31–44. https://doi.org/10.5194/bg-14-31-2017
- Krause-Jensen, D.; Duarte, C. (2014). Expansion of vegetated coastal ecosystems in the future Arctic. *Frontiers in Marine Science*, *1*. https://doi.org/10.3389/fmars.2014.00077
- Kroeker, K.J.; Micheli, F.; Gambi, M.C. (2013). Ocean acidification causes ecosystem shifts via altered competitive interactions. *Nature Climate Change*, *3*(2), 156–159. https://doi.org/10.1038/nclimate1680
- Krumhansl, K.; Scheibling, R. (2011). Detrital production in Nova Scotian kelp beds: Patterns and processes. *Marine Ecology Progress Series*, 421, 67–82. https://doi.org/10.3354/meps08905
- Krumhansl, K.A.; Okamoto, D.K.; Rassweiler, A.; Novak, M.; Bolton, J.J.; Cavanaugh, K.C.; Connell, S.D.; Johnson, C.R.; Konar, B.; Ling, S.D.; Micheli, F.; Norderhaug, K.M.; Pérez-Matus, A.; Sousa-Pinto, I.; Reed, D.C.; Salomon, A.K.; Shears, N.T.; Wernberg, T.; Anderson, R.J.; Barrett, N.S.; Buschmann, A.H.; Carr, M.H.; Caselle, J.E.; Derrien-Courtel, S.; Edgar, G.J.; Edwards, M.; Estes, J.A.; Goodwin, C.; Kenner, M.C.; Kushner, D.J.; Moy, F.E.; Nunn, J.; Steneck, R.S.; Vásquez, J.; Watson, J.; Witman, J.D.; Byrnes, J.E.K. (2016). Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences*, 113(48), 13785–13790. https://doi.org/10.1073/pnas.1606102113

- Kumagai, N.H.; García Molinos, J.; Yamano, H.; Takao, S.; Fujii, M.; Yamanaka, Y. (2018). Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proceedings of the National Academy of Sciences*, *115*(36), 8990–8995. https://doi.org/10.1073/pnas.1716826115
- Kvile, K.Ø.; Gundersen, H.; Poulsen, R.N.; Sample, J.E.; Salberg, A.-B.; Ghareeb, M.E.; Buls, T.; Bekkby, T.; Hancke, K. (2024). Drone and ground-truth data collection, image annotation and machine learning: A protocol for coastal habitat mapping and classification. *MethodsX*, *13*, 102935. https://doi.org/10.1016/j.mex.2024.102935
- Lan, X.; Tans, P.; Thoning, K.W. (2024). Trends in globally-averaged CO2 determined from NOAA Global Monitoring Laboratory measurements. Version Tuesday, 05-Nov-2024 13:17:54 MST. https://doi.org/10.15138/9N0H-ZH07
- Leigh, E.G.; Paine, R.T.; Quinn, J.F.; Suchanek, T.H. (1987). Wave energy and intertidal productivity. *Proceedings of the National Academy of Sciences*, 84(5), 1314–1318. https://doi.org/doi:10.1073/pnas.84.5.1314
- Lima, F.P.; Wethey, D.S. (2012). Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nature Communications*, *3*(1), 704. https://doi.org/10.1038/ncomms1713
- Ling, S.D.; Scheibling, R.E.; Rassweiler, A.; Johnson, C.R.; Shears, N.; Connell, S.D.; Salomon, A.K.; Norderhaug, K.M.; Pérez-Matus, A.; Hernández, J.C.; Clemente, S.; Blamey, L.K.; Hereu, B.; Ballesteros, E.; Sala, E.; Garrabou, J.; Cebrian, E.; Zabala, M.; Fujita, D.; Johnson, L.E. (2015). Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 20130269. https://doi.org/10.1098/rstb.2013.0269
- Littler, M.M.; Martz, D.R.; Littler, D.S. (1983). Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Marine Ecology Progress Series*, 11(2), 129–139. http://www.jstor.org/stable/24814583
- Lubsch, A.; Burggraaf, D.; Lansbergen, R. (2020). Feasibility study on remote estimation of biomass in a seaweed cultivation farm applying sonar: technical report. *Wageningen Marine Research rapport C110/20*. 22 p.
- Lüning, K. (1991). Seaweeds: their environment, biogeography, and ecophysiology. John Wiley & Sons.
- MacDiarmid, A.B.; Freeman, D.; Kelly, S. (2013). Rock lobster biology and ecology: contributions to understanding through the Leigh Marine Laboratory 1962–2012. *New Zealand Journal of Marine and Freshwater Research*, 47(3), 313–333. https://doi.org/10.1080/00288330.2013.810651
- Mak, W.; Hamid, N.; Liu, T.; Lu, J.; White, W.L. (2013). Fucoidan from New Zealand Undaria pinnatifida: monthly variations and determination of antioxidant activities. *Carbohydrate Polymers*, 95(1), 606–614. https://doi.org/10.1016/j.carbpol.2013.02.047
- Mangan, S.; Tait, L.W.; Gerrity, S.; Schiel, D.R. (2023). Loss and replacement of macroalgal standing stock and productivity after a major environmental disturbance. *Ecosphere*, *14*(10), e4674. https://doi.org/10.1002/ecs2.4674
- Mann, K.H. (1972). Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. *Marine Biology*, *14*(3), 199–209. https://doi.org/10.1007/BF00348280
- Mann, K.H. (1973). Seaweeds: Their Productivity and Strategy for Growth. *Science*, *182*(4116), 975–981. https://doi.org/10.1126/science.182.4116.975
- Mann, K.H. (1986). The Role of Detritus at the Land-Sea Boundary. In P. Lasserre & J.-M. Martin (Eds.), *Elsevier Oceanography Series 43*:123–140. https://doi.org/10.1016/S0422-9894(08)70750-5
- Marinovich, J.K.; Shears, N.T.; Parsons, D.M. (in press). Big fish, big mouths, big impacts: gape size of a fish predator determines size of urchins eaten. *Marine Ecology Progress Series*
- Martínez, B.; Arenas, F.; Rubal, M.; Burgués, S.; Esteban, R.; García-Plazaola, I.; Figueroa, F.L.; Pereira, R.; Saldaña, L.; Sousa-Pinto, I.; Trilla, A.; Viejo, R.M. (2012). Physical factors driving intertidal macroalgae distribution: physiological stress of a dominant fucoid at its southern limit. *Oecologia*, 170(2), 341–353. https://doi.org/10.1007/s00442-012-2324-x

- McCarthy, G.J.; Jowett, T.W.D.; Wing, S.R. (2024). Shifts in species composition in kelp forest communities: implications of differences in total phenolic composition among species. *Marine Ecology Progress Series*, 744, 17–31. https://doi.org/10.3354/meps14662
- McGonigle, C.; Grabowski, J.H.; Brown, C.J.; Weber, T.C.; Quinn, R. (2011). Detection of deep water benthic macroalgae using image-based classification techniques on multibeam backscatter at Cashes Ledge, Gulf of Maine, USA. *Estuarine, Coastal and Shelf Science*, 91(1), 87–101. https://doi.org/10.1016/j.ecss.2010.10.016
- McPeak, R.H.; Glantz, D.A. (1984). Harvesting California's kelp forests. *Oceanus*, 27(1), 19–26.
- Meehl, G.A.; Zwiers, F.; Evans, J.; Knutson, T.; Mearns, L.; Whetton, P. (2000). Trends in extreme weather and climate events: issues related to modeling extremes in projections of future climate change. *Bulletin of the American Meteorological Society*, 81(3), 427–436.
- Middelboe, A.L.; Sand-Jensen, K. (2000). Long-term changes in macroalgal communities in a Danish estuary. *Phycologia*, *39*(3), 245–257. https://doi.org/10.2216/i0031-8884-39-3-245.1
- Mieszkowska, N.; Kendall, M.A.; Hawkins, S.J.; Leaper, R.; Williamson, P.; Hardman-Mountford, N. J.; Southward, A.J. (2006). Changes in the range of some common rocky shore species in Britain a response to climate change? In K. Martens, H. Queiroga, M.R. Cunha, A.Cunha, M.H. Moreira, V. Quintino, A.M. Rodrigues, J. Seroôdio, R.M. Warwick (Eds.), Marine Biodiversity: Patterns and Processes, Assessment, Threats, Management and Conservation (pp. 241–251). Springer Netherlands. https://doi.org/10.1007/1-4020-4697-9
- Miller, K.I.; Balemi, C.A.; Blain, C.O.; Spyksma, A.J.P.; Shears, N.T. (2024). Sea urchin roe quality within urchin barrens and improvement through kelp restoration. *Ecosphere*, 15(6), e4911. https://doi.org/10.1002/ecs2.4911
- Miller, R.J.; Reed, D.C.; Brzezinski, M.A. (2011). Partitioning of primary production among giant kelp (*Macrocystis pyrifera*), understory macroalgae, and phytoplankton on a temperate reef. *Limnology and Oceanography*, 56(1), 119–132. https://doi.org/10.4319/lo.2011.56.1.0119
- Miller, S.L.; Abraham, E.R. (2011). Characterisation of New Zealand kina fisheries. *New Zealand Fisheries Assessment Report 2011/7*. 95 p.
- Ministry for the Environment and Stats NZ. (2018). New Zealand's Environmental Reporting Series: Our land 2018. ME 1350
- Montie, S., Thoral, F., Smith, R. O., Cook, F., Tait, L. W., Pinkerton, M. H., Schiel, D. R., & Thomsen, M. S. (2024). Seasonal trends in marine heatwaves highlight vulnerable coastal ecoregions and historic change points in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 58(2), 274-299. https://doi.org/10.1080/00288330.2023.2218102
- Mori, N.; Shimura, T.; Yasuda, T.; Mase, H. (2013). Multi-model climate projections of ocean surface variables under different climate scenarios—Future change of waves, sea level and wind. *Ocean Engineering*, 71, 122–129. https://doi.org/10.1016/j.oceaneng.2013.02.016
- Morrison, M.A.; Jones, E.G.; Parsons, D.P.; Grant, C.M. (2014). Habitats and areas of particular significance for coastal finfish fisheries management in New Zealand: A review of concepts and life history knowledge, and suggestions for future research. *New Zealand Aquatic Environment and Biodiversity Report No. 125.* 202 p.
- Morrison, M.A.; Lowe, M.L.; Parsons, D.M.; Usmar, N.R.; McLeod, I.M. (2009). A review of land-based effects on coastal fisheries and supporting biodiversity in New Zealand. *New Zealand Aquatic Environment and Biodiversity Report No. 37* . 100 p.
- Nau, A.W.; Lucieer, V.; Schimel, A.C.G.; Kunnath, H.; Ladroit, Y.; Martin, T. (2025). Advanced Detection and Classification of Kelp Habitats Using Multibeam Echosounder Water Column Point Cloud Data. *Remote Sensing*, 17(3), 449. https://doi.org/10.3390/rs17030449
- Nelson, W.; Duffy, C.; Trnski, T.; Stewart, R. (2018). Mesophotic *Ecklonia radiata* (Laminariales) at Rangitāhua, Kermadec Islands, New Zealand. *Phycologia*, *57*, 534–538. https://doi.org/10.2216/18-9.1
- Nelson, W.A. (1994). Distribution of Macroalgae in New Zealand An Archipelago in Space and Time. *Botanica Marina*, *37*(3), 221–234. https://doi.org/10.1515/botm.1994.37.3.221
- Nelson, W.A.; D'Archino, R.; Neill, K.F.; Robinson, N.M. (2021). Introduced marine macroalgae: new perspectives on species recognition and distribution in New Zealand. *Botanica Marina*, 64(5), 379–393. https://doi.org/10.1515/bot-2021-0042

- Nelson, W.A.; Neill, K.F.; D'Archino, R. (2023). Chapter 3. Kingdom Chromista, phylum Ochrophyta, and kingdom Plantae, phyla Prasinodermatophyta, Chlorophyta, and Rhodophyta (macroalgae). In Kelly, M.; Mills, S.; Terezow, M.; Sim-Smith, C.; Nelson, W. (Ed.), The Marine Biota of Aotearoa New Zealand. Updating our marine biodiversity inventory. NIWA Biodiversity Memoir 136, 494 p.
- Neushul, M. (1963). Studies on the Giant Kelp, Macrocystis. II. Reproduction. *American Journal of Botany*, 50(4), 354–359. https://doi.org/10.2307/2440152
- Neverman, A.J.; Donovan, M.; Smith, H.G.; Ausseil, A.-G.; Zammit, C. (2023). Climate change impacts on erosion and suspended sediment loads in New Zealand. *Geomorphology*, 427, 108607. https://doi.org/10.1016/j.geomorph.2023.108607
- Newcombe, E.M.; Taylor, R.B. (2010). Trophic cascade in a seaweed-epifauna-fish food chain. *Marine Ecology Progress Series*, 408, 161–167. https://doi.org/10.3354/meps08589
- Ní- Longphuirt, S.; Eschmann, C.; Russell, C.; Stengel, D.B. (2013). Seasonal and species-specific response of five brown macroalgae to high atmospheric CO2. *Marine Ecology Progress Series*, 493, 91–102. https://doi.org/10.3354/meps10570
- North, W.J. (1984). Biology of the Macrocystis resource in North America. FAO Fisheries Technical Paper (FAO) Issue 281.
- North, W.J.; Hubbs, C.L. (1968). Utilization of kelp-bed resources in southern California. *Fisheries Bulletin*, 1–264.
- North, W.J.; Pearse, J.S. (1970). Sea urchin population explosion in southern California coastal waters. *Science*, 167(3915), 209. https://doi.org/10.1126/science.167.3915.209-a
- Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuysen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C., & Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, *9*(1), 1324. https://doi.org/10.1038/s41467-018-03732-9
- Orr, J.C.; Fabry, V.J.; Aumont, O.; Bopp, L.; Doney, S.C.; Feely, R.A.; Gnanadesikan, A.; Gruber, N.; Ishida, A.; Joos, F.; Key, R.M.; Lindsay, K.; Maier-Reimer, E.; Matear, R.; Monfray, P.; Mouchet, A.; Najjar, R.G.; Plattner, G.K.; Rodgers, K.B.; Sabine, C.L.; Sarmiento, J.L.; Schlitzer, R.; Slater, R.D.; Totterdell, I.J.; Weirig, M.F.; Yamanaka, Y.; Yool, A. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, *437*(7059), 681–686. https://doi.org/10.1038/nature04095
- Paul, L.J.; O Maolagain, C.; Francis, M.P.; Dunn, A.; Francis, R.I.C.C. (2000). Age, growth, mortality, and yield per recruit of butterfish (*Odax pullus*) in Cook Strait, New Zealand. *New Zealand Fisheries Assessment Report 2000/6*. 30 p.
- Pearse, J.S.; Hines, A.H. (1979). Expansion of a central California kelp forest following the mass mortality of sea urchins. *Marine Biology*, 51(1), 83–91. https://doi.org/10.1007/BF00389034
- Pedersen, M.F.; Borum, J. (1996). Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Marine Ecology Progress Series*, 142, 261–272. https://doi.org/10.3354/meps142261
- Pedersen, M.F.; Nejrup, L.B.; Fredriksen, S.; Christie, H.; Norderhaug, K.M. (2012). Effects of wave exposure on population structure, demography, biomass and productivity of the kelp *Laminaria hyperborea. Marine Ecology Progress Series*, *451*, 45–60. https://doi.org/10.3354/meps09594
- Peleg, O.; Blain, C.O.; Shears, N.T. (2023). Long-term marine protection enhances kelp forest ecosystem stability. *Ecological Applications*, *33*(7), e2895. https://doi.org/https://doi.org/10.1002/eap.2895
- Pérez-Matus, A.; Micheli, F.; Konar, B.; Shears, N.; Low, N.H.N.; Okamoto, D.K.; Wernberg, T.; Krumhansl, K.A.; Ling, S.D.; Kingsford, M.; Navarrete-Fernandez, T.; Ruz, C.S.; Byrnes, J.E.K. (2025). Kelp forests as nursery and foundational habitat for reef fishes. *Ecology*, 106(2), e70007. https://doi.org/10.1002/ecy.70007
- Pérez-Matus, A.; Shima, J.S. (2010a). Disentangling the effects of macroalgae on the abundance of temperate reef fishes. *Journal of Experimental Marine Biology and Ecology*, 388(1), 1–10. https://doi.org/10.1016/j.jembe.2010.03.013

- Pérez-Matus, A.; Shima, J.S. (2010b). Density- and trait-mediated effects of fish predators on amphipod grazers: potential indirect benefits for the giant kelp *Macrocystis pyrifera*. *Marine Ecology Progress Series*, 417, 151–158. https://doi.org/10.3354/meps08820
- Pessarrodona, A.; Assis, J.; Filbee-Dexter, K.; Burrows, M.T.; Gattuso, J.-P.; Duarte, C.M.; Krause-Jensen, D.; Moore, P.J.; Smale, D. A.; Wernberg, T. (2022). Global seaweed productivity. *Science Advances*, 8(37), eabn2465. https://doi.org/10.1126/sciadv.abn2465
- Petraitis, P.S.; Dudgeon, S.R. (2004). Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology*, 300(1), 343–371. https://doi.org/10.1016/j.jembe.2003.12.026
- Pirker, J.G. (2002). Demography, Biomass Production and Effects of Harvesting Giant Kelp Macrocystis pyrifera (Linnaeus) in Southern New Zealand. University of Canterbury PhD Thesis http://dx.doi.org/10.26021/6442
- Porse, H.; Rudolph, B. (2017). The seaweed hydrocolloid industry: 2016 updates, requirements, and outlook. *Journal of Applied Phycology*, 29(5), 2187–2200. https://doi.org/10.1007/s10811-017-1144-0
- Pörtner, H.O.; Farrell, A.P. (2008). Physiology and Climate Change. *Science*, *322*(5902), 690–692. https://doi.org/10.1126/science.1163156
- Reed, D.C. (1987). Factors affecting the production of sporophylls in the giant kelp *Macrocystis* pyrifera (L.) C.Ag. *Journal of Experimental Marine Biology and Ecology*, 113(1), 61–69. https://doi.org/10.1016/0022-0981(87)90082-7
- Reed, D.C.; Kinlan, B.P.; Raimondi, P.T.; Washburn, L.; Gaylord, B.; Drake, P.T. (2006). A Metapopulation Perspective on the Patch Dynamics of Giant Kelp in Southern California, in Marine Metapopulations (Cambridge, Massachusetts: Academic Press), 353–386.
- Reed, D.C.; Rassweiler, A.; Carr, M.H.; Cavanaugh, K.C.; Malone, D.P.; Siegel, D.A. (2011). Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. *Ecology*, *92*(11), 2108–2116. https://doi.org/10.1890/11-0377.1
- Rogers-Bennett, L.; Catton, C.A. (2019). Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Scientific Reports*, 9(1), 15050. https://doi.org/10.1038/s41598-019-51114-y
- Ruz, C.S.; Muth, A.F.; Tala, F.; Pérez-Matus, A. (2018). The herbivorous fish, *Aplodactylus punctatus*, as a potential facilitator of dispersal of kelp, *Lessonia trabeculata*, in Chile. *Journal of Experimental Marine Biology and Ecology*, *500*, 112–119. https://doi.org/10.1016/j.jembe.2017.12.007
- Sabadel, A.J.M.; Durante, L.M.; Wing, S.R. (2020). Stable isotopes of amino acids from reef fishes uncover Suess and nitrogen enrichment effects on local ecosystems. *Marine Ecology Progress Series*, 647, 149–160. https://doi.org/10.3354/meps13414
- Saderne, V.; Fietzek, P.; Herman, P.M.J. (2013). Extreme Variations of pCO2 and pH in a Macrophyte Meadow of the Baltic Sea in Summer: Evidence of the Effect of Photosynthesis and Local Upwelling. *PLOS ONE*, *8*(*4*), e62689. https://doi.org/10.1371/journal.pone.0062689
- Salomon, A.K.; Shears, N.T.; Langlois, T.J.; Babcock, R.C. (2008). Cascading effects of fishing can alter carbon flow through a temperate coastal ecosystem. *Ecological Applications*, 18(8), 1874–1887. https://doi.org/10.1890/07-1777.1
- Scheibling, R. (1986). Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. *Oecologia*, 68(2), 186–198. https://doi.org/10.1007/bf00384786
- Schiel, D.R. (1980). A demographic and experimental evaluation of plant and herbivore interactions in subtidal algal stands. PhD Thesis University of Auckland. 166 p.
- Schiel, D.R. (1990). Macroalgal assemblages in New Zealand: structure, interactions and demography. *Hydrobiologia*, 192(1), 59–76. https://doi.org/10.1007/BF00006227
- Schiel, D.R. (2013). The other 93%: trophic cascades, stressors and managing coastlines in non-marine protected areas. *New Zealand Journal of Marine and Freshwater Research*, 47(3), 374–391. https://doi.org/10.1080/00288330.2013.810161

- Schiel, D.R.; Andrew, N.L.; Foster, M.S. (1995). The structure of subtidal algal and invertebrate assemblages at the Chatham Islands, New Zealand. *Marine Biology*, *123*(2), 355–367. https://doi.org/10.1007/BF00353627
- Schiel, D.R.; Foster, M.S. (1986). The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology Annual Review*, *24*, 265–307.
- Schiel, D.R.; Foster, M.S. (2006). The Population Biology of Large Brown Seaweeds: Ecological Consequences of Multiphase Life Histories in Dynamic Coastal Environments. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 343–372. https://doi.org/10.1146/annurev.ecolsys.37.091305.110251
- Schiel, D.R.; Foster, M.S. (2015). *The biology and ecology of giant kelp forests*. Univ of California Press. Oakland California. 395 p.
- Schiel, D.R.; Gerrity, S.; Orchard, S. (2023). Allocations, quota and abalone fishery management: the tragedy of the commons revisited. *New Zealand Journal of Marine and Freshwater Research*, 1–18. https://doi.org/10.1080/00288330.2023.2273468
- Schiel, D. R., Gerrity, S., Orchard, S., Alestra, T., Dunmore, R. A., Falconer, T., Thomsen, M. S., & Tait, L. W. (2021). Cataclysmic Disturbances to an Intertidal Ecosystem: Loss of Ecological Infrastructure Slows Recovery of Biogenic Habitats and Diversity. *Frontiers in Ecology and Evolution*, 9. https://doi.org/10.3389/fevo.2021.767548
- Schiel, D.R.; Kingsford, M.J.; Choat, J.H. (1986). Depth distribution and abundance of benthic organisms and fishes at the subtropical Kermadec Islands. *New Zealand Journal of Marine and Freshwater Research*, 20(4), 521–535. https://doi.org/10.1080/00288330.1986.9516173
- Schiel, D.R.; Nelson, W.A. (1990). The harvesting of macroalgae in New Zealand. *Hydrobiologia*, 204, 25–33.
- Schiel, D.R.; Wood, S.A.; Dunmore, R.A.; Taylor, D.I. (2006). Sediment on rocky intertidal reefs: Effects on early post-settlement stages of habitat-forming seaweeds. *Journal of Experimental Marine Biology and Ecology*, 331(2), 158–172. https://doi.org/10.1016/j.jembe.2005.10.015
- Schimel, A.C.G.; Brown, C.J.; Ierodiaconou, D. (2020). Automated Filtering of Multibeam Water-Column Data to Detect Relative Abundance of Giant Kelp (*Macrocystis pyrifera*). *Remote Sensing*, 12(9), 1371. https://doi.org/10.3390/rs12091371
- Schlenger, A.J.; Beas-Luna, R.; Ambrose, R.F. (2021). Forecasting ocean acidification impacts on kelp forest ecosystems. *PLOS ONE*, *16*(4), e0236218. https://doi.org/10.1371/journal.pone.0236218
- Schlieman, C.D.; Wing, S.R.; O'Connell-Milne, S.A.; McMullin, R.M.; Durante, L.M.; Kolodzey, S.; Frew, R.D. (2022). Catchment modifications influence the composition of basal organic matter supporting suspension-feeding bivalves. *Estuarine, Coastal and Shelf Science*, 275, 107989. https://doi.org/10.1016/j.ecss.2022.107989
- Shears, N.T.; Babcock, R.C. (2002). Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia*, *132*(1), 131–142. https://doi.org/10.1007/s00442-002-0920-x
- Shears, N.T.; Babcock, R.C. (2003). Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series*, 246, 1–16. https://doi.org/10.3354/meps246001
- Shears, N.T.; Babcock, R.C. (2004). Community composition and structure of shallow subtidal reefs in northeastern New Zealand, *Science for Conservation No. 245.* 22 p.
- Shears, N.T.; Babcock, R.C. (2007). Quantitative description of mainland New Zealand's shallow subtidal reef communities. *Science for Conservation No. 280.* 126 p.
- Shears, N.T.; Babcock, R.C.; Salomon, A.K. (2008). Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. *Ecological Applications*, 18(8), 1860–1873. https://doi.org/10.1890/07-1776.1
- Shelamoff, V.; Layton, C.; Tatsumi, M.; Cameron, M.J.; Wright, J.T.; Johnson, C.R. (2022). Restored kelp facilitates lobster recruitment but not other mid-trophic macroinvertebrates. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 32(7), 1115–1125. https://doi.org/10.1002/aqc.3825
- Smale, D.A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytologist*, 225(4), 1447–1454. https://doi.org/https://doi.org/10.1111/nph.16107

- Smale, D.A.; Vance, T. (2015). Climate-driven shifts in species' distributions may exacerbate the impacts of storm disturbances on North-east Atlantic kelp forests. *Marine and Freshwater Research*, 67(1), 65–74. https://doi.org/10.1071/MF14155
- Smith, H.G.; Neverman, A.J.; Betts, H.; Spiekermann, R. (2023). The influence of spatial patterns in rainfall on shallow landslides. *Geomorphology*, 437, 108795. https://doi.org/10.1016/j.geomorph.2023.108795
- Springer, Y., Hays, C., Carr, D., Mackey, M., & Bloeser, J. (2006). Ecology and Management of the Bull Kelp, Nereocystis Luetkeana: A Synthesis with Recommendations for Future Research. https://www.researchgate.net/publication/228379251_Ecology_and_Management_of_the_Bull Kelp Nereocystis Luetkeana A Synthesis with Recommendations for Future Research
- Spyksma, A.J.P.; Taylor, R.B.; Shears, N.T. (2017). Predation cues rather than resource availability promote cryptic behaviour in a habitat-forming sea urchin. *Oecologia*, *183*(3), 821–829. https://doi.org/10.1007/s00442-017-3809-4
- Stats NZ. (2021). Environmental-Economic Accounts: Fish monetary stock account 1996-2020. https://www.stats.govt.nz/information-releases/environmental-economic-accounts-2020-tables
- Steneck, R.S.; Graham, M.H.; Bourque, B.J.; Corbett, D.; Erlandson, J.M.; Estes, J.A.; Tegner, M.J. (2002). Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, 29(4), 436–459. https://doi.org/10.1017/S0376892902000322
- Suárez-Jiménez, R.; Hepburn, C.D.; Hyndes, G.A.; McLeod, R.J. Taylor, R.B.; Hurd, C.L. (2017). The invasive kelp *Undaria pinnatifida* hosts an epifaunal assemblage similar to native seaweeds with comparable morphologies. *Marine Ecology Progress Series*, *582*, 45–55. https://doi.org/10.3354/meps12321
- Swanson, A.K.; Fox, C.H. (2007). Altered kelp (Laminariales) phlorotannins and growth under elevated carbon dioxide and ultraviolet-B treatments can influence associated intertidal food webs. *Global Change Biology*, *13*(8), 1696–1709. https://doi.org/10.1111/j.1365-2486.2007.01384.x
- Tait, L.W. (2019). Giant kelp forests at critical light thresholds show compromised ecological resilience to environmental and biological drivers. *Estuarine, Coastal and Shelf Science*, 219, 231–241. https://doi.org/10.1016/j.ecss.2019.02.026
- Tait, L.W.; Bind, J.; Charan-Dixon, H.; Hawes, I.; Pirker, J.; Schiel, D. (2019). Unmanned Aerial Vehicles (UAVs) for Monitoring Macroalgal Biodiversity: Comparison of RGB and Multispectral Imaging Sensors for Biodiversity Assessments. *Remote Sensing*, 11(19), 2332. https://www.mdpi.com/2072-4292/11/19/2332
- Tait, L.W.; Mangan, S. (2024). *Guidance for using drones to monitor coastal ecosystems* https://tohora.org.nz/documents/164
- Tait, L.W.; Thoral, F.; Pinkerton, M.H.; Thomsen, M.S.; Schiel, D.R. (2021). Loss of Giant Kelp, *Macrocystis pyrifera*, Driven by Marine Heatwaves and Exacerbated by Poor Water Clarity in New Zealand. *Frontiers in Marine Science*, 8. https://doi.org/10.3389/fmars.2021.721087
- Taylor, R.B. (1998). Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Marine Ecology Progress Series*, *172*, 37–51. https://doi.org/10.3354/meps172037
- Taylor, R.B.; Cole, R.G. (1994). Mobile epifauna on subtidal brown sea-weeds in northeastern New Zealand. *Marine Ecology-Progress Series*, 115, 271–282. https://doi.org/10.3354/meps115271
- Teagle, H.; Hawkins, S.J.; Moore, P.J.; Smale, D.A. (2017). The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology*, 492, 81–98. https://doi.org/10.1016/j.jembe.2017.01.017
- Tegner, M.J.; Dayton, P.K. (2000). Ecosystem effects of fishing in kelp forest communities. *ICES Journal of Marine Science*, *57*(3), 579–589. https://doi.org/10.1006/jmsc.2000.0715
- Thompson, G.A.; Schiel, D.R. (2012). Resistance and facilitation by native algal communities in the invasion success of *Undaria pinnatifida*. *Marine Ecology Progress Series*, 468, 95–105. https://doi.org/10.3354/meps09995

- Thomsen, M.S.; Mondardini, L.; Alestra, T.; Gerrity, S.; Tait, L.; South, P.M.; Lilley, S.A.; Schiel, D.R. (2019). Local extinction of bull kelp (Durvillaea spp.) due to a marine heatwave *Frontiers in Marine Science*, 6. https://doi.org/10.3389/fmars.2019.00084
- Thomsen, M.S.; Mondardini, L.; Thoral, F.; Gerber, D.; Montie, S.; South, P.M.; Tait, L.; Orchard, S.; Alestra, T.; Schiel, D.R. (2021). Cascading impacts of earthquakes and extreme heatwaves have destroyed populations of an iconic marine foundation species. *Diversity and Distributions*, 27(12), 2369–2383. https://doi.org/10.1111/ddi.13407
- Thoral, F.; Pinkerton, M.H.; Tait, L.W.; Schiel, D.R. (2023). Spectral light quality on the seabed matters for macroalgal community composition at the extremities of light limitation. *Limnology and Oceanography*, 68(4), 902–916. https://doi.org/10.1002/lno.12318
- Tillin, H.M.; Mason, E.; Jones, M.; Burrows, M.; Smale, D. (2023). *Developing a method to estimate the macroalgal (Kelp/Ascophyllum nodosum) standing stock in England and Wales* https://www.researchgate.net/publication/387822649_Developing_a_method_to_estimate_the macroalgal KelpAscophyllum nodosum standing stock in England and Wales
- Timmer, B.; Reshitnyk, L.Y.; Hessing-Lewis, M.; Juanes, F.; Costa, M. (2022). Comparing the Use of Red-Edge and Near-Infrared Wavelength Ranges for Detecting Submerged Kelp Canopy. *Remote Sensing*, *14*(9), 2241. https://doi.org/10.3390/rs14092241
- Traiger, S.B.; Cohn, B.; Panos, D.; Daly, M.; Hirsh, H.K.; Martone, M.; Gutierrez, I.; Mucciarone, D.A.; Takeshita, Y.; Monismith, S.G.; Dunbar, R.B.; Nickols, K.J. (2022). Limited biogeochemical modification of surface waters by kelp forest canopies: Influence of kelp metabolism and site-specific hydrodynamics. *Limnology and Oceanography*, 67(2), 392–403. https://doi.org/10.1002/lno.11999
- Udy, J.; Wing, S.; O'Connell-Milne, S.; Kolodzey, S.; McMullin, R.; Durante, L.; Frew, R. (2019a). Organic matter derived from kelp supports a large proportion of biomass in temperate rocky reef fish communities: Implications for ecosystem-based management. *Aquatic Conservation:*Marine and Freshwater Ecosystems, 29(9), 1503–1519. https://doi.org/10.1002/aqc.3101
- Udy, J.A.; Wing, S.R.; O Connell-Milne, S.A.; Durante, L.M.; McMullin, R.M.; Kolodzey, S.; Frew, R.D. (2019b). Regional differences in supply of organic matter from kelp forests drive trophodynamics of temperate reef fish. *Marine Ecology Progress Series*, 621, 19–32. https://doi.org/10.3354/meps12974
- Umar, M.J.; McCook, L.J.; Price, I.R. (1998). Effects of sediment deposition on the seaweed Sargassum on a fringing coral reef. *Coral Reefs*, *17*(2), 169–177. https://doi.org/10.1007/s003380050111
- Ummenhofer, C.C.; Meehl, G.A. (2017). Extreme weather and climate events with ecological relevance: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1723), 20160135. https://doi.org/10.1098/rstb.2016.0135
- Valentine, J.; Johnson, C. (2004). Establishment of the introduced kelp Undaria pinnatifida following dieback of the native macroalga Phyllospora comosa in Tasmania, Australia. *Marine and Freshwater Research*, 55, 223–230. https://doi.org/10.1071/MF03048
- Vásquez, J.A.; Zuñiga, S.; Tala, F.; Piaget, N.; Rodríguez, D.C.; Vega, J.M.A. (2014). Economic valuation of kelp forests in northern Chile: values of goods and services of the ecosystem. *Journal of Applied Phycology*, 26(2), 1081–1088. https://doi.org/10.1007/s10811-013-0173-6
- Ventura, D.; Grosso, L.; Pensa, D.; Casoli, E.; Mancini, G.; Valente, T.; Scardi, M.; Rakaj, A. (2023). Coastal benthic habitat mapping and monitoring by integrating aerial and water surface low-cost drones. *Frontiers in Marine Science*, 9. https://doi.org/10.3389/fmars.2022.1096594
- Vergés, A.; Steinberg, P.D.; Hay, M.E.; Poore, A.G.B.; Campbell, A.H.; Ballesteros, E.; Heck, K.L.; Booth, D.J.; Coleman, M.A.; Feary, D.A.; Figueira, W.; Langlois, T.; Marzinelli, E.M.; Mizerek, T.; Mumby, P.J.; Nakamura, Y.; Roughan, M.; van Sebille, E.; Gupta, A.S.; Smale, D.A.; Tomas, F.; Wernberg, T.; Wilson, S.K. (2014). The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 20140846. https://doi.org/10.1098/rspb.2014.0846
- Vetter, E.W.; Dayton, P.K. (1998). Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep Sea Research Part II: Topical Studies in Oceanography*, 45(1), 25–54. https://doi.org/10.1016/S0967-0645(97)00048-9

- von Biela, V.R.; Arimitsu, M.L.; Piatt, J.F.; Heflin, B.; Schoen, S.K.; Trowbridge, J.L.; Clawson, C.M. (2019). Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave of 2014-2016. *Marine Ecology Progress Series*, 613, 171–182. https://doi.org/10.3354/meps12891
- Walton, M.E.M.; Browne, R.; Griffiths, J.N.; Cartwright, D.; Robins, P.; Malham, S.K.; Le Vay, L. (2022). Kelp detritus: Unutilized productivity or an unacknowledged trophic resource? Science of The Total Environment, 820, 153191. https://doi.org/10.1016/j.scitotenv.2022.153191
- Wang, X.L.; Feng, Y.; Swail, V.R. (2014). Changes in global ocean wave heights as projected using multimodel CMIP5 simulations. *Geophysical Research Letters*, 41(3), 1026–1034. https://doi.org/10.1002/2013GL058650
- Waters, J.M.; King, T.M.; Fraser, C.I.; Craw, D. (2018). An integrated ecological, genetic and geological assessment of long-distance dispersal by invertebrates on kelp rafts. *Frontiers of Biogeography 10 (3–4)*. https://doi.org/10.21425/F5FBG40888
- Wernberg, T.; Bennett, S.; Babcock, R.C.; de Bettignies, T.; Cure, K.; Depczynski, M.; Dufois, F.; Fromont, J.; Fulton, C.J.; Hovey, R.K.; Harvey, E.S.; Holmes, T.H.; Kendrick, G.A.; Radford, B.; Santana-Garcon, J.; Saunders, B.J.; Smale, D.A.; Thomsen, M.S.; Tuckett, C.A.; Tuya, F.; Vanderklift, M.A.; Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, 353(6295), 169–172. https://doi.org/doi:10.1126/science.aad8745
- Wernberg, T.; Connell, S.D. (2008). Physical disturbance and subtidal habitat structure on open rocky coasts: Effects of wave exposure, extent and intensity. *Journal of Sea Research*, 59(4), 237–248. https://doi.org/10.1016/j.seares.2008.02.005
- Wernberg, T.; Russell, B.D.; Thomsen, M.S.; Gurgel, C.; Frederico, D.; Bradshaw, C.J.A.; Poloczanska, E.S.; Connell, S.D. (2011). Seaweed Communities in Retreat from Ocean Warming. *Current Biology*, 21(21), 1828–1832. https://doi.org/10.1016/j.cub.2011.09.028
- Wernberg, T.; Smale, D.A.; Tuya, F.; Thomsen, M.S.; Langlois, T.J.; de Bettignies, T.; Bennett, S.; Rousseaux, C.S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, *3*(1), 78–82. https://doi.org/10.1038/nclimate1627
- Wheeler, T.; Major, R.; Ogilvie, S.; South, P.; Romanazzi, D.; Adams, S. (2021). Stocktake and characterisation of New Zealand's seaweed sector: Species characteristics and Te Tiriti o Waitangi considerations. Report for Sustainable Seas National Science Challenge project Building a seaweed sector: developing a seaweed sector framework for Aotearoa New Zealand. (Project code 2.5)
- White, L.N.; White, W.L. (2020). Seaweed utilisation in New Zealand. *Botanica Marina*, 63(4), 303–313. https://doi.org/10.1515/bot-2019-0089
- Williams, G.J.; Cameron, M.J.; Turner J.R.; Ford, R.B. (2008). Quantitative characterisation of reef fish diversity among nearshore habitats in a northeastern New Zealand marine reserve. *New Zealand Journal of Marine and Freshwater Research*, 42(1), 33–46. https://doi.org/10.1080/00288330809509934
- Williams, J.P.; Claisse, J.T.; Pondella II, D.J.; Williams, C.M.; Robart, M.J.; Scholz, Z.; Jaco, E.M. Ford, T.; Burdick, H.; Witting, D. (2021). Sea urchin mass mortality rapidly restores kelp forest communities. *Marine Ecology Progress Series*, 664, pp.117–131.
- Willis, T.J.; Anderson, M.J. (2003). Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Marine Ecology Progress Series*, 257, 209–221. https://doi.org/10.3354/meps257209
- Wing, S.; Jack, L. (2012). Resource specialisation among suspension-feeding invertebrates on rock walls in Fiordland, New Zealand, is driven by water column structure and feeding mode. *Marine Ecology Progress Series*, 452, 109–118. https://doi.org/10.3354/meps09588
- Wing, S.R.; Beer, N.A.; Jack, L. (2012). Resource base of blue cod *Parapercis colias* subpopulations in marginal fjordic habitats is linked to chemoautotrophic production. *Marine Ecology Progress Series*, 466, 205–214. https://doi.org/10.3354/meps09929
- Wing, S.R.; Shears, N.T.; Tait, L.W.; Schiel, D.R. (2022). The legacies of land clearance and trophic downgrading accumulate to affect structure and function of kelp forests. *Ecosphere*, *13*(12), e4303. https://doi.org/10.1002/ecs2.4303

