



Linking marine fisheries species to biogenic habitats in
New Zealand: a review and synthesis of knowledge

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M.A. Morrison
E.G. Jones
M. Consalvey
K. Berkenbusch

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EXECUTIVE SUMMARY

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Fisheries research and management has traditionally been focussed on the fish populations, while the habitats and environments which underpin their production have been largely ignored. This situation is changing, with an increasing awareness that habitats are important and can be degraded through human activities, both marine and land-based. While the wider field of marine ecology has been researching such fish-habitat themes for a number of decades, the species worked on are often small, site-attached, and relatively short-lived; while fisheries species tend to be larger bodied, and operate over much larger spatial and temporal scales. Given this, quantitatively linking fisheries species to habitats is a challenge, and an active field of research. One type of habitat that appears to be especially important for many demersal species are those referred to as 'biogenic' habitats.

These biogenic habitats are formed by plants and animals, and occur from the inter-tidal out to the deep sea. Well known biogenic habitats include salt marshes, mangrove forests, seagrass meadows, kelp forests, bryozoan fields, and shellfish beds. For the purposes of this review, biogenic habitats are defined as a) those living species that form emergent three-dimensional structure, that separate areas in which they occur from surrounding lower vertical dimension seafloor habitats and b) non-living structure generated by living organisms, such as infaunal tubes and burrows. A sub-set of these habitats are biogenic "reefs", which are visually imposing, and are defined as "solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms."

The functions provided by these habitats are diverse, and can include the elevation of biodiversity, benthic-pelagic coupling, sediment baffling, protection from erosion, nutrient recycling, the provision of shelter and food for a wide range of other organisms, and even the creation of geological features over longer time scales. They also directly underpin fisheries production for a range of species, through: 1) the provision of shelter from predation, 2) the provision of associated prey species, and in some cases, 3) the provision of surfaces for reproductive purposes e.g. the laying of elasmobranch egg cases; as well as, 4) indirectly in the case of primary producers through trophic pathways.

In New Zealand, historical data on biogenic habitat extents and changes over time are very poor, and largely limited to shallow estuarine systems where change is visually observable (e.g. salt marsh, mangroves, seagrass and oyster beds), and/or where the biogenic species is actively harvested (e.g. green-lipped mussels), or strongly associated with fish catches (e.g. the bryozoan beds of Separation Point, and off Torment Bay with coastal finfish; and the bryozoan reefs of Foveaux Strait with dredge oysters). For such species where data is available (often 'just' anecdotal accounts), strong declines have occurred, which appear largely attributable to land-based effects (e.g., sedimentation and elevated nutrient levels), and fishing impacts. Examples include the extensive loss of seagrass meadows (e.g. large areas in Whangarei, Waitemata, Manukau, Tauranga and Avon-Heathcote estuaries), green-lipped mussel beds (about 500 km² in the Hauraki Gulf), bryozoan beds (about 80

km² in Torrent Bay, about 800 km² in Foveaux Strait), and deep-water coral thickets on sea-mounts. Mangrove forests, in contrast, are one of the few biogenic habitat habitats which have greatly expanded in extent, following initial losses during European settlement through land reclamation and the building of infrastructure. Cumulatively, the magnitude and extent of biogenic habitat losses are likely to have been very substantial, but are unknown, and probably will never be able to be calculated. Other biogenic habitat species for which evidence points to historical losses include horse mussels, kelp forests, oyster beds, and sponges, both in assemblages where they tend to dominate, and as part of mixed biogenic habitat assemblages.

In the New Zealand context, there is currently no marine habitat classification system at the scale of biotopes (defined as recognisable and re-occurring natural associations of plants and animals), with the sole exception being a validated broad level habitat classification for shallow north-eastern New Zealand rocky reefs (including kelp forests and algal mats). This makes the formal and systematic evaluation of biogenic habitats problematic, and so in this review we work our way through biogenic habitats based on their intuitively obvious visual identities, and associated habitat quality variations where quantified. World-wide, biogenic habitats have seriously declined in extent and quality over time scales of decades to centuries, with global reviews (subject to some geographic data gaps) all showing serious regional and global declines in wetlands, sea-grasses, kelp forests, and oyster reefs; other biogenic habitats, including subtidal ones, may also be in decline but data is unavailable. The many functions and species associated with these habitats have by association also been lost or severely reduced. These fundamental changes in ecosystem structure and functioning have until recently been largely ignored or overlooked, partly through the phenomena of ‘sliding environmental baselines’, where each succeeding human generation has a different view of what is ‘natural’ in the oceans.

Quantitative links between fisheries species and seafloor habitats are poorly known in New Zealand. Most of the fish-habitat work has been completed in:

- Estuaries, where fish-habitat associations have been quantified for habitats such as:
 - mangroves (juvenile short-finned eels, grey mullet, and parore)
 - sub-tidal seagrass (northern New Zealand; juvenile snapper, trevally, parore, piper)
 - horse mussels (northern New Zealand; juvenile snapper, trevally).
- In more coastal locations, associations include:
 - biogenic pits and burrows (Hauraki Gulf) (juvenile snapper)
 - kelp forest edges and sponge gardens (Hauraki Gulf) (juvenile snapper)
 - bryozoan mounds at Separation Point and Torrent Bay (the latter now eliminated) (juvenile tarakihi, leatherjackets, snapper, blue cod and red cod)
 - tubeworm mounds and sponges, Port Underwood (Marlborough Sounds) (juvenile and adult blue cod)
 - Otago Shelf bryozoans (juvenile blue cod, red cod, and southern pigfish)
 - Biogenic assemblages (sponges, tubeworms, horse mussels and others) on the east coast continental shelf, South Island (juvenile tarakihi)
 - Foveaux Strait bryozoans (juvenile and adult blue cod)
 - Ninety Mile Beach foliose red algae and hydroid beach cast (green-lipped mussel spat).
- In deeper water, fish-biogenic habitat associations are effectively unknown.

In terms of reproductive links, the only observations available were the attachment of elasmobranch egg cases (e.g. skates in the Marlborough Sounds and Paterson Inlet, Stewart Island; and elephant fish

in the inshore Canterbury area), the attachment of piper/garfish egg masses to seagrass; and of Broad squid egg masses to shallow water kelp plants.

There is effectively no knowledge of how biogenic habitats may provide elevated food sources for fisheries species, aside from recent work in seagrass meadows, where a mixture of benthic and pelagic food sources are utilised by the associated small fish assemblages, including juvenile snapper and trevally. There is some evidence of the importance of habitat quality: recent experimental work using artificial habitat mimics has shown that increasing seagrass blade density attracts higher juvenile fish densities (up to a threshold for snapper and trevally); artificial horse mussel with epifauna mimics also elevate juvenile snapper numbers. Some of the above work is semi-quantitative in nature, which makes it difficult to generate metrics such as densities, to feed into modelling frameworks. Other key metrics, such as survival and growth rates relative to habitat, have not been quantified at all, due partially to the difficulties associated with estimating them under realistic field conditions. Without such measures of how different habitats contribute to adult populations, it is not possible to scale up to the fish population and associated fisheries level.

New Zealand's understanding of how biogenic habitats may contribute to fisheries production is at a very early stage, and the data only rarely exists to explicitly link habitats to production. The only exception to this is the snapper stock SNA 8 (the west coast of the North Island), where otolith chemistry (albeit for the 2003 year class only) has linked most of the adult snapper taken in the fishery back to the Kaipara Harbour as their natal nursery. Detailed fish-habitat survey work within the Kaipara Harbour has shown that high juvenile snapper densities are strongly associated with biogenic habitat structure on the seafloor, especially sub-tidal seagrass meadows, horse mussels, sponges, and an invasive bryozoan. The Kaipara Harbour is known to be under increasing pressure from land-based impacts such as sedimentation, and historical ecology work has revealed that large changes have occurred in the harbour in living memory, including the loss of areas of sub-tidal seagrass beds from the Kaipara Harbour (and presumably their associated juvenile fish contributions to the SNA 8 and other fish stocks).

There is robust evidence that some biogenic habitats have been greatly reduced in their extent and quality, ranging from the intertidal out to seamounts, although the magnitude of these losses are very poorly known. There is also empirical evidence that a number of demersal fish species are strongly associated with biogenic habitats during their juvenile life phases (e.g. snapper, trevally, blue cod, tarakihi, leatherjackets), with these habitats likely to be providing advantages in terms of growth and/or survival of these juvenile phases (the latter based largely on overseas work). In turn, it is logical, (although with the exception of the Kaipara Harbour no hard empirical data exist to support this), that these reductions in biogenic habitats are causing reductions in subsequent juvenile recruitment into adult fished populations. We would argue that this lack of evidence is due to a fundamental lack of targeted work in New Zealand aiming at linking fisheries species productivity to their underpinning habitats, rather than this dynamic not being important – a viewpoint shared in the international literature (see Armstrong & Falk-Petersen 2008).

Several areas of research are suggested to further advance our knowledge of such dynamics, with the aim being to better manage these systems so as to protect and enhance fisheries production. These are as follows:

- developing a national (fish-) habitat classification

- developing ways to detect and map biogenic habitats
- improved habitat modelling and associated predictive habitat maps
- a better understanding of threats and stressors
- the explicit quantifying of fisheries-biogenic habitat links from habitat patches to the fishery scale
- a better understanding of how selected biogenic habitats function as living organisms.

Several selected species (areas or stocks) are suggested for targeted research, being:

1. Juvenile snapper and biogenic habitats associated with the SNA 8 West Coast North Island, where the stock has failed to recover despite quota cuts and associated modelling predictions, detailed juvenile nursery habitat data exists, and mapping of some key habitats (i.e., sub-tidal seagrass meadows) has been completed.
2. Juvenile snapper in the SNA 1 stock, where a large amount of background knowledge exists, New Zealand's largest recreational fishery is based (e.g., useful in informing wider society about land-based impacts), and many other end-users and agencies also have a strong interest in biogenic habitats.
3. Blue cod, in a selected localised region, given their suspected juvenile phase reliance on biogenic habitats, which are susceptible to both land and marine-based impacts – the Marlborough Sounds is one obvious choice, given the management concerns around the sustainability of the recreational fishery, and the suspicion that land-based effects may be significant.
4. Tarakihi at the national scale, given that this fishery of approximately 6000 t per year is showing signs of stress, that there is background information suggesting that juvenile tarakihi are strongly associated with biogenic habitat nurseries (which are also under stress), and that the stock is thought to be operating at the national scale.

INTRODUCTION

The world's coasts and oceans are coming under increasing pressure from human activities, both through direct use of the marine environment, and indirectly through changes and intensification in land mass uses, and cascading effects into the world's climate and atmospheric chemistry. Natural resource based industries such as fishing are often considered to be fully exploited (sometimes over-exploited), with the underlying ecosystems on which they depend becoming more and more impacted from a range of cumulative pressures. Against this environmental context, economies still need to gain economic and social value from the fisheries they possess. New Zealand is in a comparatively fortunate position relative to much of the rest of the world, with an internationally lauded Quota Management System (QMS) to regulate total biomass removals from its 636 recognised species / stock complexes. Combined with this are a range of input controls and spatial restrictions designed to further regulate for healthy and sustainable fisheries.

However, as ideas and concepts about fisheries (and wider) ecosystem management continue to evolve, a new paradigm is taking shape that involves a more holistic view of fisheries as being an integral component of the wider ecosystem. Generically, this is referred to as Ecosystem Based Fishery Management (EBFM). A number of authors have attempted to define exactly what it is, including lists and rules of what good EBFM should incorporate, and guidelines as to its development and implementation. However, as an emerging concept that is yet to be fully refined and adapted through iterative management regimes, it is still in its relative infancy, and debate continues as to what it really is, the need for it, and the (perceived or otherwise) large amounts of data and knowledge needed to successfully 'drive' it. Reality suggests that the eventual new order that emerges will be a hybrid between traditional single species approaches, and more holistic ecosystem ones. Whatever the case, there is now general agreement that fisheries management needs to take a broader ecosystem based approach than it has done in the past. This also includes linking the fisheries sector into the wide management framework of Marine Spatial Planning (MSP) initiatives.

One of the central themes to emerge from this new viewpoint is the role of 'habitat' in supporting fisheries production, and the need to better integrate its maintenance and protection as part of sustainable management. Many nations are now recognising this, with the most widely known example coming from the United States, where the Manguson-Stevens Fishery Conservation and Management Act requires that all 'essential fish habitat' should be identified and protected (Benaka 1999). Such policies explicitly recognise the link between fauna, flora and habitat, and require appropriate strategies for classifying aquatic habitats and assessing their relative importance and condition (Diaz et al. 2004). In this review, we focus on the known and potential role of biogenic (living) habitats in helping underpin and support New Zealand's marine fisheries, from the intertidal out to seamounts, as a critical component of moving towards EBFM.

1.1 Objectives

OVERALL OBJECTIVES:

- 1 To review available information on the ecosystem value, functioning, and location of biogenic habitats important to marine fisheries production, and identify threats and information gaps relevant to an ecosystem approach to fisheries management.

SPECIFIC OBJECTIVES:

1. To collate and review available information on the location, value, functioning, threats to, and past and current status of biogenic habitats that may be important for fisheries production in the New Zealand marine environment.
2. To identify information gaps, in the New Zealand context, and recommend measures to address those important to an ecosystem approach to fisheries management.

1.2 Scope and limitations of review

Written material, from both the primary and grey literature, was sourced using a combination of key word web search engines (Web of Science, Google), manual searches of New Zealand science journals, and professional contacts in both science and regulatory agencies. The quality and type of material varied widely across different sources. Grey literature is included as this holds important information in the New Zealand context that does not exist in other forms. We have been systematic in our use of New Zealand material, but given its patchy nature (including many significant information gaps), have augmented it wherever possible with relevant international knowledge, to establish an overall framework. This is especially true for deep-water (defined here as water depth over 200 m) biogenic habitat links to fisheries, as knowledge of these is scant even at the global level. For very shallow water systems (less than 10 m) there is an immense scientific literature on biogenic habitats in general, which includes fished species, but which is generally not specifically about fisheries *per se*. Much of this work is focussed on tropical systems, especially around coral reefs, mangrove forests, and seagrass meadows. For the purposes of this review, we have only included international work from temperate systems, and have been quite selective in its use, as a full review of all the different work areas is well beyond the domain of any single literature review. For example, a general review of temperate mangrove knowledge by Morrissey et al. (2010) listed 276 citations, while a more specialised review of ‘fish in mangroves’ work by Faunce & Serafy (2006) listed 50 studies.

For each individual biogenic habitat, we have preferentially included New Zealand work where available, as well as one or more relevant overseas examples to demonstrate the possible value of the habitat. However, there is no true substitute for local species and geographic region specific studies. Overseas studies may be limited in their relevance both because of the different habitat and fisheries species pools they cover, and because of the influence of continental systems, as opposed to New Zealand’s oceanic islands status. Therefore international studies provide guidance for the potential and possible values of different habitats, but cannot be simply transferred across to the New Zealand situation. For example, there has been extensive work on the fish assemblages of giant kelp (*Macrocystis pyrifera*) forests in California, where fish assemblages are dominated by speciose fish groups such as rock fishes (*Sebastes* spp.). While New Zealand’s giant kelp is the same pan-global kelp species, rock fish are absent, and a different assemblage of fishery and other fish species occurs

in association with the kelp. Similarly, most of the work on seagrass and maerl fish–habitat interactions in the Northern Hemisphere has focussed on true cod species (gadoids), which are also not present in New Zealand. Therefore, international studies should be viewed as examples of how fish can and do use such biogenic habitats, and of the mechanisms driving that use: but cannot be used as direct proxies for what exists in the New Zealand situation. Only empirical field studies will answer such questions.

Biogenic habitats, in addition to helping underpin fisheries production, also fulfil many other important roles, with one of the most visually obvious ones being the enhancement of biodiversity. Species diversity often increases with increasing structural habitat complexity, and so as a secondary focus, we include such knowledge where it is available. Additional biogenic habitat functions include increased primary production, benthic–pelagic coupling, sediment and water flow baffling, carbon sequestration, mitigation of nutrient effects, and storm protection (mangroves) (e.g. Lotze et al. 2006, Airolidi & Beck (2007); however, such roles are outside the context of this review and are not covered here.

Our focus is on fisheries species, but in most (almost all) cases the New Zealand ‘marine habitat’ literature tends to focus more widely on species assemblages in general, and so where relevant these are included. We do not include work on very small bodied adult fish (e.g., ‘triple-fins’), nor on general small invertebrate assemblages. We also exclude truly pelagic fish species from this review – but note the use of drifting pelagic biogenic debris by some demersal species such as larval/juvenile juvenile pelagic parore, leatherjackets, kingfish, blue warehou, and hapuka/bass (see Morrison et al. 2014). At the request of the Ministry of Fisheries (now Ministry for Primary Industries), we have also included a discrete section on the potential role and value of burrows and other non-emergent biogenic structures on the seafloor. As the literature on this is very limited with respect to direct links to fisheries species, this section is more generic, and highlights the functioning of such elements in seafloor ecology, which in turn link to fisheries production. This review is also a companion document of sorts to two recent New Zealand focussed reviews: the first on the effects of land-based activities on coastal fisheries and associated biodiversity (Morrison et al. 2009), and the second on habitats and areas of particular significance for coastal finfish fisheries management in New Zealand, with a central focus on fish life histories (Morrison et al. 2014).

Our hope is that this review will help act as a catalyst for new research and management initiatives which explicitly include the fundamental role of biogenic (and other) habitats, and that a more habitat-based ecosystem management of marine fisheries will eventually emerge.

1.3 What is (biogenic) habitat?

Habitat does not simply equate to the substrate, but involves a complex interplay between the broader environmental context, and the life history and behaviour dynamics of the species examined, across a range of spatial and temporal scales (see figure 1 of Diaz et al. 2004). Overlaid on these local dynamics are a range of other, broader scale, drivers such as bio-geography, meta-population dynamics including source-sink frameworks, and oceanographic variability. In this review our primary focus is on biogenic habitats at a local scale, but these other factors are also important, and are discussed when sufficient information exists.

Defining habitats to a level where they can be meaningfully incorporated into management regimes requires classification system(s), which incorporate all of the scales mentioned above. Diaz et al.

(2004) noted that the development of a “*system capable of assessing the quantity, quality and functional value of marine systems, irrespective of location, is not a trivial task*”. Implicit in such classification schemes is the need to incorporate habitat quality, beyond just the presence/absence of a putative habitat. Many factors can affect the use of such habitats, at both patch (e.g., size, and perimeter/area ratios), and landscape (e.g., inter-patch distances, habitat type contiguous-ness) scales. The development of functional habitat classification schemes is an internationally active field of research, and some large scale systems exist (e.g. the pan-European ‘European Union Nature Information System’ (EUNIS), and linked to this, the MNCR BioMar classification for Britain and Ireland) see <http://jncc.defra.gov.uk/page-3083>. Efforts are also being made in Australia to develop a classification system around managing fisheries impacts, though the approach and habitat scales are quite different from the European system (see figure 2 of Williams et al. 2011). However, much work remains to be done, including the collection of appropriate empirical data to populate and help adaptively improve habitat classifications. In New Zealand, the only coastal habitat classification that has been created (and validated) is one for the shallow rocky reef habitats of north-eastern New Zealand (Shears et al. 2004), based on the original work of Ayling (1978). At the national scale, an environmental domain classification exists, the Marine Environmental Classification (MEC) (Snelder et al. 2007) and subsequent developments such as the Benthic Optimised MEC (BOMECE), but this does not include a ‘biotope’ classification (recognisable and re-occurring natural associations of plants and animals; not included due to a lack of data), nor does it include geomorphological meso-habitat features such as canyons, hills, plateaus, holes, ridges, and knolls. We note the viewpoint of Diaz et al. (2004): “*how can one accurately evaluate the relative value, in a temporal and/or spatial sense, of a specific habitat when no attempt has been made to objectively define the type and extent of the habitat itself?*” Current work in the MBIE programme ‘Coastal Conservation Management’ (CCM) is focussed on building a (fish-) habitat classification for New Zealand’s estuarine and coastal zone, using both a ‘top-down’ and ‘bottom-up’ approach based on empirical field campaigns, which addresses this issue. However, that is a work in progress at the time of writing this review.

In the absence of a habitat classification framework for New Zealand, we work our way through biogenic habitats based on their intuitively obvious visual identities, and associated habitat quality variations where quantified. We use the following pragmatic working definition of what a generic biogenic habitat is:

“Biogenic habitats encompass both a) those living species that form emergent three-dimensional structure, that separate areas in which it occurs from surrounding lower vertical dimension seafloor habitats and b) non-living structure generated by living organisms, such as infaunal tubes and burrows”

Obvious subsets of such habitats are biogenic “reefs”, which are visually imposing, and have been defined (Holt et al. 1998) by the Joint Nature Conservation Council (JNCC) of the United Kingdom as:

"Solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms."

The species creating these biogenic habitats are also found in other contexts; including as occasional individuals/colonies; and as a small component of diverse assemblages of habitat-forming species. The presence of individuals of a habitat-forming species does not automatically equate to the provision of important habitat. For example, the deep-water coral *Lophelia pertusa* is widely distributed in the northern hemisphere (Howell et al. 2011), and can occur as isolated colonies on boulders, cobbles, sand ripples, and on flat seabed where hard substrates for attachment are present (Wilson 1979, Mortensen & Buhl-Mortensen 2004a, b, Hovland 2005). However, its real conservation/habitat importance is associated with its ability to form large biogenic reefs. Howell et al. (2011) modelled the occurrence of *L. pertusa* on Haddon and George Blight banks (United Kingdom), and reported that while 7.17% of the total area was classified as high suitability for coral presence, only 0.56% of the area was classified as such for reef structures. That is, the dense biogenic *L. pertusa* reef distribution was a highly restricted subset of the wider distribution of *L. pertusa*, and simple presence/absence modelling of this species did not give an accurate representation of its potential areas of greatest importance as biogenic habitat. In the New Zealand context parallels occur for most other biogenic habitat species, such as other deep water coral species (e.g. Tracey et al. 2011), and horse mussels (*Atrina novaezelandiae*) which occur widely across estuarine and coastal environments down to about 120 m water depth, but which occur as dense beds only in sub-sets of this overall range.

1.4 Why does (biogenic) habitat matter to fisheries?

Traditionally the role of habitat has been largely ignored in fisheries management. However, in recent decades the impacts of fishing activities on seafloor habitats and associated assemblages (beyond just the targeted species) has become the focus of a great deal of research (e.g., Auster et al. 1996, Auster & Langton 1999, Kaiser 1998, Watling & Norse 1998, Hall 1999, Ball et al. 2000, Collie et al. 1997, Collie et al. 2000a, b, Kaiser & de Groot 2000). While impacts vary across different systems, assemblages, and fisheries types, the overall consensus is that impacts are generally significant in magnitude and extent, and are one of the greatest human impacts on both coastal and deep-water ecosystems (Thrush & Dayton 2002, Kaiser et al. 2006, Tillin et al. 2006). In this review we do not cover fishing impacts *per se*, but note that a number of international science reviews and meta-analyses exist as listed above. One of the key collective findings of such studies is that large, emergent three-dimensional organisms (biogenic habitat formers) are especially vulnerable to damage and loss from bottom trawling and dredging. The question now emerging is ‘so-what’?

The link between habitat presence, extent, and quality and the abundance and production of fisheries species, although intuitively obvious, is not yet a well-developed concept in the realm of fisheries research and management. Habitat considerations are not yet included in the stock assessment of major species, either in New Zealand or internationally (e.g., Armstrong & Falk-Petersen 2008). Incorporating habitat knowledge into population dynamics, especially at the scales at which fisheries management operates, remains a major challenge. This omission automatically gives such issues less weight, as stock assessments are the central tools in fisheries management (Armstrong & Falk-Petersen 2008). As noted by these authors (resource economists), a key task required for better incorporation of habitat values into management is to tie together the modelling of human behaviour from an economic perspective, with biological or ecological models, focussing on the interaction between habitat and fisheries. Such a focus allows the ‘use value’ from fisheries to be directly tied to the ecosystem goods and services that habitats may provide. This allows for any negative impacts of fishing on habitats, which flow on to negative impacts on fish stocks, to be quantitatively linked to the use value derived by fishers undertaking the fishery (known as a ‘negative externality’). This cascade

is shown in Figure 1 (adapted from figure 1 of Armstrong & Falk-Petersen 2008). Stock assessments are generally focussed on pure harvest effects on stocks (pathway 1). More recently, quantitative and qualitative damage assessments of gear impacts have received attention (pathway 2), but the consequent cascade effect of habitat loss onto stocks (pathway 7), and then into associated fisheries yields (pathway 6) have been largely neglected.

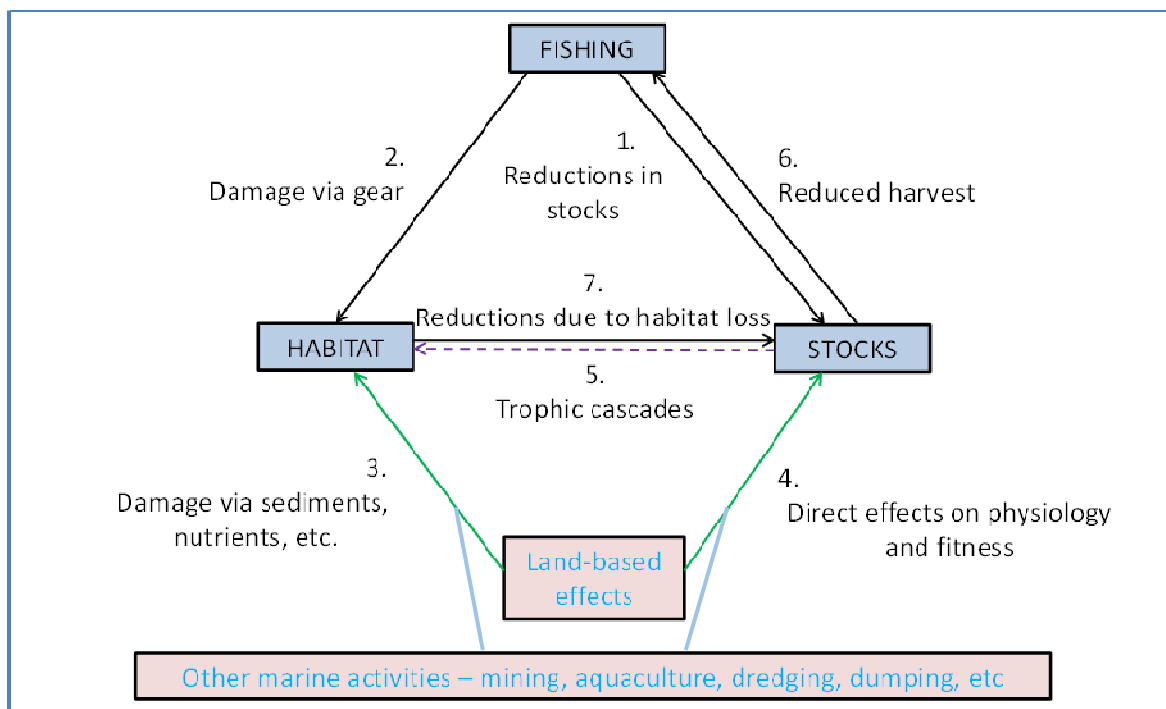


Figure 1: Inter-relationships between fishing, habitat, stocks, and land-based effects. Reductions in harvest (pathway 6) result from stock effects due to harvest (pathway 1) and habitat effects (pathway 2 and 7). Land-based impacts interact with this dynamic; including damage to habitats (pathway 3) and direct effects on harvested stocks (pathway 4). In some situations, fishing and land-based effects may interact directly, e.g. the re-suspension of fine land-derived sediments through disturbance of the seafloor by bulk fishing methods. Feed-back loops are also possible between stocks and habitat (pathway 5, the dotted line) through trophic cascades, such as seen in some situations between lobsters/large carnivorous reef fish, urchins, and kelp forests. (Source: adapted from Armstrong & Falk-Peterson 2008).

In Figure 1, we have also added another major and important stressor, land-based impacts, in particular increased sedimentation and nutrient (eutrophication) effects; as well as other marine industries. These can include both impacts on habitats (e.g., smothering, clogging of filter-feeding habitat formers, reductions in light penetration and competitive regimes for plants) (pathway 3), and direct impacts on the fisheries species themselves (e.g., reduction in physiological fitness, and impacts on foraging success (pathway 4) (see Morrison et al. 2009 for a New Zealand focussed review of these issues). While these land-based impacts do not have the same direct economic ‘negative externality’ back to the industries/activities creating them (e.g. farming, forestry, urbanisation), more broadly speaking the ‘agents’ (people) involved in those industries may still be impacted, if they value recreational fishing and marine recreation; and by a societal level loss of economic value from marine systems. Finally, in some situations there are also feedback loops from the reduction of some stocks (in abundance and size structure) into reductions in habitat type and associated productivity (pathway

5). A well-documented example in New Zealand are trophic cascades where high level predators such as snapper and rock lobsters are fished down to low levels on shallow rocky reef systems, removing their control of sea urchins by predation pressure, who then graze down kelp forests, converting them into ‘urchin barren’ habitats (Babcock et al. 1999), which have lower primary productivity (Salomon et al. 2008). However, it should be noted that such effects are context-dependent and not universal – see Shears et al. (2008a) for Hauraki Gulf examples.

1.5 Some definitions of habitat/area functions

To properly value the goods and services which habitats provide, it is necessary to adopt some formal definitions of what constitutes a given function. Generally we are interested in habitat functions that cumulatively drive population distributions and abundances: these have a clear spatial component (i.e., they are ‘place-based’). Examples include spawning aggregations (with associated migrations), settlement habitats (where the transition from larval pelagic to juvenile benthic phases occur), nursery habitats (which generally include settlement habitats), feeding grounds, ontogenetic ‘habitat chains’, and migration corridors. Biogenic habitats are often a sub-set of the overall habitats which may be involved in such functions, but may not necessarily be involved in any or all of them for a given population or species. As with habitat classifications, a clear definition (or definitions) is required to ensure that researchers, managers and others understand each other, and to avoid confusion and miscommunication caused by using multiple semantics for the same concepts and themes.

Spawning aggregations

Spawning activity may range from large spawning aggregations with associated spawning migrations, small localised groups of spawning fish, or single pairs of individuals. Species that predictably congregate in space and time can be extremely vulnerable to overexploitation (De Mitcheson et al. 2008). To date, spawning aggregations have received most attention in tropical reef fisheries (Domeier & Colin 1997, Sadovy & Domeier 2005, De Mitcheson et al. 2008).

A spawning aggregation is defined as “*a group of conspecific fish gathered for the purposes of spawning with fish densities or numbers significantly higher than those found in the area of aggregation during the non-reproductive periods*” (Domeier & Colin 1997). There are two types of spawning aggregations: resident (where fish travel short distances); and transient (where fish travel larger distances with aggregations lasting for a short portion of the year). Spawning aggregations often occur over specific topographical features and at specific times. These features and times may provide optimal gamete dispersal or larval retention near good settlement habitats, reduce egg predation, maximise larval food encounter rates, or synchronise reproduction efforts and maximise fertilisation rates. The same spawning aggregation sites can be repeatedly used year after year, with knowledge of these specific sites likely to be learnt from experienced individuals through the social transmission of knowledge (Warner 1988, 1990).

Settlement habitats

These are habitats where benthic associated fish and invertebrates with a pelagic larval phase make the transition from a pelagic to a demersal association. Kaufman et al. (1992) define this transitional phase as “*the period of time at the end of the larval phase when fish do not exhibit the colouration and behavioural characteristics of well-established juveniles*”. New Zealand fish examples include settling snapper and John dory which are very thin and transparent with long wispy fins, settling kawahai which are bright blue and silver with eight or nine dark bars on their back, and settling parore which are very dark coloured with a blue horizontal stripe along their sides; all of these species

subsequently change rapidly into the more familiar looking juveniles. McCormick & Makey (1997) divided this settlement phase into two parts for reef-associated fish: a period prior to settlement when late stage larvae explore the near-reef environment for suitable settlement sites; followed by a period after settlement as the metamorphosing fish changes to the juvenile form and behavioural patterns. Settlement habitats may be the same as nursery habitats, although many species may make rapid changes in their micro/macro habitat associations after settlement over time scales of several weeks (e.g., McCormick & Makey 1997).

Nursery habitats

The definition of what is a nursery habitat/area has received a lot of attention, following the recognition that the simple presence of juvenile fish does not automatically equate to a particular habitat or area providing an important nursery function. The conditions that need to be met in order for a habitat/area to be seen as providing a nursery function have been defined by Beck et al. (2001). Reviewing the literature, they concluded that ecological processes operating in nursery habitats, relative to those in other habitats, must support greater contributions to adult recruitment from a combination of the following four factors: (1) higher densities per unit area, (2) greater growth rates, (3) higher survival of juveniles, and (4) movement of juveniles to adult habitats. They argued that to fit to the ‘nursery-hypothesis’, species must have at least some spatial disjunction between juvenile and adult habitats, to be considered to have ‘nursery habitats’, and that in most species, movement to non-juvenile habitats was associated with reproduction. They also noted that many other life history strategies existed – and that the nursery hypothesis did not imply that, for example, seagrass meadows did not have important effects on species which spent their entire lives there (i.e., had no juvenile and adult phase spatial segregation).

A range of conditions and tests required to be met for a habitat to be considered a nursery habitat (NH) were listed by Beck et al. (2001). Even very spatially discrete habitats could qualify as important nursery habitats – as long as they produced relatively more adult recruits per unit of area than other juvenile habitats used by a species (Figure 2). Conversely, some habitats might contribute individuals to adult populations, but make a less than average contribution relative to other habitats – these would not qualify as nurseries using Beck et al.’s definition. Measuring the movement of individuals from juvenile to adult habitats was considered an essential component of nursery habitat quantification, with the best integrated measure of a given habitat’s contribution being the total biomass (i.e. production) of individuals recruiting to adult populations from that habitat. Although a habitat might support high densities of juveniles, if those individuals did not reach adult populations (e.g. the habitat was acting as a ‘sink’), then that habitat was not functioning as a productive habitat. Examples of processes which might bring about such a result included high larval settlement into sites where growth was poor, or where movement to adult habitats was risky or difficult (e.g. there were no adult habitats nearby, or there was particularly intense predation, Lipcius et al. 1997, McBride & Able 1998).

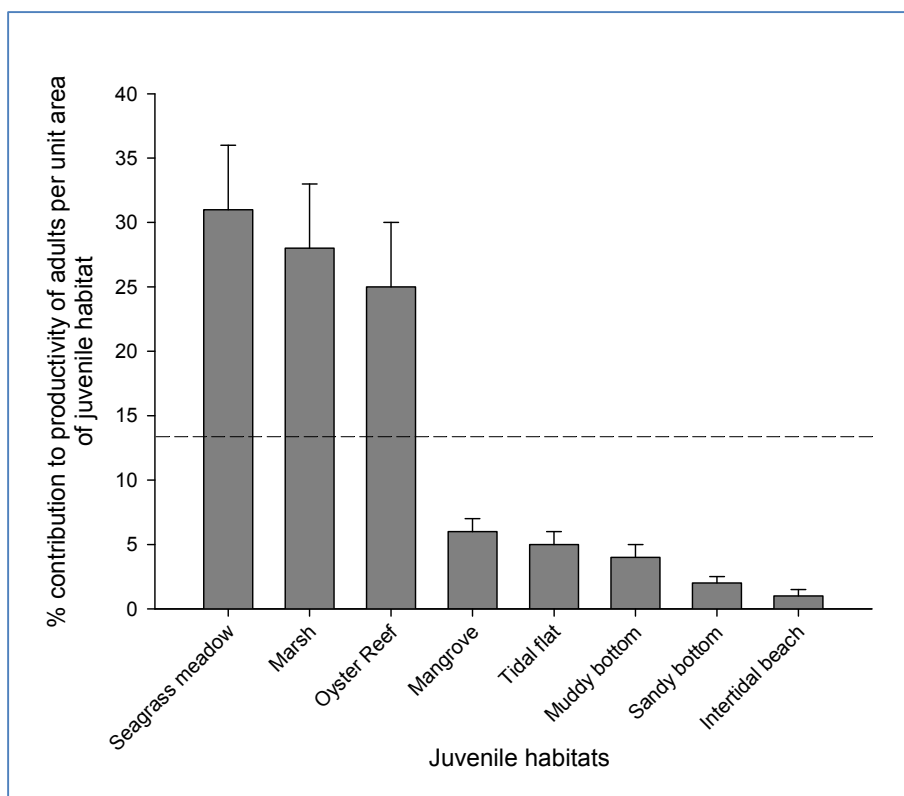


Figure 2: A hypothetical comparison of the nursery value of several different habitats. The dashed line represents the average percentage productivity of adults per unit area from all the juvenile habitats. In this example, seagrass meadows, marshes, and oyster reefs are nursery habitats (Source: figure 4 of Beck et al. 2001).

The importance of taking variation in habitat values into account, within a given habitat, and in realising that not all occurrences of a given habitat should be considered equal were also stressed by Beck et al. (2001). Examples included geographic variations in the importance of widely distributed habitats (for a New Zealand example, see the section on seagrass), in habitat quality (e.g. seagrass blade density), in larval supply and settlement, and in the local landscape configuration in which habitats were embedded (Table 1). As an example, they noted that conservation and management agencies now commonly consider all seagrass and wetlands as nurseries, and that while these broad declarations were useful for generating public interest, they hindered the actual work that needed to be accomplished by these groups because the statement lacked focus. By gaining a clearer understanding of what makes some sites more important than others as nurseries, more efficient use of limited money, time and effort could be achieved by targeting the most critical elements of the system. Beck et al. (2001) concluded that while in theory the level of evidence required for showing a habitat to be a nursery was very high and very difficult to achieve, the definition could be seen as providing a view of what a definitive test would encompass, “so that researchers could arrive at the best approximation of it”. Examples of themes researchers might best focus on included: factors of density, growth, survival, and moment in putative nursery habitats; the quantification of multiple habitats for a given species; and a better quantification of the movements of individuals between juvenile and adult habitats. They also commented that correlative and case study analyses could also yield many useful insights – such as correlations between loss of inshore habitat and decreases in offshore fisheries production (e.g., Butler & Jernakoff 1999).

Table 1: Factors that create site-specific variation in nursery value (Source: table 1 of Beck et al. 2001).

Biotic	Abiotic	Landscape
Larval supply	Water depth	Spatial pattern (e.g. size, shape, fragmentation, connectivity)
Structural complexity	Physico-chemical (dissolved O ₂ , salinity)	Relative location (e.g. relative to larval supply, other juvenile habitats, adult habitats)
Predation	Disturbance regime	
Competition	Tidal regime	
Food availability		

The nursery concept was further developed by Dahlgren et al. (2006) to allow for situations where average densities per unit of habitat might be relatively low, but where the overall extent of those habitats was such that they still provided a significant proportion of recruits to the adult population. Such habitats would not be identified as nursery habitats (NH) under the definitions of Beck et al. (2001). Dahlgren et al. proposed the term Effective Juvenile Habitat (EJH) to describe

“habitat for a particular species that contributes a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles, regardless of area coverage”.

While similar to the definition used by Beck et al. (2001), the key difference was that for EJH,

“the contribution of individuals from juvenile habitats to the adult population is based on comparisons of the overall contribution that the habitat makes, rather than the per-unit-area comparisons required for nursery habitats”.

The EJH definition does not require an estimate of the areal extent of each contributing habitat. However, the evaluation of the importance of juvenile habitats using the two classification schemes can result in considerable differences.

Dahlgren et al. (2006) argued that, given the use of natural or artificial markers, which are unique to different juvenile habitats and are preserved as animals move to adult habitats, researchers could estimate where animals were derived from, and in what proportions, providing a direct estimate of EJH. This served the purpose of broadly identifying important habitat types, and was particularly useful in focussing marine resource management, (e.g., around habitat protection, and protection of juveniles from threats such as capture as by-catch, or water quality issues), at broader spatial scales. Conversely, the NH approach, which required the mapping/areal estimation of all contributing habitats, was most suited to identifying specific high quality habitats for conservation, restoration, and management – specifically in the prioritisation required for spatially explicit management (e.g., Marine Protected Areas, MPAs, or restoration), where resources were limited. However, the need for mapping made the NH approach more intensive and expensive than the EJH approach. Which to use was context dependent, relative to the management questions being addressed, and the associated level of resourcing available.

Neither the NH or EFH concepts have (to date) been applied to New Zealand fish and invertebrates and associated fisheries, with the exception of mangrove habitats and small fish (see Mangroves), and of snapper along the west coast of the North Island (SNA 8), focussing on the nursery role of the estuaries that occur along that coast (see Seagrass).

Ontogenetic habitat chains/shifts, and the potential for habitat ‘bottle-necks’

This mechanism is widespread in fish and invertebrates, and occurs where an organism shifts with size/age between different habitats, often as a trade-off between feeding opportunities and the risk of

predation. The classic paper on this phenomenon is that of Werner & Hall (1988) who showed that blue-gill sunfish (*Lepomis macrochirus*) in lakes made several shifts between the pelagic and littoral zones during its life history, and that the density of a predator, largemouth bass (*Micropterus salmonoides*), affected at what size these shifts occurred. All species which use NH or EFH habitats by definition are making ontogenetic habitat shifts; with the potential for habitat bottlenecks to occur where the habitat available is insufficient to support the numbers of animals passing along the habitat chain (e.g. Parrish & Polovina 1994).

Feeding grounds

This is a term that refers to habitats or areas where fish preferentially occur in greater numbers to feed. No formal definition could be found in the science literature, although the term is widely used.

Migration/movement corridors

Movement in organisms is diverse, and can be categorised in many ways (see Dingle & Drake 2007 for a good overview). Here we refer specifically to annual migrations, using the definitions “*Migrations are round trips synchronized with the annual cycle; seasonal migrations are particular stages of these annual journeys.*” (Dingle & Drake 2007). Such migrations may proceed along movement corridors, which we define as the areas through which fish or other organisms move during their migrations. In some cases these corridors may be very broad, in others they may be relatively narrow, with fisheries species sometimes being targeted as they travel along these corridors, e.g. blue moki spawning migrations along the lower east North Island coast (Francis 1981; fisher observations in Langley & Walker (2004), such situations are often referred to as ‘spawning runs’).

1.6 The issue of sliding environmental base-lines

Today's conditions may be far removed from what original ecosystems were like; both in terms of the spatial extent and configuration of habitats, and of the associated plant and animal populations they supported (e.g., Dayton et al. 1998, Jackson 2001, Jackson et al. 2001). Past human impacts have been profound, but have often gone unnoticed, as each succeeding human generation has a different view of what ‘natural’ is, based on their own observations. This results in diminishing expectations of what is ‘natural’ in the oceans, i.e., sliding environmental baselines (Dayton et al. 1998). For instance, Airoldi & Beck (2007) found that coastal biogenic marine habitats of Europe, including wetlands, seagrass meadows, shellfish beds and biogenic reefs, had been virtually eliminated over the last several hundred years, with less than 15% of the European coastline considered to remain in ‘good’ condition. They also noted that historical loss estimates were conservative: “*even worse is the fact that these losses are only measured against recent distributions with little recognition of the compounding impact of centuries and millennia of habitat loss*”. Similarly, Lotze et al. (2006) assessed impacts in North America and European systems, and found human impacts to have depleted more than 90% of formerly important species, destroyed 65% of seagrass and wetland habitat, degraded water quality, and accelerated species invasions. They concluded that “*the structure and functioning of estuarine and coastal habitats has been fundamentally changed by the loss of large predators and herbivores, spawning and nursery habitat, and filtering capacity that sustains water quality*”. They offered some hope for restoration, noting that as overexploitation and habitat destruction were responsible for most historical changes, their reduction should be a major management priority; and that despite some extinctions, most species and functional groups still persisted, albeit in greatly reduced numbers, and so recovery potential remained. Where human efforts focussed on protection and restoration, recovery had occurred, although usually with significant time lags (see also Lotze et al. 2011).

New Zealand has not escaped such impacts, despite its short history of human settlement. Morrison et al. (2009) concluded that the impacts of past human land use were likely to have been high on coastal systems and species, especially through sedimentation. Parsons et al. (2009) found evidence of large reductions in the abundance and size of snapper from estuarine and very near-shore habitats where once they were commonly caught, and the probable loss of some behavioural groups. Taylor et al. (2011) used long-term diver recollections of the Poor Knights Islands Marine Reserve to show large and steady long term declines in abundances of black corals, tube sponges, packhorse lobster, and large predatory fishes. Shears (2010) highlighted changes on Meola Reef, Waitemata Harbour (Figure 3). Given the existence of sliding baselines, marine resource management including fisheries should be viewed not only in the context of managing what currently exists (at an arbitrary point in time), but also in the context of what was historically present, and what the system might look like in the future, given pragmatic and realistic mitigation and/or restoration research and management strategies.



Figure 3: Example of a sliding baseline. Western side of Meola Reef, from left: 1920s with tubeworm or gastropod mounds and rock with little sediment and no Pacific oysters (Oliver 1923); 1982 with Pacific oysters and little sediment (Dromgoole & Foster 1983); 2010 with Pacific oysters and large patches of consolidated sediment. Mangroves can also be seen to appear in the background (Source: figure 16 of Shears 2010).

NEW ZEALAND'S BIOGENIC HABITATS

Keeping the above definitions and discussions in mind, we now discuss a range of biogenic habitats, broadly grouped by type and at what depths they occur in New Zealand's marine environment. Generally we focus on specific habitat types which can be visually identified, presenting information on:

- the known extent and status of the habitat in New Zealand (with overseas examples as necessary);
- its values and functions, in particular around what fisheries (and/or other) species may be associated with the habitat; and associated international literature, where little is known in the New Zealand context;
- possible and known threats and stressors;
- information gaps, and recommendations for research to address those gaps;
- recommended measures for possible management.

Imagery is included where possible to give the reader a greater appreciation of how the habitat and associated organisms physically appear. Figure 4 shows the location of the various places mentioned through the report.

We note that to our knowledge there are no New Zealand fisheries species which are truly obligate to any specific habitats for their survival (though they may be obligate on a habitat group); rather species are facultative in their habitat use, and many may use a range of habitats for the same function. For example, juvenile snapper (under 10 cm) have been recorded across a relatively wide range of shallow estuarine and coastal biogenic habitats. However, within this wider range of habitat use, there are probably strong and consistent differences in juvenile density, and combined with the different extent of habitats, some habitats are collectively probably of much greater importance than others.

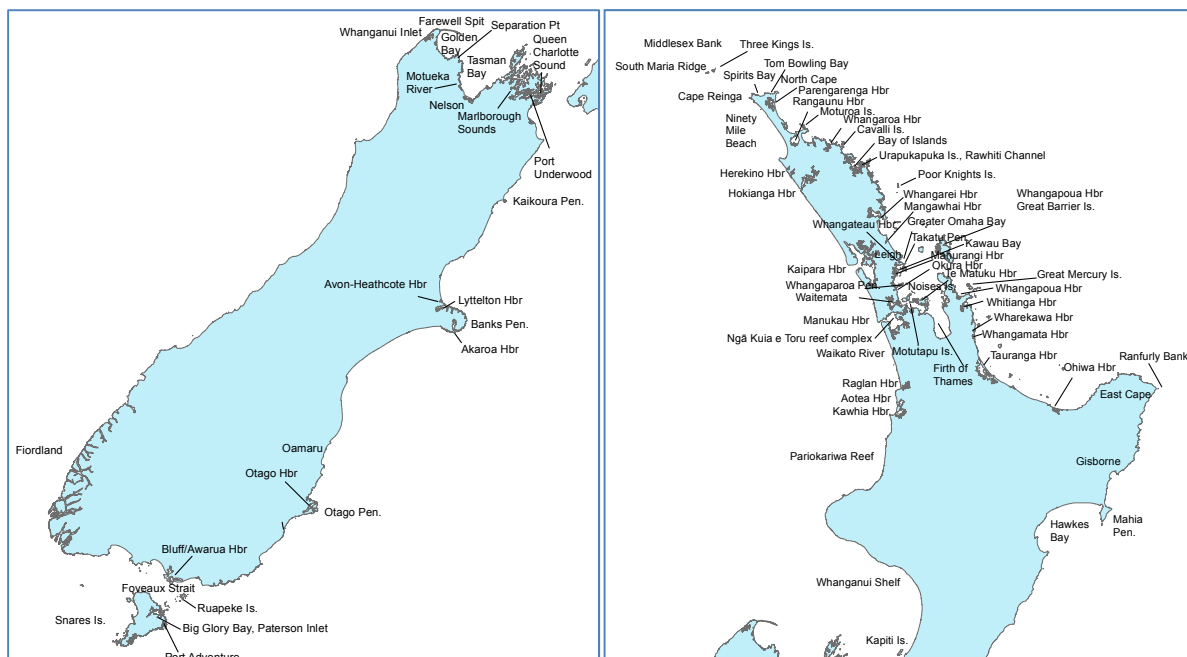


Figure 4: Locations of place names mentioned in the text, for the South and North islands respectively.

THE COASTAL ZONE

3.1 Salt Marsh

Location

Salt marsh in New Zealand occurs at the heads of estuaries, above the seagrass and mangrove zones (where present) (Morrisey et al. 2010). Salt marsh is often dominated by sea rush (*Juncus kraussii*) and jointed rush (oioi) (*Apodasmia similis*), which can form dense thickets up to 1.5 m high. Along the banks of tidal streams, the marsh ribbonwood shrub (makamaka) (*Plagianthus divaricatus*) is often present.

Two species of cord-grass, *Spartina alterniflora* (Figure 5) and *S. anglica* were introduced to New Zealand in the 1950s (along with a third species *S. townsendii* in 1913), to promote reclamation of

intertidal flats, reduce shoreline erosion, and provide for stock grazing. These have formed extensive thickets in some estuaries in the past, although they are now subject to rigorous control programmes as an unwanted species, and are much reduced in extent (Swales et al. 2004a. b).



Figure 5: Example of the introduced saltmarsh species *Spartina alterniflora* in New Zealand. Photograph taken 12th February 2011, Te Kapa Inlet, Mahurangi Harbour, Auckland. (Source: Richard Taylor, Leigh Marine Laboratory, University of Auckland).

Value and function

There are no studies that we are aware of which have directly quantified what fish species may utilise salt-marsh habitats in New Zealand. These habitats are only accessible by fish during the top of high tides, especially spring tides, and are probably of little direct value to most fish species in New Zealand (but see *Galaxias maculatus* below). In New Zealand native salt marshes (mainly rushes), fish usage is probably constrained to short periods of foraging during spring tides when they are accessible. These are probably semi-pelagic species, such as grey (*Mugil cephalus*) and yellow-eyed (*Aldrichetta forsteri*) mullets, smelt (*Retropina retropina*), and the common galaxiid *Galaxias maculatus* (inanga). *G. maculatus* (Figure 6) is the only galaxiid species which spawns in estuarine systems (C. Baker, NIWA, pers. comm.), and as with other galaxiids, it deposits its eggs among riparian vegetation and other substrates supra-tidally (at extreme upper tidal elevation, e.g. Figure 6) (McDowall & Charteris 2006). Hickford et al. (2010) sampled a number of sites around Banks Peninsula, and recorded *M. maculatus* eggs on eight plant species which prefer damp conditions – however most of those plants were not salt marsh ‘species’. There was a strong positive correlation between the density of riparian vegetation, and initial egg densities from spawning. They also found higher egg survival in riparian vegetation with dense stems and a thick aerial root-mat (*J. egdariae*, *S. phoenix*, and *H. lanatus*) which provided a cooler and more humid micro-environment, as well as probably protecting the eggs from lethal ultra-violet light (Hickford et al. 2010). These findings demonstrate the importance of biogenic habitat (supra-littoral vegetation), including aspects of habitat quality (expressed here as stem density, and aerial root thickness), to the population dynamics of *G. maculatus* (by providing optimal spawning substrates), and ultimately to fishery productivity (catch of juveniles returning from the sea as part of their catadromous life history).



Figure 6: An adult common galaxid, *Galaxias maculatus*. (Source: Cindy Baker, NIWA Hamilton); “estuarine spawning sites of *Galaxias maculatus* (arrows indicate spawning vegetation)”. (Source: figure 3 of McDowall & Charteris 2006).

The introduced cord-grass species have been reclassified as pest species due to their ability to rapidly expand across intertidal estuarine flats (following a long lag period of gradual or no expansion), with associated environmental impacts, and are being actively eradicated (Swales et al. 2004a, b). Their associated fish fauna is unknown, but is probably similar to that of mangroves (see mangroves section) given their intertidal presence in upper estuarine areas. In continental systems such as North America, these salt-marsh species form part of very extensive wetland systems, which are heavily utilised by fish, and provide important juvenile fish nursery functions. Examples include significantly enhanced growth of juvenile pinfish (*Lagodon rhomboides*, a small sparid growing to 40 cm) in association with intertidal *Spartina alterniflora* marshes, relative to bare unvegetated flats (Irlandi & Crawford 1997); and of juvenile red drum (*Sciaenops ocellatus*, which grows to 1.5 m in length) in Galveston Bay, Texas: as well as much higher red drum densities along the salt-march habitat edge, relative to unvegetated habitats (Stunz 1999). As a EFH example (Dalhgren et al. 2006), Stunz (1999) concluded that the large areal marsh extent in the Galveston Bay complex cumulatively provided the most important nursery habitat for red drum, even though on a per unit basis juvenile red drum densities in salt-marsh were relatively low relative to seagrass habitat (which was very rare in Galveston Bay) (Stunz et al. 2002).

It is unknown, but unlikely, that New Zealand fisheries species are utilising introduced cord-grass habitats in any significant way, with the ongoing pest control of cord-grass further limiting this possibility.

Past and current status and threats

As salt marsh occupies flat fertile areas which are easily reclaimed for productive agricultural land use, including farming and urban settlements, salt marsh has greatly declined in spatial extent since Europeans arrived in New Zealand. For example, in Whangarei Harbour (Northland), saltmarsh extent declined from 5.56 to 4.05 km² between 1942 and 1966, and further reduced to 1.89 km² extent by 1985, representing an overall decline of 66% (Parrish 1985, Cromarty & Scott 1995). This does not include likely high losses prior to 1942. Similarly, in Whangaroa Harbour (Northland), its extent declined from 2.4 to 0.45 km² between 1909 and 1981, a decline of 78% (Whangaroa Harbour Study 1985). *G. maculatus* juveniles contribute 90% of the New Zealand whitebait catch (four other species contributing the other 10%) (McDowall 1965), and there is a general consensus that catches have declined since the late 1950s, although little direct statistical evidence is available to attribute this to overfishing (Hickford et al. 2010). The destruction of spawning and rearing habitat is seen as a contributing factor (Taylor 1996). A significant negative relationship between the occurrence and abundance of adult *G. maculate*, and increasing catchment development, has been reported from a national wide estuarine fish survey (69 estuaries, Francis et al. 2011).

Information gaps

While no information is available on fish usage of salt marsh in New Zealand, it is like to be modest. Sampling of salt marsh in South Australia caught only one fish in pop-nets (Bloomfield & Gillanders 2005), while a study in New South Wales sampled 16 fish species, dominated by two goby species, and glassfish (*Ambassis jackoniensis*, also known as Port Jackson perchlet) (Mazumder et al. 2005). These are not commercial fisheries species, and do not occur in New Zealand. In a second New South Wales study, a number of small non-commercial fish species were found to access salt-marsh during spring tides to exploit high abundances of zooplankton, and retreat to seagrass habitats as a refuge during low tides (Saintilan et al. 2007). Similar dynamics may exist in New Zealand, but are unlike to include fisheries species.

No suggestions are made for new research.

Recommended measures

None.

3.2 Mangroves (*Avicennia marina australasica*)

Location

New Zealand has only one species of mangrove, *Avicennia marina australasica* (Figure 7a) which is present in all estuaries on the west coast of the North Island (except the Waikato River mouth) from Kawhia to Herekino, and on the east coast of the North Island from Parengarenga to west of Ohiwa Harbour. *A. marina australasica* is a native species, but also occurs in temperate Australia. Taxonomically, it is viewed as a sub-species with *Avicennia marina* (grey mangrove), which occurs in both the southern and northern hemispheres (Morrisey et al. 2007, 2010). There is no historic national

scale inventory of what New Zealand once possessed in terms of mangrove spatial distribution and extent prior to human activities. Aerial photography, the key method for assessing mangrove cover, only became available from the 1940s, and is patchy in coverage, as historical photographs did not specifically target marine habitats such as mangrove forests.

Value and function

There are no invertebrate fisheries species which use mangroves in New Zealand, in contrast with tropical regions, where prawn fisheries are often heavily reliant on mangroves as nursery grounds (e.g., Manson et al. 2005, Nagelkerken et al. 2008). Of note however, the invasive greasy-back prawn *Metapenaeus bennettiae* appears to be established and expanding in range and abundance in the Hauraki Gulf (individuals caught in Mahurangi, Okura, and Te Makatu estuaries in 2010, M.M, pers. obs.). Until relatively recently, most research examining fish in mangroves has been in tropical systems, with only one temperate system paper as of 2000. Since 2000, a further 10 studies have been published on temperate systems (nine in temperate Australia, one in New Zealand).

In the New Zealand study, fine mesh fyke nets (Figure 7a, 8a) were used to quantify small fish assemblages leaving mangrove forests with the falling tide (Morrisey et al. 2007, 2010). Eight estuaries were sampled in northern New Zealand, encompassing a (putative) environmental gradient from relatively pristine to heavily modified by human activity, across the east and west coasts.

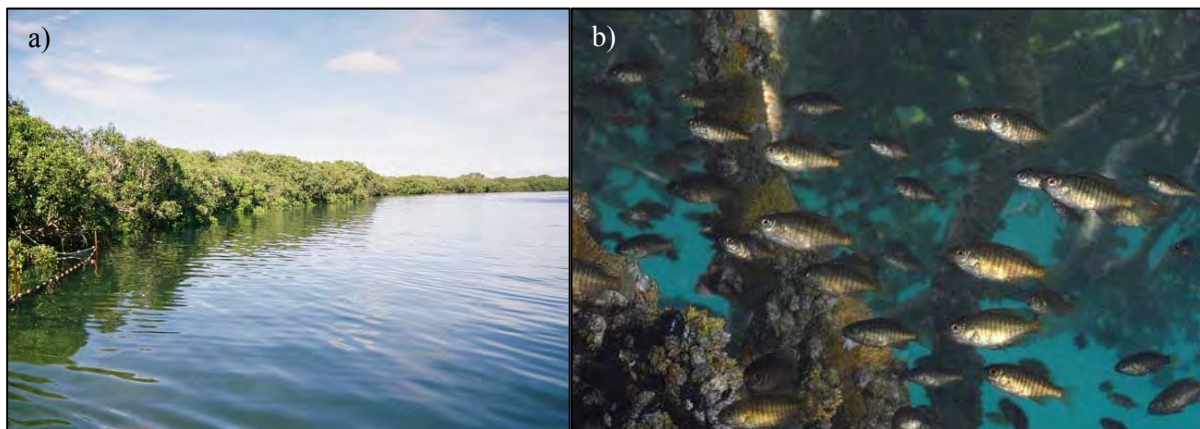


Figure 7: a) Rangaunu Harbour mangrove forest edge being sampled by fyke net, b) recently settled parore (20–25 mm) sheltering under a mangrove tree at high tide, Whangateau Harbour. (Source: M. Lowe, NIWA, and R. Grace, independent researcher).

West coast sites were generally characterised by larger, more complex trees (Figure 8b), set in an environment of high suspended sediment loads, low water clarities, higher organic carbon levels, and finer sediment grain sizes. On the east coast, some sites also displayed these characteristics, but most sites had smaller, less complex trees (Figure 8a), higher water clarities and larger mean sediment grain sizes. Nineteen fish species were sampled (17 000 individuals in total), with 88 per cent of all individuals being small semi-pelagic schooling species (mullet, pilchards, and smelt), while 98% of all individuals were juvenile life history stages. Four species dominated the catch (92%): yellow-eyed mullet (*A. forsteri*), grey mullet (*M. cephalus*), estuarine triplefin (*Grahamina nigripenne*) and the pilchard (*Sardinops neopilchardus*). Most of the remaining species were demersal fish, including short-finned eels (*Anguilla australis*), parore (*Girella triscuspidata*) (Figure 7b), sand flounder (*Rhombosolea plebia*) and yellow-belly flounder (*Rhombosolea leporina*). Only occasional

individuals of the remaining nine species were caught, including two commercial species (snapper, *Pagrus auratus*, and kahawai, *Arripis trutta*). Fish assemblage differences between coasts and among estuaries were driven more by large variations in the relative abundance of a few species, than differences in the species pool present. However, virtually all grey mullet were sampled from the west coast, and parore from the east coast, while short-finned eels were found across both coasts. There was no evidence of more (putatively) pristine estuaries having markedly different fish assemblages. Aside from grey mullet and short-finned eels (and parore as a low value species), no commercial species were common.

Individual species varied in their response to forest and physical environmental variables. Grey mullet and yellow belly flounder were positively associated with higher total suspended sediment loads, while yellow-eyed mullet were positively associated with increasing distance from the sea. Short finned eels were positively associated with increasing mangrove habitat complexity (seedlings, saplings and number of trees), while parore were associated with higher water clarities and intermediate sediment grain sizes. Collectively, these results demonstrate that the habitat quality and geographical setting of mangrove forests influence the fish assemblages that they support, and it is not just the presence of mangroves *per se* that needs to be taken into account when assessing habitat functions and values.



Figure 8: Examples of: a) short (c. 1.4 m) and dense mangrove trees towards their southern limit, Tauranga Harbour, East Coast; b) tall (c. 6–8 m) and large mangrove trees, Kaipara Harbour, West Coast, (Source: Meredith Lowe, NIWA, and Kerry Webster, NRC).

Using the nursery habitat definitions of Beck et al. (2001) and Dahlgren et al. (2006), the relative value of mangroves to fish in the context of estuaries can be assessed (albeit not to the idealised standards given by the above authors). Only short-finned eels, parore and grey mullet occurred in sufficiently high and/or widespread abundance to distinguish mangroves from other estuarine habitats (see for comparison Morrison et al. 2002, Francis et al. 2005, Morrison & Carbines 2006, Schwarz et al. 2006, Francis et al. 2011, Morrison & Francis unpubl. data, Morrison & Lowe unpubl. data). Based on the consistent and widespread numbers of short-finned eels and parore in mangroves, and low abundance in alternative estuarine habitats (but see seagrass and brown algae re parore), mangroves can probably be viewed as effective juvenile habitat (EJH) (both coasts for short-finned eels, east coast for parore). In contrast, grey mullet occurred at much higher densities/catch rates than parore and short-finned eels, and are relatively rare in other estuarine habitats at the sizes sampled (20–50

mm). Most juveniles sampled outside mangroves are larger, older juveniles (50–150 mm), which suggests a probable ontogenetic habitat shift from higher to lower complexity estuarine habitats. This suggests that mangroves on the west coast can be probably be classified as both nursery habitats (NH) and EJH for this species.

However, more recent extensive targeted field collections of juvenile grey mullet (MFish project GMU2000901 and the MBIE CCM programme) has identified a number of additional grey mullet nursery areas, some of which are not associated with mangroves (e.g. Kawhia Harbour). These surveys have used targeting methods which have a much higher probability of detecting juvenile grey mullet than randomly set mangrove fyke nets. It is now unclear whether juvenile grey mullet have a facultative relationship with mangroves, or simply co-occur with mangroves in upper estuarine muddy environments in northern New Zealand. Juvenile grey mullet do enter mangrove forests, as all of the fish sampled by fyke nets have been leaving mangrove forests as the tide recedes; and tidal migrations of juvenile mullet up into mangrove areas have been observed in some estuaries (M.M., pers. obs.). However, gut content analysis of fyke net caught fish, and of the mangrove benthos, suggests that juvenile grey mullet are largely feeding on zooplankton swept into the mangrove forests, as well as some detrital material (Morrisey et al. 2007, Lowe 2013), and receive little direct food value directly from *in situ* mangrove habitat. Juvenile grey mullet daily growth rates, as estimated across 14 estuaries, also decline significantly as the proportion of the intertidal flats occupied by mangroves increases (mangrove cover 0 to 50%, growth rate declines by a third, $R^2 = 0.50$, $P = 0.01$), although other factors are also significantly correlated with this growth rate decline (sediment, nitrogen and phosphorus inputs) (Mohd Zain 2013). It may be that a trade-off between shelter from predators (e.g. mangrove forests) and food supply (non-mangrove habitats) is operating; experimental work is now needed to assess the explicit (if any) functional relationships between grey mullet and mangroves.

New Zealand fish usage of mangroves agrees with ten studies completed in temperate Australia (Bell et al. 1984, Clynick & Chapman 2002, Hindell & Jenkins 2004, 2005, Smith & Hindell 2005, Bloomfield & Gillanders 2005, Mazumber et al. 2005, 2006, Saintilan et al. 2007, Payne & Gillanders 2009 – see Morrisey et al. (2010) for a detailed findings summary and synthesis of these studies). Collectively, these studies showed that while fish numbers can be high in mangrove forests, overall species diversity is relatively modest relative to other habitats, and that a few key species dominate numerically. These are mainly species from the families Gobiidae (gobies), Atherinidae (a group not found in New Zealand), and Mullidae (especially the yellow-eyed mullet *Aldrichetta forsteri*). While some fisheries species are found in mangroves, they are usually present in low numbers only, and the overall direct habitat value of temperate mangroves to fisheries appears to be modest.

Past and current status and threats

In strong contrast to most other countries, New Zealand's mangrove forests are expanding at a significant rate, replacing other habitats such as open sand and mud flats, causing strong and often acrimonious societal debate as to their value and what management actions are appropriate. There is strong anecdotal evidence that significant mangrove loss has occurred historically at some locations, largely to create farmland, but true losses are unknown (Morrisey et al. 2010). Documented examples include the Hokianga Harbour, where mangrove extent reduced from 6.3 to 2.7 km² (57% decline) (Shaw et al. 1990); and in the Manukau Harbour, where mangrove extent reduced from about 5.8 to 4.5 km², between 1955–60 and 1981 (22% decline) (Crisp et al. 1990). From 1977, mangroves were fully nationally protected from infilling (e.g., to create farmland), and since that time clearance of mangroves has been a controlled activity (i.e., consents are required).

The Nature Conservation Council (1984) produced a mangrove distribution inventory in 1983, using aerial photography from 1970 to 1983, with an estimated total mangrove extent of 193.43 km². Compared to the current Land Cover Database (LCDB) estimate, there is a 32 km² positive discrepancy, which may represent a net increase over the last 20 years (to 2003, Morrisey et al. 2007). However, the LCDB is known to contain errors, as well-established mangroves have been observed in areas where they are absent in the LCDB (e.g., M.M, pers. obs.). In recent decades mangroves have greatly expanded in spatial extent in many estuaries, e.g., a 117% increase in Tauranga Harbour over the last 50 years (see Morrisey et al. 2010); and the development of a large forest in the upper Firth of Thames, changing from a wide mangrove-free shelly beach in the 1950s, to a mangrove forest more than a kilometre wide, which is still expanding seawards (Swales et al. 2007). Even estuaries considered to be in good ecological condition have been affected, with Rangaunu Harbour mangroves expanding by 33% between 1944 and 1981 (Shaw et al. 1990). This forest is considered to be the largest in New Zealand at 31 km², and covers 30% of the harbour's intertidal area (May 1999). In combination with the harbour's extensive seagrass meadows, it generates more than 21 000 t yr⁻¹ of detritus dry weight (May 1999). Whether this production finds its way into trophic food webs that include fisheries is not known.

There is still debate on what is driving mangrove expansions, and why, if it is primarily sedimentation driven, there was such a time lag in response to the widespread historical clearance of land catchments. A detailed discussion of the dynamics of mangrove expansion and drivers in New Zealand, as well as known mapped changes, is given in Morrisey et al. (2007) (see table 4 for areal estimates). Overall, mangroves can be viewed as one of the very few (if not the only) marine biogenic habitats that is expanding in spatial extent in New Zealand. Given that New Zealand mangroves are at the southern-most extent of their range world-wide and that this is thought to be at least partially controlled by climate, on-going global warming also offers the possibility for them to extend their range southwards (Morrisey et al. 2010)

Information gaps

As with most biogenic habitats, we still do not know the relative contribution that mangrove forests make to fisheries productivity for the species which may utilise this habitat during some stage of their life history (e.g. grey mullet, short-finned eels, and parore). Nor do we know what happens as habitat extent and quality changes through time, e.g., mangrove extent increases at the 'expense' of other habitats. In an Australian study, an assessment of commercial fish catches against different estuary types and the habitat extents within them, found that in larger estuaries an increased proportion of mangrove extent was positively associated with commercial catches of long-fin river eels (*Anguilla reinhartii*) and sand mullet (*Myxus elongates*) (Saintilan 2004). However, overall it was suggested that the role of mangroves in supporting commercial fisheries was modest in this temperate region.

Suggestions for new research include:

- Experimental work to assess if juvenile grey mullet have a positive facultative relationship with mangrove forests: or alternatively whether increases in intertidal flats mangrove coverage (and/or associated environmental changes) may be adversely affecting the productivity and health of juvenile grey mullet nurseries.
- Combined empirical and modelling approaches to assess whether changing mangrove extents provide a net benefit or loss to juvenile fish production, as the habitat landscape shifts within estuaries (mangroves increase, others habitats shrink). This is not a mangrove specific

suggestion, as a range of other habitats would also be included (e.g. seagrass meadows); the question involves all estuarine habitats, and how they operate as a habitat landscape.

- Assessment of whether the provision of mangrove habitat to short-finned eels is significant in the context of the wider freshwater dominated population habitat dynamics of this species

Recommended measures

As part of the wider ongoing societal debate on and management of mangroves, fisheries researchers and managers can provide input on the relative value of mangroves to fisheries, and what mangrove control might mean in this context. As mangroves are on the increase, arguably this biogenic species is not of concern in terms of habitat loss: conversely, other habitat extents are being reduced. Associated environmental changes are also important e.g. habitat quality degradation through sedimentation, increasing turbidity; and potential adverse affects on some fisheries species such as flounders (loss of foraging areas) and perhaps even grey mullet; although short-finned eels may benefit.

3.3 Seagrass (*Zostera capricorni*)

Location

Seagrasses are true flowering plants (Angiospermae), with stems, leaves, and roots which have become specialised to grow rooted and submersed in estuarine and shallow coastal environments (Turner & Schwarz 2006). *Z. capricorni* occurs around the North, South, Stewart, and Chatham Islands (as well as in Australia), and is largely an inter-tidal species, but where water conditions permit, can grow sub-tidally, down to a known New Zealand maximum water depth of about 7 m (e.g. Ruapuke Island, Foveaux Strait). It is predominantly found on soft sediments, and can form extensive beds, or mosaics of discrete patches, on estuarine tidal-flats at mid to low levels (e.g. Figure 9a). It also occurs as patches on open coast intertidal rock platforms, including the lower East Coast North Island, and Kaikoura Peninsula (e.g., Woods & Schiel 1997; Ramage & Schiel 1998, 1999, Morrison et al., in review).

Value and Function

There are approximately 60–70 species of seagrass world-wide, which collectively are considered to be one of the most valuable of all habitats in the estuarine/coastal zone (Costanza et al. 1997), providing a wide range of goods and services: including primary production to detrital and grazing food-webs, altering water flow, nutrient recycling, increasing biodiversity, and the creation of critical habitats for many species, including the juveniles of many recreational and commercial fisheries species. The increased faunal densities within seagrass habitats are possibly largely driven by protection from predation (Horinouchi 2007), though other factors such as foraging opportunities may also play a role. In some regions of the world, they are also important as food sources for marine mega-herbivores, such as green sea turtles, dugongs, and manatees (Orth et al. 2006).

In northern New Zealand seagrass meadows, sub-tidal seagrass components consistently support different fish species assemblages relative to surrounding less structured habitats (i.e., sand and mud-flats) including the juveniles of some fisheries species such as snapper, trevally, and parore (Schwarz et al. 2006, Francis et al. 2005, 2011, Morrison et al., in review a). In the case of the Kaipara Harbour (Figure 9b), otolith chemistry work has shown that this estuary is the main source of juvenile snapper for the west coast of the North Island (Morrison et al. 2009). Recent mapping of the southern Kaipara

Harbour seagrass meadows has reported 30 km² of seagrass to be present, of which one-third (10 km²) is sub-tidal (Morrison et al. 2014b).

In the lower North Island (Porirua Harbour) and South Island seagrass meadows, the warmer water species (species where the small juveniles prefer warmer water) of snapper, trevally and parore are effectively absent, although juvenile snapper nurseries may also occur at the top of the South Island (Nelson/Marlborough) in other biogenic habitats (Morrison et al, in review a). Juvenile spotties and piper (*Hyporhamphus ihi*) are found across subtidal seagrass meadows nationally (albeit patchily), while juvenile leatherjackets (*Parika scaber*) become more common in lower South Island seagrass meadows (noting that for this species seagrass represents a trivial fringe habitat, as their main nursery habitat appear to be the frond-heads of kelps such as *Ecklonia radiata* (see macro-algae section).

As well as being an important nursery habitat for juveniles, seagrass also acts as a settlement habitat for fish larvae making the transition from the water column to the seafloor, with very small (about 8–10 mm) snapper having been caught in seagrass which are still semi-transparent, with long trailing fins (late larval form), as well as parore of a similar size with a blue stripe along their side, a feature known to disappear soon after settlement (Morrison 1990). Fine scale observational and experimental work in New Zealand is limited. Detailed experiments using artificial seagrass units (ASUs) have shown that very high densities of small fish, including juvenile snapper and trevally, are attracted and/or settle to these seagrass mimics (Figures 9c, d). Increasing seagrass blade density invoked different responses from different fish species: including monotypic linear increases (mottled triplefins, and overall fish species richness) increasing to an asymptote (spotties, snapper, parore, trevally, red mullet), parabolas (sand and exquisite gobies), and flat responses (clingfish). Subsequent work by Parsons et al. (2013) confirmed this effect of blade length, and also provided some potential evidence of a recruitment shadow effect, where ASUs closer to the incoming larval source may have depleted the larval supply for ASUs located further away.

One of the responses of seagrass meadows to environmental degradation, prior to the complete loss of the bed, is a reduction in seagrass blade densities (Turner & Schwarz 2006). The obvious conclusion from these results is that habitat quality (in this case seagrass blade density) is an important component of fish habitat usage, and that in this case habitat quality is directly related to the value of a specific habitat (seagrass) as a juvenile fish nursery.

In a study of fisheries catch across a range of temperate Australian estuaries, Saintilan (2004) concluded that “*as estuaries infill and the area of seagrass and mud basin declines [and mangroves increase], so too does the catch of species dependent upon these habitats*”, and that “*the results strongly suggest that seagrass is a critically important habitat for a range of commercially important species, and that declines in seagrass area resulting from natural or anthropogenic disturbance should lead directly to decreases in stocks of these species*”. Blandon & zu Ermgassen (2014) used a meta-analysis of temperate Australian fish in seagrass studies to estimate the economic value of fish enhanced by seagrass habitat. They identified 13 species which were ‘recruitment-enhanced in seagrass habitat’, 12 of which had sufficient life history information to allow for estimation of total biomass enhancement. These species were enhanced in seagrass by 0.98 kg m⁻² y⁻¹, equivalent to \$AUS 230 000 ha⁻¹ y⁻¹ (ha = 10 000 m²).

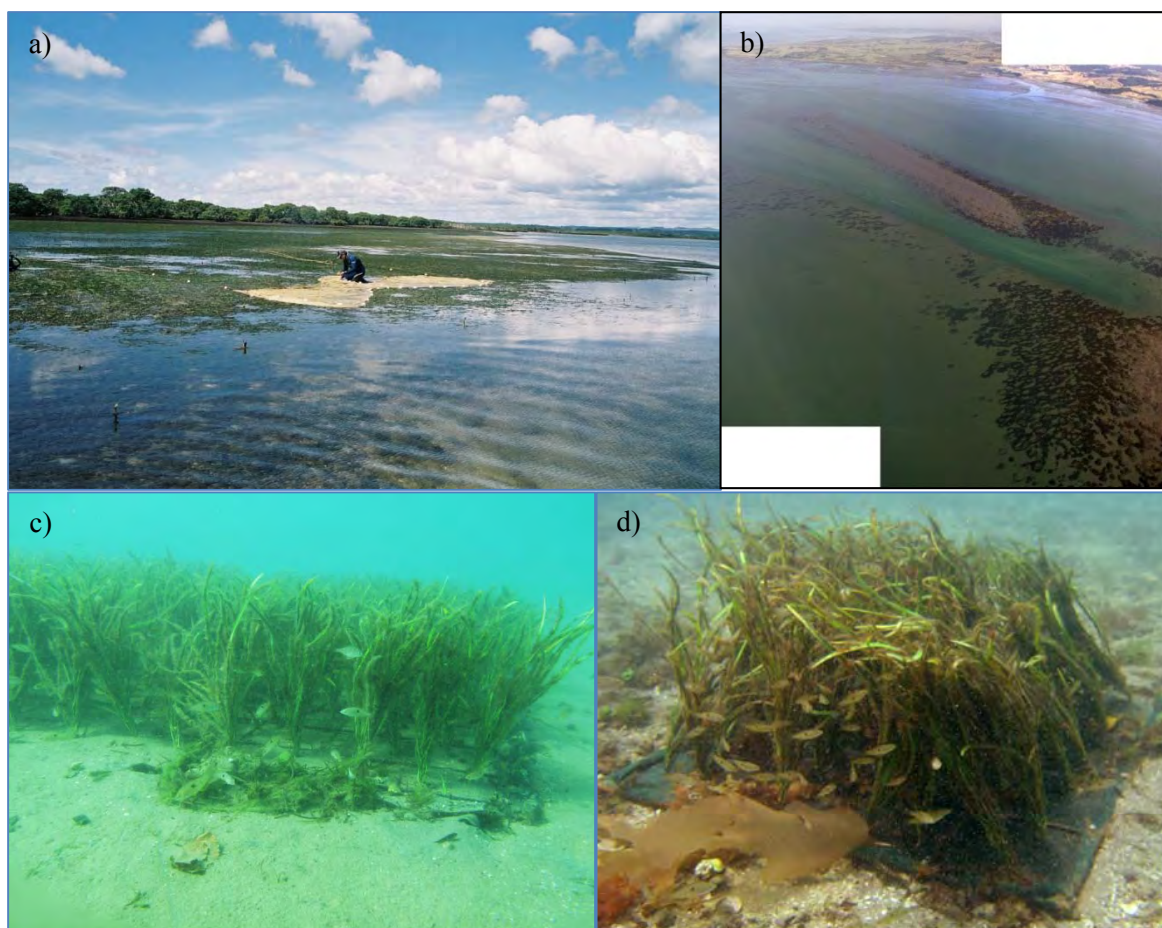


Figure 9: Seagrass meadows and fish associations in the upper North Island, a) intertidal seagrass meadow with sub-tidal fringe abutting mangrove forest, Rangaunu Harbour, East Northland, b) large scale of sub-tidal seagrass mosaic (patches 20–50 m diameter) in the southern Kaipara Harbour, c) fish assemblage, associated with 3 m² Artificial Seagrass Unit (ASU), and, d) juvenile spotties sheltering behind 0.25 m² ASU (Whangapoua Harbour, east Coromandel). (Sources: a, c, d, C. Middleton, NIWA; b, Biomarine Ltd).

Past and current status and threats

Spalding et al. (2003) estimated that there is about 44 km² of seagrass habitat in New Zealand, but the accuracy of this estimate is questionable, as systematic mapping data are not available, although the order of magnitude is probably correct. Unfortunately, seagrasses are in global decline from the effects of many cumulative stressors, the dominant ones being excess nutrients (eutrophication) and sedimentation, as well as invasive species, intensive coastal development including reclamation and the hardening of shorelines (e.g. walls, break-waters, marinas, roads), and aquaculture operations. The loss of higher level consumers (mega herbivores) has also been implicated as having cascading trophic effects in some systems (Heck et al. 2000, Jackson et al. 2001), indicating that both top-down and bottom-up processes are operating (Heck & Orth 2006).

Reported global seagrass loss has increased almost 10-fold over the last four decades, leading to the conclusion by many seagrass researchers that this plant group is in global crisis (Orth et al. 2006). Waycott et al. (2008) compiled quantitative data from 215 sites (including two northern New Zealand studies), encompassing 1128 observations from around the world, covering the time period 1879–2006. These observations were heavily dominated by studies from around the eastern seaboard of

North America, the coastline of Western Europe, and temperate Australia, with only one study outside of Australasia in the Southern Hemisphere (South Africa) (see figure 2 of Waycott et al. 2008). Analysis of these observations found that seagrass meadows had declined in all areas where data was available, starting from the earliest records in 1879. There were significantly more declines in seagrass meadows than predicted by chance. Across the overall time period there was a mean annual decline of 1.5% per yr⁻¹, with a cumulative 3370 km² of seagrass being lost (27 km² per yr⁻¹) (29% of the overall 11 592 km²). With some caveats, Waycott et al. estimated by inference a total world area of seagrass of about 177 000 km². Using their derived loss value of 29%, they suggested that globally more than 51 000 km² of seagrass had been lost over the last 127 years (to the year 2008). Loss rates accelerated over the last eight decades, from a 1% yr⁻¹ decline before 1940, increasing to 5% yr⁻¹ after 1980, and to 35% of total seagrass loss occurring from 1980 onwards. Seventy seven of the 128 sites declining had evidence of decline causes documented, with the two major causes being direct impacts from coastal development and dredging activities (21 sites), and indirect impacts from declining water quality (35 sites). Natural processes such as storm damage and biological disturbance were implicated for 6 sites. Twenty nine of the 51 sites showing increases had attributed causes, including improved water quality and habitat remediation (11 sites), and recovery from storm damage or episodes of wasting disease (Waycott et al. 2008).

New Zealand seagrass meadows, consistent with the international studies, have declined in abundance over the last 100 or so years. Large seagrass meadows remain in east Northland (Parengarenga, Ranganui, and Kaipara harbours), the upper west coast Northland Island (Aotea and Kawhia Harbours), the Bay of Plenty (Tauranga Harbour), the north-western tip of the South Island (Farewell Spit, Wanganui Inlet), and in Southland (Bluff Harbour; Paterson Inlet, Stewart Island). Smaller beds also exist in many smaller estuaries (e.g., see figure 1 in Inglis 2003), although most are not documented in the scientific literature. Historical losses are thought to have been large, although they are poorly documented, and many cases have probably gone unrecorded. Probable mechanisms include increased sedimentation, and associated reductions in water column light levels, and overgrowth by epiphytic algae benefiting from higher nutrient levels from land run-off preventing adequate light reaching seagrass blades (Turner & Schwarz 2006). Known large-scale losses include: significant declines in some eastern Bay of Islands sub-tidal seagrass meadows (Matheson et al. 2010); all of Whangarei Harbour's 12–14 km² of seagrass in the late 1960s following the dumping of 5 million tonnes of sediment 'fines' into the estuary from port expansion and a cement works (Figures 10a, b) (Morrison 2003); large meadows in the Waitemata ("*lush beds more than a mile across*", Morton & Miller 1973) and Manukau harbours (Powell 1936); 34% of Tauranga's seagrass between 1959 and 1996 (Park 1999), and all of the Avon-Heathcote Estuary's (Christchurch) seagrass (Inglis 2003). However, Whangarei Harbour has shown a major increase in subtidal seagrass since 2008, from nominally none, to a 3.5 km² area composed of numerous large patches (D. Parsons, NIWA, pers. comm.). The southern Kaipara Harbour's seagrass has also increased since the early 2000s (Bulmar et al. 2012, M.M. pers. obs.) while new areas of seagrass have also appeared in the Waitemata Harbour (albeit still limited in extent, and with only a small component being subtidal; M.M. & M. Lowe, unpubl. data.)

Work in Tauranga Harbour (Figure 10c) and the Bay of Islands (Figure 10d) both point to land-based effects from either sediments or nutrients as causing this decline. In Tauranga Harbour (Park 1999), loss rates in the sub-estuaries were positively correlated with suspended sediment input loadings scaled by relative area. There was also a reasonably strong (but not statistically significant), negative correlation with sediment mud content, and nutrient loads of phosphorous and nitrogen coming from the catchments. Earlier analysis of seagrass distribution in Tauranga Harbour found that seagrass was

generally absent once the mud content of surface sediments reached 13% (Park 1994, in Park 1999). Park also noted that substantial losses might have already occurred before 1959. However, there was some recent evidence for some possible recovery, in places such as the Tuapiro sub-estuary. More recent work in the eastern Bay of Islands assessed changes in sub-tidal seagrass beds between 1961 and 2004–05 (Matheson et al. 2010). Seagrass extent in the mainland bays near Rawhiti (Kaimarama Bay, Hauai Bay and Kaingahoa Bay) declined from about 320 000 m² to less than 10 000 m² between 1961 and 2004–05, a 97% loss. In contrast, sites on the offshore islands (Otiao and Urupukapuka) showed little change, with about 170 000 m² seagrass cover between them in 1961, and 2004–05. Collectively, two monitored factors (increased phytoplankton and epiphytic algal biomass) were considered to be linked to nutrient enrichment from septic tank leachate, stream and storm-water inflows, water currents moving contaminants from the inner Bay of Islands, boat effluent, and grey water (which often contains phosphorus) discharges (Matheson et al. 2010). In addition, a significantly greater proportion of fine sand sediments (125–250 µm) were found at the mainland sites, suggesting that seagrass within these bays had been detrimentally affected by activities such as land clearance and development in the surrounding catchments, with associated increased levels of fine sediment runoff and deposition. Matheson et al. (2008) provides a description of New Zealand seagrass stressors in general, and discuss in particular the impacts of black swan grazing on Tauranga Harbour seagrass, as well as the implication of a slime mould (*Labyrinthula zosterae*) in seagrass loss in the 1960s in the wider Waitemata Harbour and Christchurch (Armiger 1964).

There is a clear issue of seagrass loss over time through environmental decline, with Turner & Schwarz (2006) listing some of the factors driving those losses. Their relative contribution of juveniles to coastal fisheries stocks remains unknown, but is likely to be very substantial in some areas, given the densities of juveniles per unit area, and the extent of seagrass meadows (e.g. Southern Kaipara, Parengarenga, and Rangaunu Harbours; and now Whangarei Harbour). Given the documented historical losses from some systems (e.g. Whangarei, Waitemata, and Manukau Harbours), substantial past reductions in juvenile fish production have almost certainly occurred. Some restoration may be possible as seagrass transplant trials in Whangarei Harbour have been successful (at the metres to tens of metres scale), although these were intertidal patches (Matheson et al., in prep).

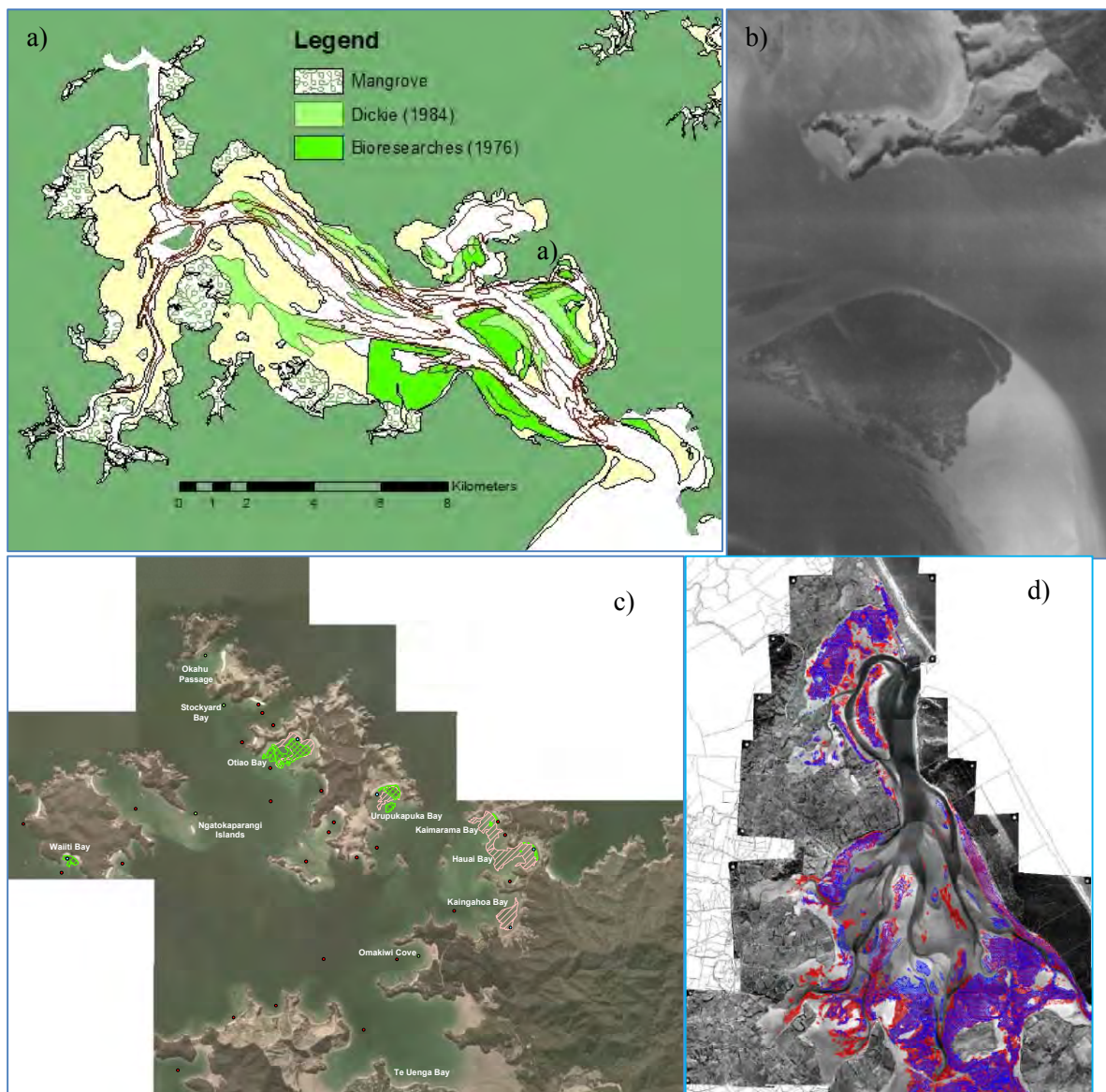


Figure 10: Examples of historical seagrass loss (note figures vary in scale): a) historical seagrass meadow extents in Whangarei Harbour, Northland, based on 1966 aerial photographs, from two sources (Dickie 1984, Bioresearches 1976; the latter only covers the lower harbour). Seagrass historically covered 12–14 km² of the harbour’s 100 km², with much of the seagrass being sub-tidal (as indicated by depth contours) with associated high fish nursery values (Source: Morrison 2003); b) 1942 aerial photograph, Snake Bank, Whangarei Harbour, showing extensive seagrass (Source: Reed et al. 2004); c) eastern Bay of Islands (all sub-tidal seagrass, 1961 (pink shading) and 2004–05 (green). Red dots denote ground-truthed sites with no seagrass, green dots sites with low seagrass cover, blue dots intensively sampled sites. The 1961 aerial images did not cover Waititi Bay or Cooks Cove (Source: figure 2, Matheson et al. 2010, finer scale imagery of each site is available in that reference); d) northern Tauranga Harbour showing seagrass presence in 1959 (red) and 1996 (blue) (Source: figure 3.1, Park 1999).

Information gaps

In terms of research to help better management of seagrass meadows as important fisheries species nurseries (i.e. snapper and trevally), the key systems to focus on are the southern Kaipara, Parengarenga, Rangaunu and Whangarei harbours, in northern New Zealand. These choices are based on recent aerial/satellite imagery/mapping of the harbours finding extensive sub-tidal seagrass

meadows, followed by ground-truthing and sampling of associated small fish assemblages using fine mesh beach seine nets. Other northern harbours such as the Manukau, Waitemata, and Tauranga also probably had high seagrass fish habitat functions in the past, and potentially might also be restored (probably largely through general environmental quality improvements rather than active transplanting) some way back to their original seagrass fish nursery functions.

Suggestions for new research include:

- Using natural markers such as otolith chemistry to assess what proportion of total recruitment these seagrass systems contribute to adjacent coastal fisheries, versus alternative nursery habitats (in the sense of either the Beck et al. 2001, or Dahlgren et al. 2006 approaches).
- Determine what specific components of the subtidal seagrass meadows contribute the most (e.g. high blade density sub-tidal fringes, or extensive shallow sub-tidal flat expanses; seagrass habitat edges or interiors), in terms of fish numbers, and growth and survivorship rates.
- Quantify how these seagrass complexes vary over time, both in response to direct human land and marine based activities, and indirect impacts such as storm frequencies and intensities increasing with climate change, as well as through natural long term cycles (suspected to operate at decadal scales).
- Incorporate the above into habitat landscape models of fisheries productivity (see mangrove suggestions section).
- Estimate the economic value of seagrass for fisheries species, as a per unit area metric (in the sense of Peterson et al. 2003, Blandon & zu Ermgassen 2014).
- Develop a national inventory of seagrass distribution, integrating with a current DOC project assembling data and maps on seagrass, and incorporating Local Ecological Knowledge (LEK) on historical distribution.

Recommended measures

Seagrass restoration is a complicated and expensive undertaking, with no guarantee of success, and so protection of what currently exists, as well as efforts to increase general environmental conditions, remain the best approaches in the short term. As seagrass meadows provide a range of valuable ecological goods and services in addition to those associated with fisheries, there is good potential to work with other agencies to also safeguard other processes such as the maintenance of biodiversity, high primary productivity, and nutrient recycling.

3.4 Macro-algae

New Zealand's macroalgal species range from encrusting forms through to the giant kelp *Macrocystis pyrifera*, and are one of the most conspicuous coastal biogenic habitats. Species can occur individually and/or as algal meadows and kelp forests. Macroalgae could occupy an entire review in their own right, with ecological work having included assemblage surveys (e.g., Choat & Schiel 1982, Schiel & Hickford 2001, Shears 2007, Shears & Babcock 2004, 2007) species interactions (Schiel 1988), and an evaluation of their use in biogeographic classification schemes (Shears et al. 2008b). As this review is targeted at fisheries species, we focus primarily on habitat occurrence, threats and stressors, and linkages to associated species.

Red algae – e.g., *Gracilaria* spp., *Adamsiella chauvinii*, and maerl/rhodoliths

Location

Red algae are common in shallow sub-tidal locations, including rocky reefs, and can form extensive beds ('meadows'), from the intertidal out to coastal depths of about 70 metres where light levels permit. There are numerous species, many of which are not yet described (W. Nelson, NIWA, pers. comm.). Three species/species groups for which some information is available are discussed here as examples. In estuarine systems, *Gracilaria chilensis*, a species with fine straight serrated blades, often forms large beds in west coast harbours such as the Manukau (along with a second, invasive and as yet unnamed *Gracilaria* species (W. Nelson, pers. comm.)). Large biomasses may occur at times, and during spring tides large volumes of algae may detach from the seafloor and form drifting masses, creating a major nuisance to net fishers, and preventing fishing at some locations and times (according to some local Manukau Harbour flounder fishers, as discussed with M.M.).

The endemic red algae *Adamsie*

lla chauvinii (formerly *Lenormandia chauvinii*) forms dense permanent canopies up to 20 cm high on soft sediments, attaching to stones and shells buried in the sediment (Kregting et al. 2008). In the South Island, large beds occur in some of the bigger estuaries (e.g., Otago, Kregting et al. 2008), sheltered embayments (Paterson Inlet, Willan 1981, Smith et al. 2005), and Sounds (e.g., Marlborough Sounds, Davidson et al. 2010). Batham (1969) noted extensive red algae cover (primarily *A. chauvinii*) in Glory Cove; while more broadly across Paterson Inlet, Willan (1981) reported a widespread and extensive algal canopy assemblage (*A. chauvinii* and two *Rhodymenia* spp., similar red algal species), covering up to 100% of the seafloor in some areas (Figure 11) (a non-vegetated habitat of sand and bryozoan patches also occurs). In the Marlborough Sounds, seven *A. chauvinii* beds have been reported from water depths of 8 to 24 metres, covering 75 to 100% of the seafloor where they occur, with bed extents ranging from 37 000 to 205 000 m² (Davidson et al. 2010, 2011).



Figure 11: Fauna associated with *A. chauvinii* in Paterson Inlet, including starfish, brittle-stars, hydroids, ceranthid anemone, sea cucumber, and fan scallop. (Source: C. Hepburn, Otago University).

Maerl/rhodoliths is a collective term for free-living, non-geniculate (meaning jointed or articulate), calcified coralline red algae. Rhodoliths often form large beds of living and dead individuals, with

underlying mud, pebble, or sand substrates (Figure 12). Four species occur in New Zealand (Harvey et al. 2005, Farr et al. 2009). Usually reported from shallow locations, they can extend down to at least 286 m water depth globally (references in Nelson 2009), and have been recorded in New Zealand waters down to water depths of 90–100 m depth at Middlesex Bank, north of the Three Kings Islands (Nelson et al. 1984, M.M and E.J., unpubl. data). Nelson & Hancock (1984) investigated South Maria Ridge (including Middlesex Bank and the Three Kings Islands), and recorded calcareous algae (“probably *Lithothamnium* sp.”) as three ‘forms’, in the shallower areas (less than 120 m depth); encrusting skeletal material; multi-lamellar, small algal reefs; and sub-spherical nodules (or rhodolites) which formed a semi-continuous lag pavement. They stated that living rhodophytes occurred down to 120 m, and that individuals below this depth were transported and/or relic from the past when sea-levels were much lower (Nelson & Hancock 1984). Dead (relic?) rhodoliths from deeper water were also sampled during the TAN1105 voyage from the Three Kings by rock dredge (E.J. & M.M., unpubl. data).

On the East Northland coast, rhodolith beds have been recorded in eastern Rangaunu Bay (M. Lowe and M.M., NIWA, unpubl. data) at the Cavalli Islands (Grace & Hayward 1980, M. Lowe & M.M., NIWA, unpubl. data) and the south-eastern Bay of Islands (Hayward et al. 1981, Hewitt et al. 2010, M. Lowe and M.M., unpubl. data). In the Hauraki Gulf, rhodolith beds have been found in Kawau Bay (see figure 24 of Morrison et al. 2009), Whangaparoa Peninsula (Basso et al. 2010), the Noises Islands (Figure 12) (Dewas & O’Shea 2011) and around the Motuihe Channel (Morrison et al. 2003). In the Coromandel, they have been reported from The Sisters, Mercury Cove, Great Mercury Island (J. Williams, NIWA, pers. comm.), and in the Wellington region from Kapiti Island (W. Nelson, NIWA, pers. comm.). In the Marlborough Sounds, Davidson et al. (2010) recorded five rhodolith beds in water depths of 6 to 26 metres, on relatively gently sloping seafloors, with almost 100% cover of the seafloor, ranging in extent from 19 000 to 223 000 m² (Figure 12).

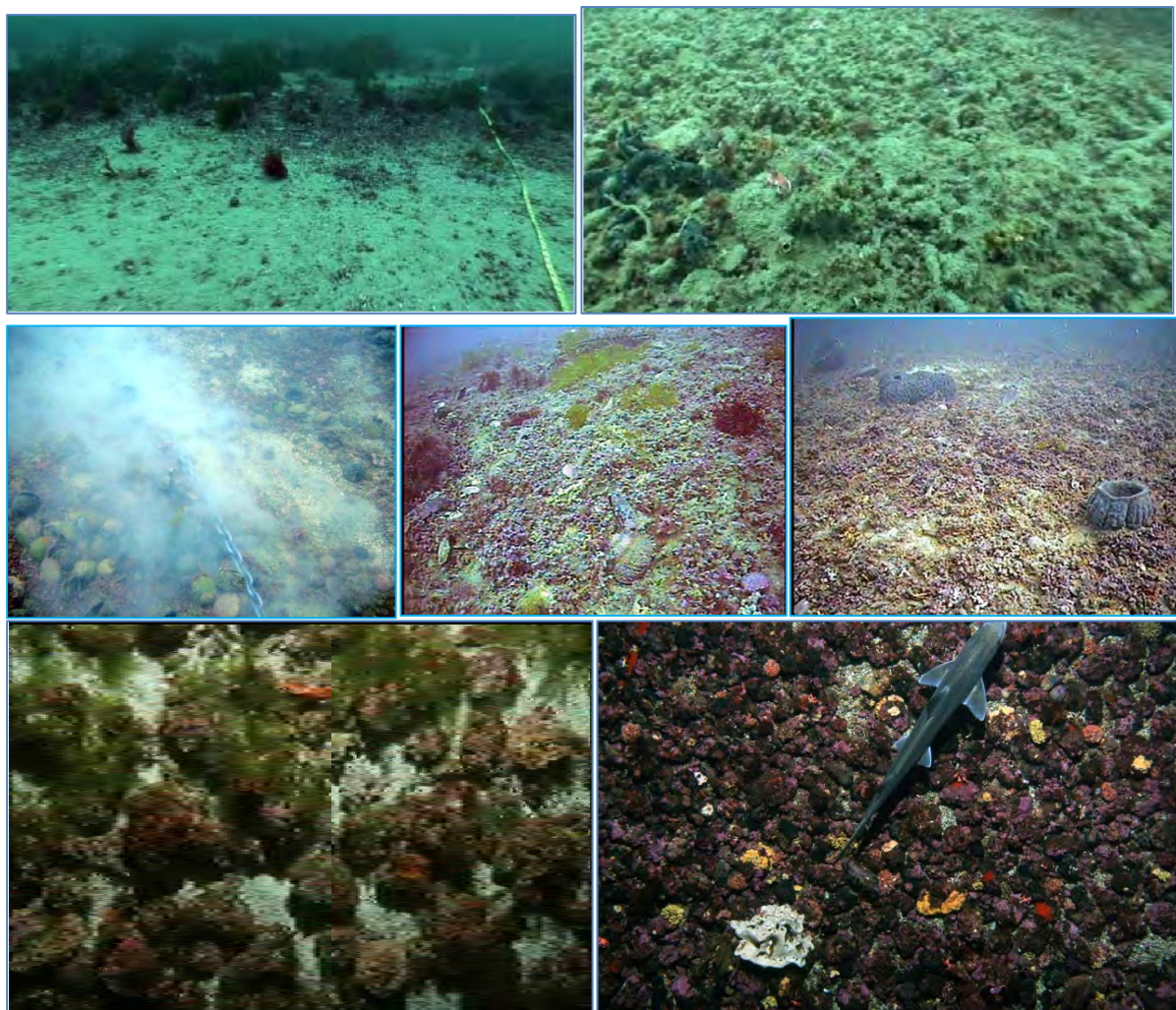


Figure 12: Top row) clean rhodolith bed with associated macro-algae and shell hash; sediment covered rhodolith bed with tubeworms and sponge (Bay of Islands); Middle row: left, small boat anchor disturbance of mixed rhodolith and dog cockle (*T. laticostata*) bed at Otara Islands, Noises Islands, inner Hauraki Gulf; middle and right, rhodolith beds with associated sponges and red and green macro-algae, Marlborough Sounds; bottom, deeper water rhodolith beds at Three Kings Islands (Sources: top, Hewitt et al. 2010; middle left, S. Severne, AUT; middle middle right, Rob Davidson, Davidson Environmental Ltd; bottom, DTIS, E.J. & M.M., TAN1105).

Value and function

For *Gracilaria* species, there is little information on what finfish fisheries species may associate with these habitats. National scale small estuarine fish sampling did not suggest any notable effect of largely intertidal red algae on species diversities or abundances (Francis et al. 2005, 2011). However, more recent sampling of subtidal *Gracilaria* sp. canopies growing on subtidal Asian date mussel beds in the Kaipara Harbour suggested a potential juvenile (under 10 cm) snapper habitat role, with densities being similar to those of adjacent subtidal seagrass meadows (mussel beds without algal canopies held only low or no snapper numbers) (Morrison et al. 2014b). In Jervis Bay Australia, sampling of subtidal (15–18 m) red drift algae (*Gracilaria verrucosa*) returned relatively few associated species, with those present being mainly a subset of the species found in shallower adjacent seagrass (*Posidonia australis*) beds (Langtry & Jacoby 1996). They concluded that these habitats were “not serving as a nursery ground for numerous species of fish”. Studies of *G. verrucosa* beds in

Chile and South Africa reached the same conclusion (Pequeno 1987, D. Keats & A. Groener, pers. comm. respectively; both cited in Langtry & Jacoby 1996).

A. chauvinii beds have associated larger-bodied epifaunal assemblages. In Paterson Inlet, this includes fan scallops (*Chlamys gemmulata* form *suteri*) and brachiopods (*Terebratella sanguinea*), as well as echinoderms (Willan 1981). Large concentrations of unidentified larval fish have also been seasonally observed in close association with these *A. chauvinii* canopies (L. Chatterton, pers. comm.). In Otago Harbour, abundant associated faunal assemblages include bryozoans, ascidians, sponges, crabs, snails and fish (Kregting et al. 2008). In the Marlborough Sounds, associated epifauna includes sea cucumbers, horse mussels, snake stars, soft tube tubeworms, and scallops (Davidson et al. 2010, 2011). Potential linkages to fisheries species are unknown, although skate (probably rough skate *Zearaja nasuta*) and elephant fish (*Callorhynchus milii*) egg cases have been observed in the beds (Davidson et al. 2010, 2011, C. Duffy, pers. comm.). No fish counts or measures have been undertaken in these habitats.

Rhodoliths often provide complex habitats for a wide diversity of small invertebrates and algae (including rare species) (Bosence & Wilson 2003, Steller et al. 2003, Foster et al. 2007), with their habitat value increasing as rhodolith complexity increases (Steller et al. 2003, Grall et al. 2006, Figueiredo et al. 2007, Foster et al. 2007). Species associations with rhodolith beds in New Zealand are poorly known. Associated fauna may include sponges, sea-stars, gastropods, and blue cod. Dense bivalve-maerl bed associations also occur, the most common being dense beds of the dog cockle *Tucetona laticostata* buried below the surface of shallow water maerl beds (Morrison et al. 2009, Dewas & O'Shea 2011). Overseas, work on the possible role of maerl in supporting fisheries species is limited to a couple of key examples. Kamenos et al. (2004a) reported significantly higher numbers of juvenile queen scallops (*Aequipecten opercularis*) and other juvenile invertebrates in pristine maerl beds, relative to adjacent habitats. Kamenos et al. (2004b) used fyke nets to assess the juvenile abundances of three gadoid species (cod, *Gadus morhua*; saithe, *Pollachius virens*; pollack, *Pollachius pollachius*) over maerl, relative to gravel with associated algae cover, and found that gadiods preferentially foraged over the maerl habitats. Maerl might play a similar role for some fish species in New Zealand, but aside from an observation of some juvenile blue cod in association with a maerl bed at Kapiti Island (W. Nelson, NIWA, pers. comm.), there is no data available with which to assess this. Small fish beam trawl sampling in March/April 2014 of the Te Rawhiti Channel (Bay of Islands) and Cavalli Passage has found small snapper and other species juveniles associated with maerl and/or red algal meadows, these data were being collected at the time this report was finalised (M. Lowe & M.M., unpubl. data).

Red algae (and hydroids) provide an important function for green-lipped mussel settlement on the west coast of Northland, especially the Ninety Mile Beach region (and probably elsewhere). Buchanan (1994) found mussel juveniles distributed on algal substrates according to mussel size and degree of branching of the filamentous macroalgae. Analyses of drift material with attached spat collected from the surf zone along Ninety Mile Beach also showed a significant inverse relationship between mussel size and degree of branching of the substrate (Alfaro & Jeffs 2002). A detailed review of green-lipped mussel dynamics including their interactions with red algae is given by Alfaro et al. (2011).

Past and current status and threats

No information is available for *Gracilaria* species, nor for *A. chauvinii* beds.

Rhodoliths have received a great deal more attention (largely internationally), especially in Europe, where a dedicated research programme (BIOMAERL) undertook work in Scotland, Brittany, Spain, and Malta (Nelson 2009). One of the major threats for maerl beds in that region are dredge fisheries for bivalves, as shellfish densities and quality are often high in such habitats. Maerl appears to be a group that is especially sensitive to disturbance. A comparison between dredged and un-dredged ('pristine') maerl beds found that dredged areas had a reduced structural complexity, resembling more a gravel bottom in structure than live maerl (Kamenos et al. 2003). Even a single pass of towed gear can bury maerl under sediment, killing it through lack of light (Hall-Spencer & Moore 2000). Other threats include the harvesting of maerl for agricultural and industrial purposes (e.g. as lime fertiliser), with centuries of harvesting having taken place in Ireland, Cornwall, and France (Briand 1991). Aquaculture operations are also a concern in some areas, as they value the same high water quality and high tidal current speed conditions as maerl does. Hall-Spencer et al. (2006) examined the effects of three salmon farms located over maerl (*Phymatolithon calcareum*) habitats, reporting a build-up of waste organic matter, and 10 to 100 fold higher abundances of scavenging fauna, relative to six reference maerl beds. All of the farms caused significant reductions in live maerl cover, and associated reductions in infaunal biodiversity, especially of small crustaceans (ostracods, isopods, tanaids and cumaceans), while organic enrichment tolerant species (polychaetes) increased in abundance. These impacts occurred despite the presence of high tidal currents, and the farms, which had been in operation for 4–12 years, were concluded to have done long-term environmental damage (Hall-Spencer et al. 2006).

Experimental work by Wilson et al. (2004), using photosynthetic capacity as a diagnostic of stress, found that maerl was less susceptible than previously thought to extremes of salinity, temperature, and heavy metal pollution, but that burial, particularly by fine or anoxic sediments, had significant stress and lethal effects. They concluded that smothering by sediment, produced by human activities such as trawling and maerl harvesting, sewage discharges, shellfish and finfish farm wastes, and sedimentation from tidal flow disruptions, was the main anthropogenic threat to live maerl and their associated high biodiversity assemblages. One of the major concerns around such damage, with its flow on effects to biodiversity and fisheries species (see below) is that even if the stressors are subsequently removed, rhodolith growth rates are very slow, generally ranging from 0.5–1 mm per year (references in Nelson 2009). This means that recovery rates need to be viewed on time-scales from multiple decades to centuries, leading to the idea that maerl beds need to be viewed as a non-renewable resource (Bosence & Wilson 2003).

Information gaps

Fish sampling on any of the above red algae species, or others, would be of benefit in better quantifying what fisheries species functions they might provide. Some current survey work (as of March 2014) includes red algae species/meadows on soft sediments in the eastern Bay of Islands and Cavalli Passage, East Northland. South Island red algal habitats are effectively unknown in terms of possible fisheries species functions; nor is their distribution and abundance well documented, especially in the context of habitat maps for management purposes.

Suggestions for new research include:

- A compilation of known red algae beds (any species) through marine user surveys/interviews would be useful; little published information was able to be located as part of this review.

- Undertake fish-habitat surveys of selected red algal habitats in the South Island, in particular of species such as *A. chauvinii* in sheltered environments (Marlborough Sounds, Otago and Bluff harbours, Paterson Inlet). Rhodolith fish associations are also largely unknown.
- Undertake general habitat mapping of selected species as appropriate, where they form a sufficient cover to be amenable to remote sensing approaches (see Morrison et al. 2014b, for Kaipara Harbour example). Incorporate appropriate environmental measurements to help define their growing requirements (e.g., water column light levels, degree of sedimentation).

Recommended measures

Red algae have been largely overlooked as a component of habitat management, although in a fisheries species context it is not yet known whether they provide an important biogenic habitat for supporting fisheries productivity. If this link can be established, then more effort will be needed to incorporate them into ecosystem based management approaches, especially around the mitigation of threats and stressors such as sedimentation, eutrophication, and mechanical disturbance.

Green algae e.g. *Caulerpra* spp.

Location

While green algae are less speciose than red algae, a number of species can occur in sufficient densities to form biogenic habitat. Here we use the *Caulerpa* genus as an example. There are nine New Zealand species in this genus, with growth forms composed of stolons or runners along the substrate, which send up fronds at regular intervals (Figure 13 upper panel). Shears et al. (2004) reported *Caulerpa* (mainly *C. flexilis*) as occurring in water depths of 3–12 m (but usually more than 6 m), and forming dense mats, usually at the rock-sand interface, in north-eastern New Zealand; this pattern was also reported from Bay of Islands reefs (Parsons et al. 2010), as well as mats being found on adjacent shallow coarse soft sediments (Bowden et al. 2010). In the Marlborough Sounds, *Caulerpra brownii* has been recorded as a small scale habitat former in association with other macroalgae on rock walls in the outer region and entrances to the sounds (R. Davidson, Davidson Environmental Ltd, pers. comm.), as well as in Fiordland (Willis et al. 2010), and at the Snares Islands (Hoho Bay, D. Freeman, DOC, pers. comm.). *Caulerpra sedoides* (grape weed) occurs as patches in many areas of the Marlborough Sounds, but never as large extents (R. Davidson, Davidson Environmental Ltd, pers. comm.).

Another example is *Microdictyon umbillicatum*, a delicate green algae which has recently formed high biomass beds in Tryphena Harbour, Great Barrier Island (Figure 13 lower panel). These beds had an abundant associated fish assemblage (not quantified), and also supported high numbers of amphipods (N. Shears, Leigh Marine Laboratory, pers. comm.), one of the main dietary components for juvenile fish (Lowe 2013). The appearance of these beds caused concern in the local community about possible nutrient enrichment issues, suggesting that such high biomasses are relatively uncommon. Nevertheless, they might contribute a fisheries species nursery function in some contexts.

Value and function

No information is available on what fisheries species may associate with *Caulerpra* spp., nor other green algal species.

Past and current status and threats

No information is available.

Information gaps

A NIWA small fish-habitat field programme (March–April 2014) in East Northland has sampled *C. flexilis* beds as encountered, as part of a wider survey effort.

Suggestions for new research include:

- A compilation of known green algae beds (any species) through marine user surveys/interviews would be useful; little published information was able to be located as part of this review.
- Any fish-habitat survey including green algae as biogenic habitat formers would be useful, with the same general points as given for red algae.

Recommended measures

As for red algae.



Figure 13: Top row, *Caulerpra* sp. bed, and close-up; bottom row, *M. umbilicatum* bed with spotties and larger juvenile snapper, and close-up, Great Barrier Island (Source: upper left, Debbie Freeman, DOC; upper right, Kate Neill, NIWA; lower, Nick Shears, Leigh Marine Laboratory, University of Auckland).

Brown kelp forests – *Ecklonia radiata*, *Carpophyllum* spp., *Macrocystis pyrifera*, and others

Location

Brown kelp forests are widespread around New Zealand, and a relatively large amount of research has been done in describing their general distribution and abundance at various spatial scales, from regional to national (see references at start of Algae section). Reviewing these studies is beyond the scope of this review; for more detail the reader is directed in particular to the work of D.R. Schiel (University of Canterbury) and N.T. Shears (University of Auckland). Key larger biogenic habitat formers include *Ecklonia radiata*, *Lessonia* spp., *Carpophyllum* spp., *Sargassum* spp., *Durvillea antarctica* (bull kelp), and *Macrocystis pyrifera* (giant kelp). *M. pyrifera* is globally distributed in cold temperate waters (Graham et al. 2007), and is New Zealand's largest kelp species. Given current interest and debate around its introduction into the Quota Management System as a harvestable resource, we include more detail on this species. In New Zealand, *M. pyrifera* is restricted to the colder waters of the lower North Island (upper limits: Kapiti Island west coast, Castle Point east coast), the entire South Island, the Chatham Islands, and the sub-Antarctic islands (Auckland, Bounty, and Campbell); and is considered to co-occur with the Southland Current along the South Island (Hay 1990a). At finer spatial scales, it can be patchily distributed, limited by suitable rocky seabed substrates on which to attach. For example, along the central South Island's eastern coast it is only found around Banks Peninsula, and about 60 km to the north at Motunau (Pirker 2002). Locally common on open coast systems as extensive beds, it also extends as a 'fringing habitat' into sheltered embayments and harbours. At off-shore locations with very clear waters, such as the Chatham Islands, it can extend down to depths of 30 metres (Schiel 1990, Schiel & Hickford 2001), but in mainland coastal waters, depth ranges are reduced due to the relatively turbid waters with associated suspended sediment loads, a consequence of land run-off and the outflows of the South Island's large braided river systems (Pirker 2002).

Value and function

Arguably, there are no New Zealand studies which have explicitly linked brown kelp forests to fisheries production, although numerous studies have examined ecological fish-habitat associations and underlying processes. Choat & Ayling (1987) looked at eleven shallow (4–10 m) reef locations across north-eastern New Zealand encompassing 1000 km of coastline (Three Kings Islands to Hahei, one Wellington site) using visual fish counts. Macroalgae reefs supported large numbers of small fish, mainly labrids, and few large benthic-feeding fishes. Conversely, echinoid-dominated reefs ('urchin barrens') supported a different fish fauna, with more large benthic-feeding species. More detailed sampling of eight sites along an environmental exposure gradient at a single locality (Takatu Peninsula, north of Auckland) matched the larger scale pattern. The positive relationship between small fish (less than 50 mm) and plant density was significant (plants per m² (range 0–20), versus mean fish density (range 0–150); $r = 0.79$, $P < 0.01$, $n = 8$ sites). Conversely, the negative relationship between larger carnivorous fish and plant density was also significant (plants per m² (range 0–20), versus mean fish density (range 0–11); $r = -0.55$, $P < 0.05$, $n = 8$ sites). Detailed behavioural observations at a reef site (Waterfall Reef, Leigh Marine Reserve) also suggested that larger benthic-feeding reef fishes were less likely to feed within macroalgae stands. Experimental reductions of grazing invertebrates designed to produce brown algal stands on echinoid-dominated reef flats supporting these observations (Choat & Ayling 1987). While the species involved were dominated by wrasses (especially the spotty *N. celidotus*), they showed that the presence of kelp forests affected fish

species composition and size-related habitat use. Jones (1984) also found this relationship for small fish, with spotties being positively associated with the density of macroalgae. Recruit densities decreased when kelp was removed, and increased with kelp addition (mediated through the removal of urchins). Similarly, juvenile leatherjackets settle into *E. radiata* kelp-heads, maintaining a very close association for several months following settlement from the plankton (Ackley 1988). Juvenile (and adult) butterflyfish (*Odax pullus*) are also largely associated with kelp forests (Clements 1985, Meekan 1986, Bader 1998).

Anderson & Miller (2004) sampled temperate reef fish assemblages in north-eastern New Zealand, at several spatial scales using visual counts, over two years. Two habitat types were compared; kelp forest (*E. radiata*) and barrens habitats, with significant differences being found in their respective fish assemblages. It was noted that there was a significant habitat–location interaction, with the effects of habitat not occurring at all locations. Spatial variation was large relative to inter-annual variation (minimal), and kelp forest as a biogenic habitat consistently influenced fish assemblages through time (over the two years).

Williams et al. (2008) sampled five habitats (shallow kelp, deep kelp, sand, algal turf, and sponge flats) in the Cape Rodney-Okakari Point Marine Reserve, New Zealand (Leigh). Different fish assemblages characterised most of the habitat comparisons. Kelp was characterised by leatherjackets, red moki, spotties, and several triplefin species; sponge flats were characterised by leatherjackets, blue cod, and goatfish; and algal turf was characterised by spotties (note: the general fish species diversity of Leigh is less than along the more exposed coastal areas as sampled by Anderson & Miller 2004).

Along the north-eastern coast of the South Island, Hickford & Schiel (1995) examined the relationships between gill-netting and shallow rocky reef fish (by visual census). They defined five habitat types, being mixtures of reef or sand, algae, and water depth. Eleven fish species were recorded, with spotties being the most abundant for all habitats except rocky reef with crustose coralline algae. Abundances varied significantly across habitats, with the highest densities being recorded in sandy bottom and patch reefs (about 16 per 100 m²). Two species of deeper water wrasses, scarlet wrasses and girdled wrasse (*N. cinctus*) occurred at significantly higher densities in deeper habitat (rocky reef, coralline algae, 15–20 m water depth). Three large carnivorous species (tarakihi, blue moki *Latridopsis ciliaris*, and blue cod) occurred in significantly higher densities over sandy bottom with small patch reefs with sparse algae. The banded wrasse (*Notolabrus fucicola*) was common across all habitats.

Win (2011) looked at three distinct macroalgal habitats and their epifaunal and fish assemblages within the East Otago Taiapure (24 km²), north of Dunedin. These habitats were *Carpophyllum flexuosum* and *Cystophora* spp. beds (0–3 m); *M. pyrifera* forest (3–10 m); and *E. radiata* beds (10–15 m). The dominant fish species were spotties, blue moki, and banded wrasse. Consistently rare species were trumpeter (*Latris lineata*), leatherjacket, girdled wrasse, scarlet wrasse, tarakihi, and marble-fish. Blue moki were present in the highest numbers as small juveniles (10–40 cm, referred to as ‘schooling size’), and along with smaller juveniles and adult blue moki, were associated with deeper habitats (*M. pyrifera* and *E. radiata*). Blue moki varied in abundance seasonally, with adult fish (over 40 cm) being most common in summer, and absent in winter and autumn, suggesting an offshore spawning migration (Francis 1981). Smaller fish were present throughout the year, with higher numbers in spring suggesting recruitment. Blue cod and low abundances of trumpeter (10–40 cm size class) were also only found in the deeper habitats, Butterflyfish were present at very low abundances across all habitats, and banded wrasses at similar low numbers in the two deeper habitats.

While limited information is available on *Macrocystis* fish associations in New Zealand, substantial work has been done in Northern America; especially on the rockfish (*Sebastes*) species group (not found in New Zealand). Two examples are given here to show how fisheries species can rely on giant kelp; although whether such relationships occur in New Zealand is unknown. Anderson (1994) looked at the relationships between the kelp perch *Brachyistius frenatus* and *M. pyrifera*. He found clear ontogenetic habitat shifts: small fish initially recruited into the floating kelp canopy, then moved down into the water column with increasing age/size, where fish associated more loosely with bundles of fronds, eventually being distributed as adults across several distinct depth strata. Juvenile densities were positively related to kelp canopy percentage cover. Carr (1994) examined spatial and temporal recruitment variation in kelp bass (*Paralabrax clathratus*) relative to giant kelp. Recruitment was positively related to kelp density, but was asymptotic at high plant densities, indicating that recruitment saturated at intermediate kelp densities (about 100–130 stipes per 30 m²). Field experiments demonstrated that recruitment responded linearly to the local abundance of kelp structure (the number and biomass of over-lapping kelp blades), indicating that both the quantity and quality of the recruitment habitat limited larval recruitment. The structural complexity per unit length of plant (blade biomass per unit plant length – a form of volume) was inversely related to plant density (i.e. plants changed their physical form with increasing density). This relationship was responsible for the asymptotic recruitment limits seen in the field (i.e. overall plant biomass did not increase beyond a certain point once a critical density of plants were present).

An example of a chain of algal habitat use by a fish (parore)

As a New Zealand example of finfish use of multiple algal habitats, Morrison (1990) examined the ontogenetic habitat use of the northern temperate reef fish parore (*Girella tricuspidata*) in the Leigh region. In January-February, large numbers of post-settlement juveniles appeared along intertidal reef edges which drop into the adjacent sub-tidal channels (Whangateau Estuary) (Figure 14). The majority of fish occurred along the reef crest/edge micro-habitat, in close association with *Hormosira banksii* patches (Neptune's Necklace, a brown furoid macroalgae). Fish were seen to eat passing zooplankton (confirmed by diet analysis), fleeing to *H. banksii* when disturbed. In March, these fish disappeared at the same time as fish of the same size appeared about 1000 m away on steep boulder reefs with the brown kelp *Carpophyllylum flexuosum*, just inside the harbour entrance. Fish inhabited the boundary zone between the upper kelp forest edge, and the narrow intertidal bare boulder habitat, in shallow water (less than 2 m at high tide), where they continued to feed on zooplankton. Over the next 9 months, their distribution shifted down through the kelp canopy (and associated depths), until they were concentrated in schools along the bottom edge of the kelp forest, in kelp clearings with a broken boulder substrate, at about 11 m depth. Their diet shifted to include small hydroids, and small red algae. At around 100 mm in size, they disappeared from these habitats, at the same time as schools of the same size fish appeared on shallow subtidal reefs in the entrance of the harbour (large broken rock slabs, with some algal cover), some 100–200 m away. At around 150–200 mm size, dense schools appeared at Waterfall Reef, Leigh Marine Reserve, about 15 km away. Parore less than 100 mm were never observed along the open coast reef systems, despite extensive free-ranging searches, as well as formal visual transect sampling. At 200–250 mm, fish started to appear across a wider range of coastal reefs, and by 300 mm were widespread across most areas. Fish less than 300 mm (not yet adults) were not seen at remote reef systems separated by large expanses of sand (e.g. the Te Arai reef system mid-way along the exposed coastline of Pakiri Beach), nor were they seen at semi-oceanic islands lacking any sheltered estuarine environments (e.g. the Mokohinau and Poor Knights Islands), where adult parore in general were very rare, suggesting that barriers to movement existed.

This example, while of a species of limited commercial value (although in the QMS), shows that habitat chains exist, and that potential habitat degradation at one location (in this case estuarine algal habitats) could potentially cascade through into large adult population declines at other locations some distance away (in this case open rocky reef systems, including a fully protected marine reserve, at the scale of tens of kilometres). As an additional point, subsequent to this work, juvenile parore were also found to utilise other biogenic estuarine habitats (sub-tidal seagrass meadows, and mangrove forests), as well as floating wharf pontoons with algae and invertebrate epifauna in sheltered harbours, showing that they are not obligate on one specific habitat type (a dynamic that appears true for all New Zealand coastal fishfish fisheries species, Morrison et al. 2014a). Juveniles of other species associated with the small reef complexes in the mid Whangateau Harbour included larger juvenile trevally (large schools up in in adjacent water column), spotties (on the reef edge and drop), and snapper (in small schools at the reef-sand interface, M.M., pers. obs.).



Figure 14: Juvenile parore (30–50 mm) in association with *H. banksii*, at Horseshoe Island reef high-tide, Whangateau Harbour. (Source: Natalie Usmar, SMS Ltd).

Parore are a long-lived species that can live for 35 years or more (Gillanders et al. 2012). While this provides buffering against risk from poor years of recruitment through the presence of many age classes, it also suggests that the consequences of degradation of nursery habitats, i.e., reductions in recruitment, may take a long time to be noticed, with a time lag on the scale of perhaps a decade. This is true for all longer lived species, although as many of them have had their population age structure truncated through the removal of larger and older fish, this risk buffering strategy is much reduced, meaning that adverse effects will manifest much more swiftly. Stewart (2011) gives examples of such reductions in age structure for eleven reef-associated fisheries species from New South Wales, Australia, including snapper, kingfish (*Seriola lanandi*), porae/grey morwong (*Nemodactylus douglasii*), sweep (*Scorpius lineolatus*), red (or blackspot) pigfish (*Bodianus unimaculatus*), Maori wrasse (*Ophthalmolepis lineolatus*), and a trevally species (*Pseudocaranx georgianus*). Even in heavily fished species with strongly truncated age/size distributions, there is still a time lag between settlement and recruitment to the fishery, e.g., 3–4 years for west coast North Island snapper (SNA 8), 4–5 years for Hauraki Gulf snapper, and about 6 years for tarakihi.

Past and current status and threats

Here we focus on giant kelp as a specific example. Work on New Zealand *M. pyrifera* beds has been relatively limited, and focussed largely on the plants themselves rather than their faunal and floral associations. The PhD thesis of Pirker (2002) is the largest single body of work, and examined spatial and temporal biomass dynamics, including recruitment and growth rates, around Banks Peninsula, as well as some limited work in Tory Channel, Marlborough Sounds. Experimental work included algal removals to assess impacts on the algal understory and mobile benthic invertebrates (mimicking potential effects from large-scale algal harvesting), and small scale experiments to examine the effects of nutrients, light and grazing on *M. pyrifera* early life history.

Pirker (2002) found Akaroa Harbour *M. pyrifera* beds to be composed of short-lived plants (*i.e.* annual) which rarely lived more than 12 months, with strong seasonal canopy declines over the summer months. This was attributed to a combination of warmer water temperatures, nutrient limitation, and sediment inputs. A combination of aerial photography and ground-based biomass measures were used to scale up to the bed scale. Biomass varied widely over time, along with loss of the structural complexity of the kelp forests. For example, at Wainui (Figure 15), a 32 000 m² *M. pyrifera* bed declined in biomass from 144 t to 21 t (85% loss) over a period of one year (October 1995–October 1996), while another bed at Ohinepeka Bay declined from 31 t to 0.06 t (98%) over six months the following year. In the Wainui example, the greatest biomass reductions were associated with a greatly increased sediment delivery period from the adjacent land due to boat ramp construction activities, which physically smothered the sea surface canopy, covered the seafloor, and prevented kelp recruitment for over a year (Pirker 2002). Summer deteriorations of the surface canopy were also partially attributed to nutrient depletion effects, driven by warmer water temperatures.

Further south, Fyfe et al. (1999) researched the potential of using remote sensing (aerial photographs) to quantify *M. pyrifera* forest extent and biomass in a Taiapure off Pleasant Point, North Otago, from 1994 to 1998. Plants lived longer than in Pirker's study, with plants being tracked to at least 2 years of age. Estimated plant biomass in November 1995 was 8100 ± 1000 t, covering 3 km². In contrast to Pirker (2002), significant bed loss was seen during winters as a result of winter storms, and no large-scale summer declines were reported.

Pirker (2002) and Fyfe et al. (1999)'s work shows that *M. pyrifera* beds and associated biomasses vary widely over season and years, in agreement with Northern Hemisphere studies (Ebeling et al. 1984, Dayton et al. 1992, North 1994, Graham et al. 1997). *Macrocystis* is a very fast growing species, with its high daily growth rates allowing for relatively quick recoveries from one-off disturbances. Pirker (2002) reported frond elongation rates of up to 22–24.5 mm per day from Akaroa Harbour; while Brown et al. (1997) measured rates of 12–14 mm for submerged fronds, and 19–20 mm for canopy fronds, in Otago Harbour. In central California, full recovery can occur within 3 months given the right environmental conditions, depending on the severity of disturbance and level of forest exposure (Graham et al. 1997), while at its southern limit in Baja California, recovery can take decades, due to higher mortalities, reduced recruitment, substratum limitations, and competing algae (Edwards & Hernandez-Carmona 2005).

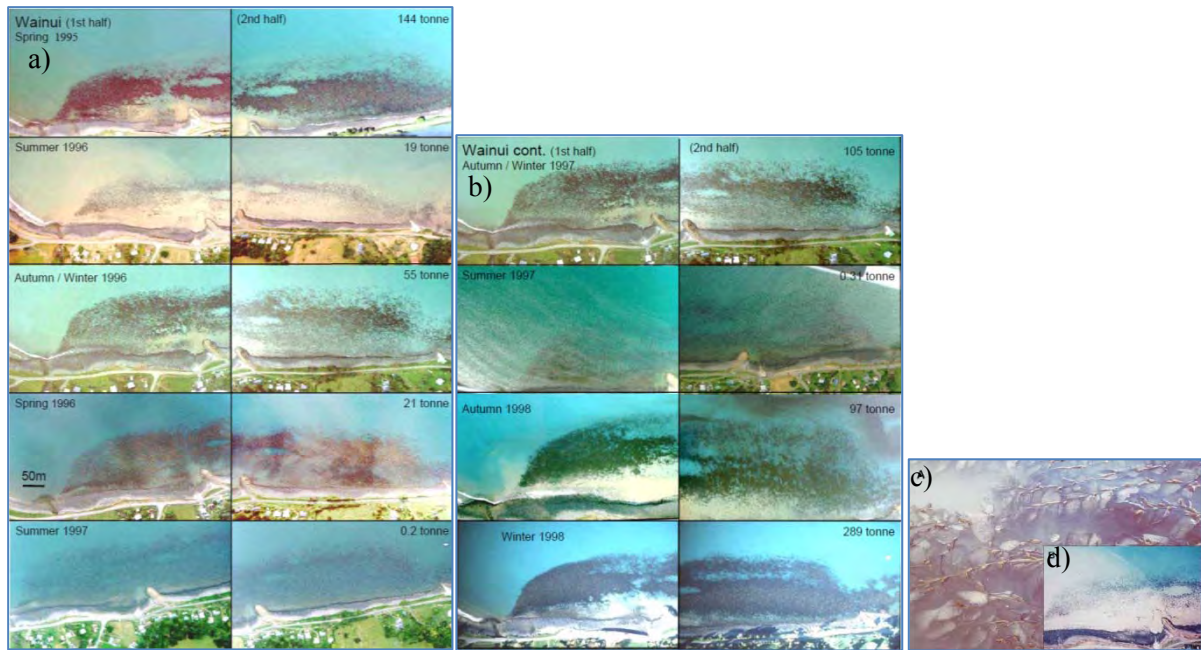


Figure 15 a, b) Aerial photographs of the Wainui kelp forest taken at 610 metres altitude in successive seasons, spring 1995–winter 1998. Total forest sea-surface canopy biomass estimates, based on above aerial photographs and in situ measurements (metric tons), are shown for each forest in the top right corner for each season, c) a close up view of the thick sediment layer on the surface of sea-surface canopy fronds, and d) an aerial photograph showing severe sedimentation of the Wainui Bay kelp forest through February 1996. Note the position of the breakwater at the lower right of the photo (total length about 50 m). (Source: figures 3.22 and 3.25, from Pirker 2002)

Information gaps

While there are many knowledge gaps around brown algae, the relevant central one here is to what extent brown algal forests contribute to fisheries species production. The various research covered above demonstrates that fisheries species utilise these habitats, but no attempt has yet been made to link this work to the fisheries themselves.

Suggestions for new research are:

- Work towards assessing how selected brown algae species (e.g., giant kelp or *Ecklonia*) may support selected fisheries species production, through functions such as providing nursery habitat, and foraging. A careful selection of geographic area, with associated fisheries species pool, will need to be made. Giant kelp may be the most tractable species to work on, and has the added attraction of being able to be mapped using remote sensing approaches. However, regardless of selection, advancing this work will be quite difficult.

Recommended measures

The range of brown algae is so broad, and the associated geographical and environmental settings so diverse, that it is difficult to pick out any specific focus. Given this, it is probably best to allow direct management issues as they emerge to drive research and management measures. For example, the recent focus on industrial harvest of giant kelp has led to a research and policy focus on this species, albeit at a relatively modest scale.

3.5 Shellfish (molluscs) biogenic habitats

A conspicuous component of many near-shore coastal systems is the presence of shellfish beds, especially of bivalves, which can occur in high abundances and associated biomass. Some support commercial and/or recreational fisheries (dredge and Pacific oysters, scallops, green-lipped mussels, surf clams, tuatua, cockles, and pipi), and/or aquaculture (Pacific oysters, green-lipped mussels). In addition to their direct fisheries values, many of these and other non-fisheries species also provide important ecological goods and services. Coen et al. (2007) undertook a comprehensive review of the role of molluscs in creating habitat, and classified these habitats into three major types, 1) (*biogenic*) reefs (veneer of living and dead animals), 2) aggregations (living and dead), and 3) shell (dead) accumulations ('shell hash'). Some species can be grouped into either habitat category 2 or 3, depending on the relative abundance of dead shell versus live organisms. The authors also added a fourth category, 4) cultured ground (an American term), to acknowledge the expanding spatial extent of farmed shellfish species. Most shellfish habitat formers are bivalves (infaunal or epifaunal), but occasionally other groups such as gastropods may also contribute, in particular Vermetidae, who possess very irregular elongated tubular shells which cement to objects such as rocks and shells (Safriel 1975). Such habitats have been observed at Moturoa Islands, east Northland, where "*a profuse development of a rich mid-tidal zone of the vermetid gastropod Novastoa lamellose, consisting of a massive layer of intertwined tubes cemented in a matrix of coralline paint 100 mm or more thick, with a network of open galleries honeycombing the whole mass*" (Grace & Puch 1977). However, such habitats appear to be rare, spatially restricted, and essentially undocumented, and are not further discussed. Our focus in the following sections is on bivalve species.

The four shellfish habitat types above provide four key characteristics – hard substrate, vertical (three-dimensional) structure, food for other organisms, and water quality regulation – which collectively were argued to result in a significant enhancement of overall habitat value for many other fish and invertebrate species of (Atlantic) shelf, coastal, and estuarine waters (Loen & Grizzle et al. 2007).

Green-lipped mussels (*Perna canaliculus*)

Location

Green-lipped mussels occur throughout New Zealand, and create biogenic habitat on both soft and hard substrates. Historically, extensive beds occurred in the Hauraki Gulf (Figure 16b), Kaipara Harbour, and Tasman Bay, although most of these beds have now been fished to local extinction. Small beds also occur in smaller estuaries, such as Whangapoua Harbour (Great Barrier Island), and Ohiwa Harbour (Bay of Plenty) (McLeod 2009, McLeod et al. 2012). Once widespread on soft sediment systems at the above broader locations, green-lipped mussels are now largely confined to rocky reef habitats. Substantial populations may also exist on the upper west Northland coast, where large volumes of spat attached to drift algae are collected each year to provide spat for marine farms. A few known soft sediment beds remain, such as at Whangapoua Harbour, Great Barrier Island (Figure 16a), while some others have established beneath or adjacent to mussels farms, e.g., at Waimangu Point, Firth of Thames (McLeod 2009), and in Orchard Bay, Marlborough Sounds (Rob Davidson, Davidson Environmental Ltd, pers. comm., Figure 16c).

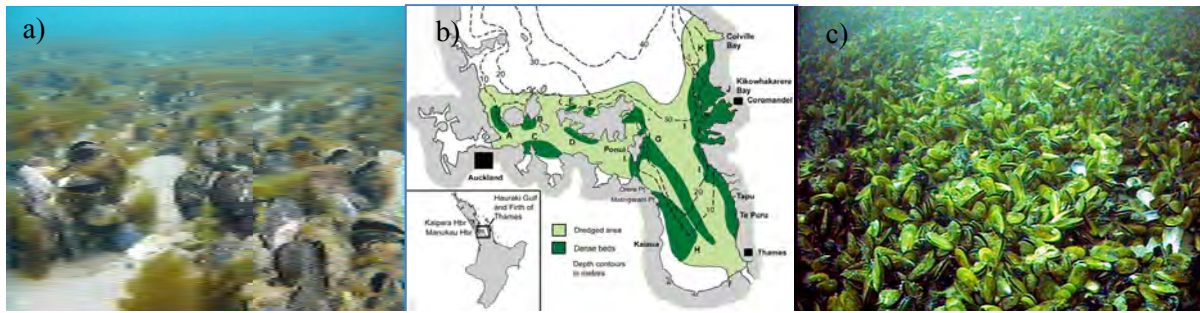


Figure 16: a) Shallow sub-tidal green-lipped mussel bed in Whangapoua Harbour, Great Barrier Island b) Historical extent of green-lipped mussel beds in the Hauraki Gulf, letter codes as follows: A) Rangitoto Channel; B) Motutapu; C) Beachlands; D) south Waiheke; E) Oneroa; F) Onetangi; G) Ponui-Thames; H) southwest Firth; I) eastern Firth and Coromandel; J) Kikowhakarere; K) Colville Bay; c) mussel bed in Orchard Bay, western side of Forsyth Island, Marlborough Sounds, associated with an adjacent mussel farm (Source: a, Ian McLeod, UoA; b, figure 5 of Paul 2012, redrawn from Reid 1969, c, Rob Davidson, Davidson Environmental Ltd)

Value and function

Little information exists on the ecological role of natural green-lipped mussel beds in New Zealand. McLeod (2009) assessed several remnant mussel beds in the Greater Hauraki Gulf and Bay of Plenty for their invertebrate and small fish assemblages (see the threats section for an account of the mussel fishery collapse). Associated small fish assemblages were dominated by mottled triplefins (*Grahamina capito*), clingfish (*Trachelochismus melobesia*), and occasional spotties (*N. celidotus*) (note: more mobile species such as juvenile snapper and trevally (if present) were not vulnerable to capture by the small diver deployed drop nets: such species are diver negative and initially move away at the approach of divers. Overall small fish densities ranged from 2 to 10 individuals m⁻² across the three locations sampled, and were about ten times greater than densities on adjacent bare sediments.

Invertebrate densities in the mussel patches (including infaunal species under the mussels) were 2 to 8 times greater than those of the adjacent bare sediments. Associated biomass values were 7 times higher. Mussel habitat species richness was also higher, especially of small crustaceans (0.5–5.6 mm) including calanoid copepods, caridean, cumacean and mysid shrimps, paguroidea (hermit crabs), porcellanidae (half crabs), pycnogonidia (sea spiders) and tanaideacea; all of which were absent in adjacent bare areas. Larger crustaceans (8.0–22.4 mm) were also much more abundant in mussel habitats, with high densities of *Petrolishes elongates* (blue half-crab) and *Halicarcinus innominatus* (pill box crab) at some sites. Such strong associations between mussels and high densities of crustaceans has been documented in a number of international studies (e.g., Dittman 1990, Moksnes et al. 1998, Ragnarsson & Raffaelli 1999, Moksnes 2002, Beadman et al. 2004, Lindsey et al. 2006), as well as the broader assemblage contrasts between mussel and adjacent non-mussel habitats (Ragnarsson & Raffaelli 1999, Duarte et al. 2006, Commito et al. 2008).

McLeod (2009) calculated the potential loss of macrofaunal invertebrate productivity associated with the historical loss of 500 km² of soft sediment mussel beds (pre-1958 estimate, Reid 1969). Two estimates of historical mussel densities were used: 1.5 per m² as calculated towards the very end of the fishery by Greenway (1969); and 120 per m² from a current day Waimangu Point mussel bed. Total small mobile invertebrate loss estimates were 370 and 33 000 tons Ash-Free-Dry-Weight y⁻¹

respectively. These estimates are conservative, as they do not include sessile invertebrates (e.g. sponges and ascidians), nor invertebrates larger than 22.4 mm (both groups more abundant on mussel reefs than adjacent bare areas in McLeod's surveys). As well as the overall gross reduction in productivity associated with mussel bed loss, other assemblage effects include shifts in the overall size distributions of invertebrates, with larger invertebrates being 20 times more abundant in mussel habitats, and the majority of these being crustaceans (especially in the 8–2.4 mm size class, which were also virtually absent from bare areas). Crustaceans larger than 1 mm are the dominant food source for small fishes (0.1–100 g wet weight) in shallow water temperate environments (Edgar & Shaw 1995).

Given these large secondary productivity declines, changes in infaunal size distributions, and the loss of crustacean components, a strong cascading effect into epibenthic carnivores including fish (e.g. snapper) was highly likely. Using the two lost productivity estimates above, McLeod (2009) estimated that the small mobile invertebrate productivity associated with the pre-1958 mussel reefs could have supported an additional biomass of between 200 and 16 000 T y⁻¹ of predatory fish above those able to be supported by 'bare' sediment areas, which replaced the reefs from the late 1960s onwards. The extra production supported by the current day Waimangu Point mussel bed (640 000 m²) was estimated to be 20 t y⁻¹.

Collectively, the above calculations show that loss of the extensive (approximately 500 km²) green-lipped mussel beds of the inner Hauraki Gulf have probably had large effects on the associated ecosystem. As well as providing direct habitat structure and food foraging, the beds could have potentially filtered the entire water volume of the Firth of Thames in less than a day, compared to over a year on the basis of current mussel biomass (McLeod 2009). Historical accounts also suggest that the Firth of Thames was once a much less turbid system; in the early days of European settlement, sailing ship crews could see the seafloor coming into Coromandel Harbour (at about 30 m water depth). Today the entrance is much shallower, and the seafloor not visible from the surface. The Firth of Thames is now a nutrient enriched system (due to land-based industries), and with the removal of the large and extensive filter-feeding mussel beds known to act as agents against nutrient-enriched algal blooms, it is only the low light levels from the sedimentation that probably prevent the outbreaks of large (and potentially toxic) algal blooms (Cloern 1999, 2001). Other sedimentation associated changes in the Firth of Thames include the development of a large mangrove forest at its head (see mangrove section), the loss of extensive pipi and cockle populations, and a general broad scale shift from sands to fine muds across the upper region of the Firth (Morrison et al. 2009).

Current catches of snapper in the Firth are around 120 t yr⁻¹, along with smaller fisheries for flatfish (yellow-belly and sand flounder). While the Firth of Thames is perceived to be an important snapper nursery ground (based on MPI trawl surveys, 1982–99), it is highly probable that the loss of the approximately 500 km² of mussel beds has severely degraded its nursery values. The extent of that impact cannot be determined with the available data, but the estimated fish productivity loss (200 to 16 000 T y⁻¹) gives some likely indication. However, there are many other unknowns around what else has changed in the Hauraki Gulf, and how those may have once influenced system functioning. For example, snapper were historically much more abundant and of a larger average size (Parsons et al. 2009), and it is not clear what role these fish filled as predators (e.g., snapper cannibalism, M.M. unpubl. data).

With the establishment of mussel farms, an alternative mussel habitat has been created (albeit a semi-pelagic one), with approximately 20 000 t now being farmed in the Firth of Thames. These farm

structures are known to attract adult snapper in northern New Zealand, and are targeted by recreational fishers as de facto 'Fish Attraction Devices' (FADs) for their elevation of catch rates (B. Hartill, pers. comm.). Morrisey et al. (2006) assessed the fish assemblages associated with mussel farms at the top of the South Island (Collingwood, Beatrix Bay, and Kenepuru Sound), and found these to be dominated by triplefins and spotties, with no commercially or recreationally important species observed. They reported anecdotal evidence of leatherjackets (*P. scaber*) and snapper (*P. auratus*) feeding on mussel spat, although none were sampled (using visual counts, ROV, and fish anaesthetic). Similar anecdotal evidence of spat predation by leatherjackets and snapper has been reported for northern New Zealand mussel farms.

Past and current status and threats

Green-lipped mussels are both a habitat former (Figure 16a) and a fisheries species. Commercial wild fisheries largely ceased in the late 1960s, and today wild populations are mainly harvested by recreational and customary fisheries. The Hauraki Gulf and Firth of Thames historically held extensive beds (Reid 1969, Greenway 1969; see Paul 2012 for a fishery history). These beds formed a spatially significant benthic habitat (approximately 500 km²), and were heavily fished using dredges from the 1920s to the 1960s. Mussel beds occurred along the entire west Coromandel Coast from Te Puru to Colville (Figure 16b). Throughout the 40 years of the fishery, 2–4 vessels operated full-time, along with casual boats, landing a high of 40 900 sacks of mussels in 1961 (about 15 million mussels). However, by 1966 the fishery had collapsed, with the beds having been serially depleted to extinction (Greenway 1969). The population collapse was attributed to unsustainable fishing pressure, including the loss of settlement surfaces for newly recruiting mussels (Greenway 1969). Broad scale acoustic and camera surveys in 2002/2003 did not locate any mussel beds, with the largest solitary patch seen being about 1 m² in extent (Morrison et al. 2002, 2003). The soft sediment green-lipped mussel populations of this region have failed to recover since being fished to functional extinction, despite some 40 years of being virtually unfished (there may have been some incidental by-catch by trawlers).

Information gaps

Given a lack of contemporary soft sediment mussel beds, potential research on these biogenic habitats is somewhat constrained. The establishment of a Mussel Restoration Trust (see following section) and associated restoration trials may provide new knowledge through time, and attempting to restore the mussel beds is a worthy objective. Aside from restoration, other suggestions are as follows.

Suggestions for new research are:

- Collate local ecological knowledge to determine where remaining soft sediment mussel reefs may still exist, in particular for areas of New Zealand such as Tasman/Golden Bays and the Marlborough Sounds. Work with regional councils and others to protect them from being lost.
- Undertake fish sampling of mobile species such as juvenile snapper and trevally, using suitable tools, to generate estimates of fish usage, and compare to other biogenic habitats such as subtidal seagrass, red algal meadows, and rhodolith beds. Use these estimates to better understand the likely relative importance of mussel beds as finfish habitat, and what habitat restoration might result in, in terms of wild fisheries improvements.

Recommended measures

Green-lipped mussel beds on soft sediments can now be considered a rare biogenic habitat in New Zealand, though they were once extensive in coastal embayments such as the Hauraki Gulf and Firth of Thames, and Tasman Bay and Marlborough Sounds. As with seagrass, there is a potential for restoration, although the costs and benefits have not yet been formally considered. Restoration through transplantations may be possible (McLeod et al. 2012). Why populations are unable to re-establish naturally is open to conjecture, but likely mechanisms include a lack of suitable hard substrates on which to settle, a lack of chemical cues from adults that may promote recruitment, and issues of sedimentation, including re-suspension from storm and other events. Strategic restoration of small patches of mussels, including the use of dead shells to provide low relief 'platforms' on the seafloor for transplanted mussels, may be possible, as a means of initialising the process, followed by a slow natural regeneration from these seed patches (over a timescale of multiple decades). Such an approach would require an evaluation of what the objectives were, what agency/ies might be responsible for the work including costs, and how other factors such as mechanical disturbance of the patches through fishing could be avoided. There is an extensive literature on restoration of shellfish habitats in North America, in particular around oysters, which could be used to inform such an approach (both in the biological and social-economics contexts). A recent initiative for the Hauraki Gulf has seen the establishment of the Mussel Reef Restoration Trust (<http://reviveourgulf.org.nz/>).

Rock (*Saccostrea commercialis*) and Pacific oysters (*Crassostrea gigas*)

Location

New Zealand has a number of native oyster species, but only two are associated with the forming of biogenic reefs: the flat (Bluff) oyster (*Ostrea edulis*); and the rock oyster (*Saccostrea commercialis*) (soft sediment, reef species respectively). The non indigenous/invasive Pacific oyster (*Crassostrea gigas*) has become a dominant feature in northern estuaries, and is thought to have displaced rock oysters in many locations, and now supports a significant aquaculture industry. Pacific oysters also form biogenic beds in Nelson-Marlborough estuaries (Rob Davidson, Davidson Environmental Ltd, pers. comm.). Anecdotally, rock oysters have declined considerably from historical abundances (this is also supported by catch histories, see Morrison et al. 2014b for the Kaipara Harbour), while Pacific oysters have expanded since their initial appearance in the 1970s, through an unknown invasive or introduced pathway. Rock and Pacific oysters have a northern distribution, while flat oysters occur around New Zealand. Bluff oysters are considered in the Bryozoan section, as they are an assemblage component rather than being a biogenic habitat former themselves.

There are no national accounts of oyster reef distributions, but the distribution of some rock oyster beds in the Kaipara Harbour have been reported (Kelly 2009). Oyster abundance and distribution was estimated remotely (video from helicopter), ground truthed by site visits. Figure 17 shows abundance contours for one of the surveyed areas, and Figure 18 some of the forms that beds take.

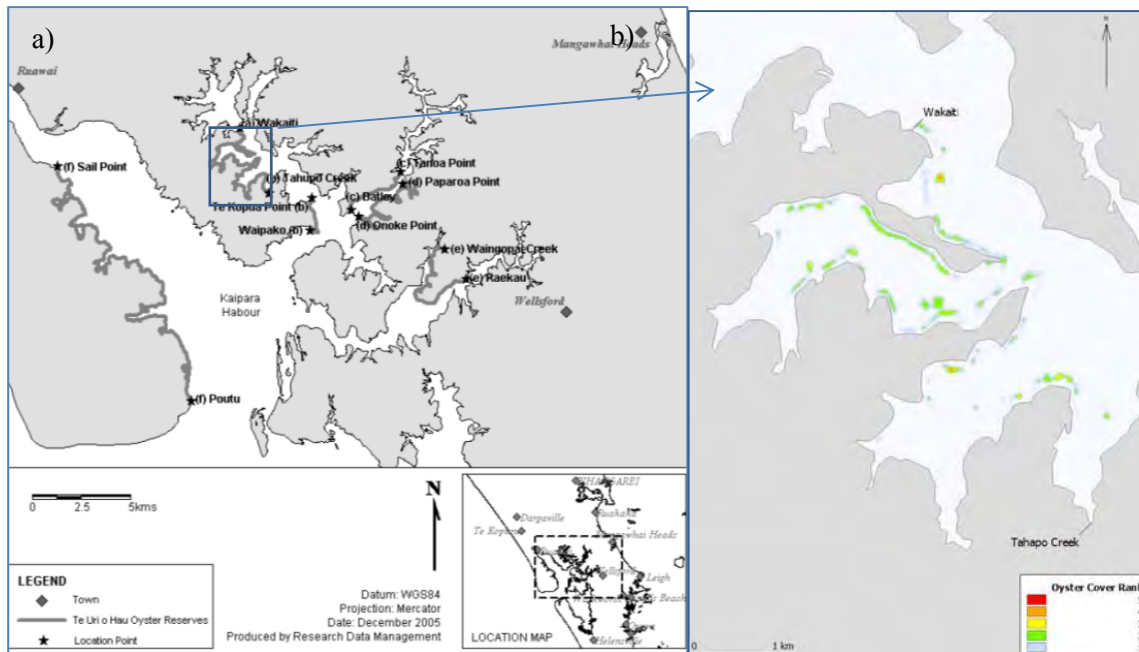


Figure 17: a) Location of the six oyster reserves in the Kaipara Harbour (Source: annex Two of Ministry of Fisheries 2005; and b) abundance contours for oyster beds in Wakaiti to Tahupo Creek, 1 lowest, 5 highest oyster cover (Source: figure 3, Kelly 2009).

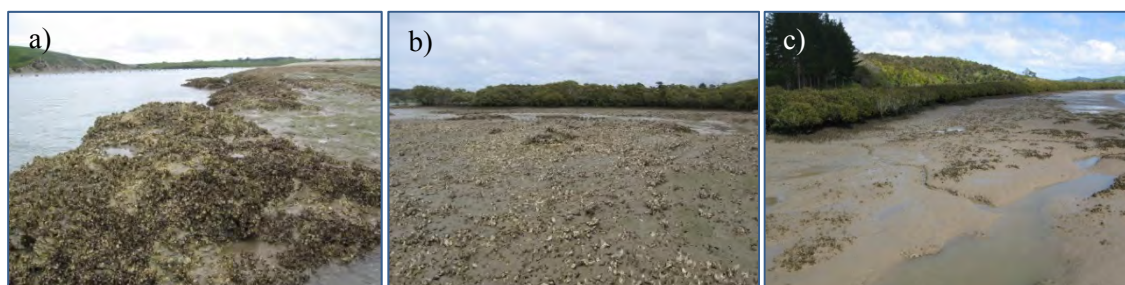


Figure 18: a, b, c) three examples of intertidal oyster reefs in Kaipara Harbour; one on rocky reef, one on reef and mud, one on mud, (Source: Shane Kelly, Coast & Catchment Ltd).

Pacific oysters dominated ground-truthed cells, while rock oysters were present in only a quarter of the cells. While the two species overlapped, rock oysters extended further the shore than Pacific oysters, and conversely Pacific oysters extended further down the shore than rock oysters. Oysters were attached to a variety of structures including mangroves, boulders, reefs, and man-made structures (largely abandoned oyster farms), as well as mud. An estimated 22.4 M oysters (95% CI, 18.2 to 26.9 M) were present in the Wakaiti to Tahupo Creek Oyster Reserve. Isolated areas within this, and the Waingopae Creek to Raekau Oyster Reserve, were found to hold ‘hotspots’ of oyster abundance, but at least some of these contained large numbers of dead oysters. This was consistent with recent mass mortalities information as described by local kaumatua, with an associated significant reduction in oysters available for harvesting (Kelly 2009).

Value and function

Beck et al. (2011) noted that oyster reefs provided a range of ecological and other goods and services. These included water filtration, the provision of food and habitat for many associated animal species (including invertebrates, fish, and birds), the stabilisation of shore-lines and associated coastal

defence, and the provision of fisheries (Grabowski & Peterson 2007, NRC 2010 – cited in Beck et al. 2011). Filtration was a key role, including the removal of suspended solids from the water column, helping maintain water clarity for species such as seagrasses, and prevent harmful algal blooms (Cloern 1999, 2001, Newell 2004, Cerrato et al. 2004, Newell & Koch 2004). The removal of excess nutrients from coastal bay waters, which facilitated the denitrification of surrounding sediments, was also highlighted as a key service in areas where nutrient removal was a key management priority (Newell et al. 2005). Further roles included the enhancement of coastal biodiversity, and the underpinning of production of some commercially important fish species. Links to socially and economically important human activities, such as marine recreation/tourism and sports (recreational) fishing were also noted, through the functioning of reefs as fish habitat, and the improvement of water quality. Beck et al. (2011) concluded that while there was an increasing recognition that shellfish (including oyster reefs) provided multiple ecosystem services, management objectives for oyster reefs were still largely focused on shellfish harvesting only, and ignored all of their other functions and values. They argued that there was very good potential for better oyster reef management, with key elements underpinning the successful management of other coastal fisheries being present, including a) the existence of extensive private rights, b) populations that could be policed near-shore, and c) clear links between the target species and ecosystem structure.

Peterson et al. (2003) calculated the per-unit area cumulative enhancement of fish and large mobile crustacean biomass expected to occur as a result of replacing an area of unstructured mud/sand estuarine bottom in the south-east USA with a restored oyster reef. They estimated the value added through the processes of enhanced recruitment, and enhanced growth. Species whose lifetime expected production was thought to be limited by the area of oyster reef (near exclusive association of recruits with reefs) were fully 'credited' to the reef, while for species whose recruitment was only modestly enhanced in abundance by oyster reefs, reefs were given fractional credit for the overall production generated by the consumption of reef-associated prey (based on gut content data and natural history information). Using this approach, it was estimated that a 10 m² area of restored oyster reef would yield an extra 2.6 kg of production per year (fish and large mobile crustaceans) more than an equivalent area of unstructured mud/sand estuarine bottom, over the functional lifetime of the oyster reef. The life-span of reefs protected from 'bottom-disturbing fishing gear' was suggested to be limited by intense storms or sedimentation, to on average 20 to 30 years. A reef (10 m²) lasting 20 to 30 years would generate a cumulative biomass amount of 38–50 kg, allowing for a discount to present-day value (3% discount per year). Peterson et al. (2003) argued that while these calculations assumed that the present day extent of oyster reef habitats limits the production of reef-associated species and crustaceans in the southeast United States, such an assumption was reasonable based on the strong associations of many fishes with oyster reef-dependent prey, and the high loss of reef habitats over the previous century. Nineteen species were identified from the science literature as being biomass enhanced by the presence of oyster habitat, with ten (three commercial) of these being recruitment-enhanced and nine (one commercial) growth enhanced. Of the extra 2.6 kg production per year, 1 kg (38%) was contributed by fisheries species. Peterson et al. (2003) noted that many other environmental benefits would also be achieved by reef restoration, including positive effects on water clarity, carbon sequestration, rate of denitrification, and oyster restocking.

The value of rock and Pacific oysters as biogenic habitat for fisheries species in New Zealand is unknown.

Past and current status and threats

No detailed work on New Zealand rock and Pacific oysters exists, outside of the aquaculture literature. Globally, few extensive wild oyster populations still exist. Kirby (2004) evaluated the historical expansion and then collapse of oyster fisheries, and found that these “*expanded and collapsed in a linear sequence*” along eastern America (*Crassostrea virginica*), western North America (*Ostreola conchaphila*), and eastern Australia (*Saccostrea glomerata*). Fishery collapses occurred initially in estuaries closest to developing urban centres (markets), before exploitation expanded down the coast. As each individual fishery collapsed, oysters from more distant estuaries were transplanted to restock the depleted estuaries, and this pattern continued through time as a ‘*moving wave of exploitation [which] travelled along each coastline until the most distant estuary had been reached and over-fished*’. He also noted that the historical degradation of these reefs still remains unappreciated today, and that this oversight could be assigned to the ‘*shifting baseline syndrome*’, with no scientist today having ever seen an undisturbed, fully functioning oyster reef. He argued that given their reported large size, wide geographic distribution, and associated multitude of suspension feeders, they probably once played a dominant ecological role in estuaries.

Beck et al. (2011) looked at the global condition of oyster reefs over the last 130 years. It was calculated that oyster reefs today represent less than 10% of their historical abundance in most bays (70%) and eco-regions (63%), and are functionally extinct (less than 1% abundance remaining) in many of these areas, especially in North America, Australia, and Europe (they consider their estimates conservative). Total cumulative global loss was estimated at 85%. New Zealand was included in this assessment, with the Foveaux Strait region (flat/Bluff oysters) being classified as in poor condition (90 to 99% historical abundance lost), while the remainder of mainland New Zealand was classified as in fair condition (50 to 89% lost). Like Kirby (2004), Beck et al. (2011) found a common decline sequence, starting with the loss of vertical relief and complexity (dredging and trawling), which then interacted with the impacts of other stressors such as anoxia, sedimentation, disease, and invasive species. Years of declining harvests were followed by introductions of non-native oysters (either direct releases or aquaculture escapees), with an end-point of overharvesting and disease leading to population crashes. Other anthropogenic influences included alterations to shorelines, changes in freshwater flows, and increased sediment, nutrient and toxin loads.

Information gaps

Rock oysters are considered to be in decline, and as inferred by Kelly (2009), have been replaced to a significant degree by the invasive/introduced Pacific oyster, now the dominant oyster species in northern estuaries. As well as being a valuable aquaculture species, Pacific oysters are also a pest, being seen as partially responsible for highly accelerated sedimentation of upper estuary areas, being a hazard to swimmers and boats, and reducing the available fishing areas for commercial netting (Morrison et al. 2014b). Our opinion is they probably do not provide a significant fisheries species habitat in such environments, given the limited available species pool that might associate with them, with the possible exception of juvenile grey mullet.

Suggestions for new research are:

- Undertake some limited sampling of Pacific oyster reefs to assess their value to fisheries species. This sampling could include oyster farms, to assess whether they potentially provide positive habitat values. This data could then be compared against other biogenic and non-biogenic habitats, to quantify the relative value of oyster beds. The approach of Peterson et al,

(2003) could potentially be used for this or any other biogenic habitats, although North American systems have significantly more data available than New Zealand equivalents.

Recommended measures

None

Horse mussel beds (*Atrina novezealandiae*)

Location

The large pinnid mussel *Atrina novezealandiae* known as the horse mussel, occurs from extreme low tide areas, out to at least 45–70 m water depth on the continental shelf (Vooren 1975, Hopkins 2002), with dead shell having been reported from 200 m water depth (Hay 1990b). Horse mussels grow to more than 40 cm in length, and anchor the lower part of their shells in soft sediments using sub-surface byssal threads. Mussel densities range from occasional scattered individuals, through to very densely packed ‘beds’, extending over hundreds to thousands of metres. They are relatively long lived (more than 10 years) (Butler & Brewster 1979, Hay 1990b, Hopkins 2002), and recruitment appears to be highly variable between years, meaning that beds may appear and disappear over decadal scales (e.g. see Hayward et al. 1997). Usually individuals within a bed are all of similar size, suggesting discrete mass recruitment events. Observations of a horse mussel recruitment event (20–30 mm individuals) in Greater Omaha Bay (about 17–22 m, sand seafloor) in 1993 found very discrete and dense clumps (more than 30–40 cm diameter, 2–3 m spacing), extending for at least one kilometre along the depth contour. Mussels grew rapidly over the next six months (to about 100 mm), and combined with individuals ‘pushing out’ laterally as well as mortality, produced patches of about 1 m, containing lower density, larger animals (Morrison 1999, M.M, pers. obs.).

While horse mussel beds occur around New Zealand and are probably common and extensive, there are no inventories or systematic maps of their distribution. They are a widespread habitat in the Hauraki Gulf (e.g. Compton et al. 2012). Some bed locations were identified as part of LEK interviews with commercial fishers in the “Continental shelf biogenic habitats” programme (ZBD200801) (41 instances), including off Clifford Bay in Cook Strait, and around Stewart Island. Other reported locations include Mahurangi Harbour (Ellis et al. 2002, Usmar 2010), the Marlborough Sounds (Davidson et al. 2010), Otago Peninsula (about 65–70 m) (Hopkins 2002), Doubtful Sound (about 12–14 m depth) (Hopkins 2002), and Oamaru (about 45 m water depth) (Vooren 1975). Hay (1990b) also noted that at Napier, following the 1931 earthquake, ‘*vast beds of horse mussels were exposed when the west shore of the Ahuriri Lagoon was uplifted 0.5–1 metre*’. They are also common in the southern Bay of Islands (Figure 19a). Horse mussel beds can be detected with side-scan sonar, making them amenable to habitat mapping and monitoring, e.g. off the Motueka Delta in Tasman Bay (Gillespie et al. 2005, Figure 19b), and between Kaikoura Peninsula and Haumari Bluffs, east coast South Island (Carter et al. 2004, Figure 20) (these were presumed to be horse mussels, but no ground-truthing was undertaken) (Figure 20).

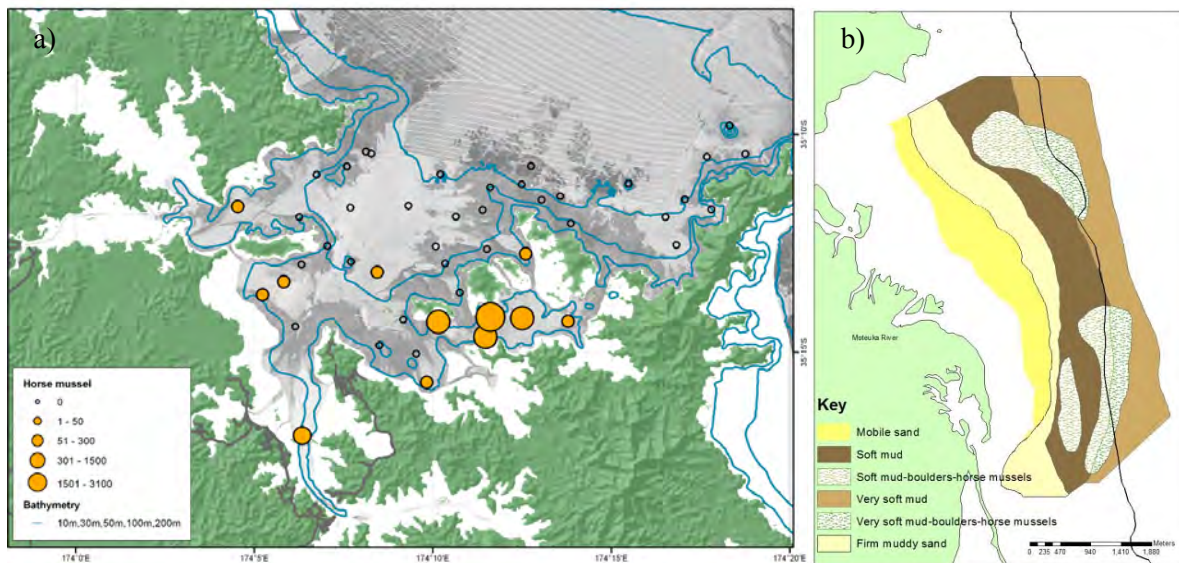


Figure 19: a) Horse mussel bed densities estimated by DTIS, Bay of Islands. Highest densities occurred in Te Rawhiti Inlet, in association with mixed shell hash and rhodoliths. Bed ranged from about 10 to 50 m water depth (minimum DTIS depth is 10 m). (Source: Bowden et al. 2010). b) Horse mussel beds (ground-truthed) mapped by side-scan sonar off the Motueka Delta, Tasman Bay (Gillespie et al. 2005). Black line is 10 m depth contour. Horse mussels occurred over soft mud with boulders, and very soft mud with boulders. Estimated bed depth band about 8–10 m. Total mapped about 15 km², with a horse mussel bed extent of 3.01 km² (20% of mapped area) (Source: Paul Gillespie, Cawthron Institute).

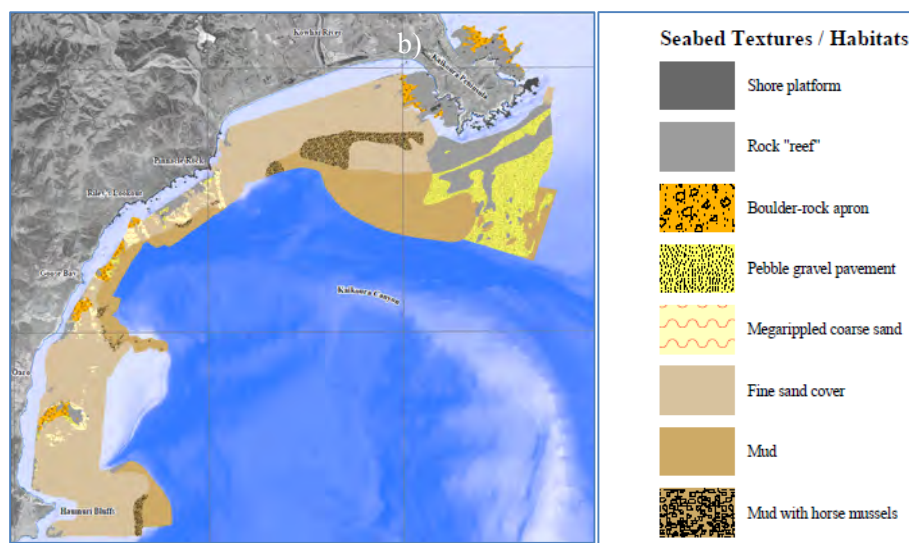


Figure 20: Horse mussel beds (presumed) mapped by side-scan sonar between Kaikoura and Haumari Bluffs, shown as brown speckled polygons, associated with about 15–40 m water depths (Source: Carter et al. 2004).

Value and function

Horse mussels were added as a commercial species to the Quota Management System (QMS) in 2004, but total annual landings average less than 1 t, taken as by-catch by trawling, Danish seining, and dredging. Discard rates are not known, nor are the levels of displacement and/or mortality of animals *in situ* on the seafloor. Horse mussels remove large volumes of plankton and suspended sediments out

of the water column, and at high densities, produce large amounts of faeces and pseudo faeces, which impact on the surrounding seafloor and biological assemblages (Cummings et al. 2001, Ellis et al. 2002). Their presence also alters fine scale boundary layer water flows (Nikora et al. 2002), meso-scale hydrodynamic interactions (Green et al. 1998), and community interactions (Keough 1984, Cummings et al. 1998, 2001).

Horse mussel beds (Figure 21a) often support diverse species assemblages of sponges, macro-algae, bryozoans, filter feeding bivalves, and soft corals, and mobile species such as sea cucumbers, hermit crabs, and small benthic fishes (Figure 21b, c), depending on environmental setting (e.g. Hay 1990b, Ellis et al. 2002, Usmar 2010). Hay (1990b) reported low density beds of *M. pyrifera* and *E. radiata* extending 2–3 m above the seafloor, growing on horse mussels in the outer Marlborough Sounds, and similar associations have been observed for *E. radiata* off south-west Motiti Island, Bay of Plenty (scallop dredge by-catch, M.M., pers. obs.). Hay (1990b) also reported dense foliose algae growing on outer Marlborough Sounds horse mussels (e.g., *Shizoseris*, *Hymenena*, *Epymenia*, *Laingia*, *Stenogramme*, and *Asparagopsis*); while in the inner sounds the associated epibenthic species were mainly animals, especially sponges and colonial tunicates. As well as creating mono-specific dense beds, both living and dead horse mussels are often a component of many other diverse biogenic seafloors, along with contributions from dog cockles, scallops, maerl, bryozoans, sponges, hydroids and macro-algae (e.g., see Davidson et al. 2010 for Marlborough Sound examples).

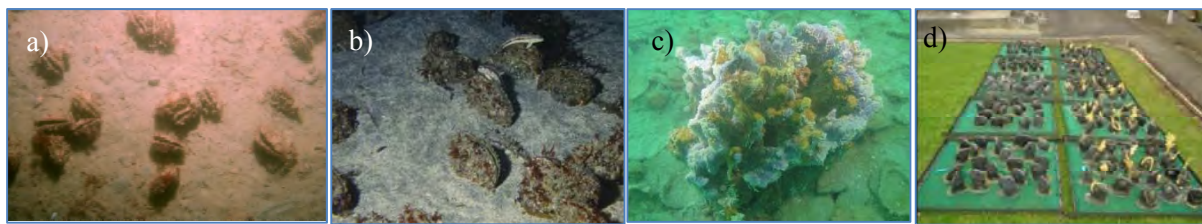


Figure 21: a) mainly dead horse mussel bed on muddy sand, Rawhiti Passage, Bay of Islands, Northland (about 20 m depth) (DTIS, OS2020 image); b) juvenile blue cod (about 8–10 cm) resting on horse mussels in Goat Island Bay, Leigh, Northland (about 30 m depth) (Source: Grant-Mackie 1987); c) horse mussel covered by sponges and hermit crabs, Tamaki Strait, Auckland (about 10 m depth) (Source: J. Williams, NIWA); d) artificial 1 m² horse mussel patches with and without epifauna analogues (Source: N. Usmar, SMS Ltd).

Fish associations with horse mussel beds have only been quantified in some local areas of northern New Zealand, aside from Hay (1990b) observing blennies, sucker fish and juvenile octopus inside dead horse mussels in the Marlborough Sounds. In high current areas in the Marlborough Sounds, he also observed that the presence of horse mussels tended to create crater-like depressions, up to 30–50 cm deep and 1–2 m wide. Seaweed, shells and debris accumulated around the mussels in the depression's centre, and blue cod and gurnard were also often present, as well as spotties, blennies, leatherjackets and opal fish.

Northern New Zealand beds provide a nursery function for juvenile snapper and trevally, as well as supporting other small fishes such as triplefins (e.g., Morrison & Carbines 2006, Jones et al. 2010, Usmar 2010, Lowe 2013). Usmar (2010) deployed artificial horse mussel patches (Figure 21d) in Mahurangi Harbour, both with and without artificial epifauna, as well as controls, and found highest snapper numbers (30–50 mm) to be associated with the horse mussels with epifauna. Mean densities were about 40–120 (\pm 30) snapper per 100 m², compared to adjacent area densities of 4.7 (\pm 3) per

100 m² (as sampled by beam trawling) a 10–30 fold difference, attributable to the artificial horse mussel structures. Other associated species included triple-fins, juvenile spotties (*N. celidotus*), goatfish (*U. lineatus*), and the invasive bridled goby (*Arenigobius bifrenatus*) (Usmar 2010).

In the inner Hauraki Gulf, horse mussels, sponges and ascidians are the dominant emergent seafloor structure in the higher current channel areas. In this environmental setting, adult snapper are positively correlated with the presence of these structures, while juvenile snapper (under 10 cm) are associated with lower tidal speed areas, in association with pits and burrows on the seafloor, away from horse mussel beds (Compton et al. 2012). Cannibalism by adult snapper (as shown by gut contents), and predation by other species might explain the absence of juvenile snapper in the more structured habitats, high flow areas. These patterns suggest that the degree of utilisation of horse mussel beds as fish nursery areas is likely to depend on environmental context.

Outside of this northern based work, there is no information available on what fish species utilise horse mussel beds around the New Zealand coast.

Past and current status and threats

Horse mussels are sensitive to high levels of suspended sediments, and have declined in locations where levels have reached some critical threshold, such as the upper Mahurangi Harbour (Ellis et al. 2002). The wider spatial scale extent of such impacts is unknown, but may be extensive (Morrison et al. 2009). Horse mussels are also relatively fragile to disturbance from towed fishing gears (e.g., trawls and dredges), as well as events such as boat anchoring. In addition to being physically caught, many individuals are probably knocked sideways *in situ*, where they can live for up to a year or more lying on the seafloor (Hay 1990b). The level of mortality generated by fishing disturbance is unknown. Anecdotal reports suggest large declines in areas that have been historically heavily fished; including in decades past the ‘conditioning’ of some fishing grounds with chains towed between vessels to remove horse mussel beds.

Hay (1990b) observed intensive commercial scallop dredging across part of a research survey transect in Guards Bay, Marlborough Sounds (15 December 1987). The fished area was described as a flat featureless area “*completely criss-crossed with the marks of the scallop dredges*”, with no live horse mussel, but abundant broken shell; while the un-dredged area (on a bank avoided by the dredgers) had horse mussel densities of 3–5 per m², with a “*lush growth of epiphytic foliose red seaweeds and Ecklonia, and abundant fish life*”. Fishers were reported to generally avoid areas of high density horse mussels due to their interference with fishing operations, but also to commonly “*flatten areas of horse mussels to render the bottom terrain more suitable for dredging and trawling in future years*” (Hay 1990b). Hay suggested that significant horse mussel habitat on the outer Marlborough Sounds, inside the Sounds (e.g., Ketu Bay), and inside Croiselles Harbour had probably been destroyed by commercial trawling and dredging.

Internationally there is also evidence for fishing impacts on other emergent bivalve populations. Similar to New Zealand’s *A. novaezelandica*, *M. modiolus* is associated with many other epifauna, including sponges, hydroids, and bryozoans (Wildish & Fader 1998, Fuller et al. 1998), and in the Gulf of Maine they provide a species refuge from predation and sea grazing, as well as supporting distinct communities, with higher densities and diversity than adjacent areas (Witman 1995, Ojeda & Dearborn 1999). Kenchington et al. (2007) examined the species presence-absence between two (1966–67, 1997) mega-benthic surveys of scallop grounds in the Bay of Fundy. Attached fragile,

epifaunal and filtering feeding taxa including horse mussels (*Modiolus modiolus*), boring sponges, scallops, fan worms and stalked tunicates declined; and were replaced by a combination of motile scavengers, motile filter-feeders, and robust burrowing filter-feeders (e.g., whelks, bivalves, toad crabs, sea urchins and brittle stars). Kenchington et al. (2007) attributed these temporal changes to physical fishing gear impacts, noting that trawling and scallop dredging in this area were “*neither intense nor new developments*”. Other possible secondary causes of change included other ecosystem effects of fishing (discards and bait subsidies), mass scallop mortalities, and a bryozoan range expansion (*Flustra foliacea*). In particular, these authors highlighted the horse mussel loss trend as “*alarming*” (p 236). This species was identified as by far the largest contributor to macrobenthic secondary production in the Bay of Fundy (Wildish & Peer 1983), and a characteristic benthos species north of the major scallop grounds (Peer et al. 1980), including biotherms (Wildish et al. 1998), which still formed much of the substrate within Kenchington’s study region (Fuller et al. 1998). (Note: these biotherms were considered analogous to historical Foveaux Strait bryozoan reefs (Cranfield et al. 1999, 2004)). Kenchington et al. concluded that for horse mussels their “*vulnerability is not to a single pass of fishing gear, or even to brief periods of intensive fishing, but to prolonged, unsustainable impacts continued over decades*”. They also noted that if mobile fishing gear was to extend into mussel biotherms areas, those biotherms could be as vulnerable to impact as the bryozoan reefs of Foveaux Strait (Cranfield et al. 2003, 2004), which they resembled in form and function.

Recreational anchoring and scallop dredging are also potential issues. Backhurst & Cole (2000) assessed anchoring impacts at nearby Kawau Island, an intensively used anchorage, and found no correlation between horse mussel densities and putative anchoring intensities across five locations. Horse mussels were in fact the most abundant epifauna (more than 1 per m²) at Mansion House Bay, one of the most heavily used sites. However, the authors noted that densities might have been still higher in the absence of anchoring. Experimental repeated dropping of an anchor onto small seafloor plots found horse mussel damage rates to rise with increasing anchoring intensity, with damaged individuals being attacked by whelks and starfish, and suffering 100% mortality. In Mahurangi Harbour, recreational yacht and launch densities reach very high levels in some discrete areas over summer; the seafloor under these areas is covered by dead horse mussel shell shards (M.M., pers. obs.). Anchor and chain damage may be creating this smashed shell cover.

Information gaps

Fish-horse mussel associations at the wider national scale are unknown; including in central and southern coastal regions, where cooler water species juveniles (e.g., blue and red cod, tarakihi, and trumpeter) become more dominant in shallow waters; and on the continental shelf nationally. In addition to providing fish habitat, horse mussel beds support many other important functions, including enhancing biodiversity and benthic-pelagic coupling. Key questions include: where do horse mussel beds occur, and why; how do the associated assemblages, including fisheries species, vary across different environmental settings (e.g., protected shallow bays versus exposed open coastal areas, with depth, and with latitude); and how do stressors such as fishing and sedimentation footprints overlap horse mussel bed distributions, and affect their various ecological functions (including fishery functions such as provision of nurseries).

Suggestions for new research are:

- Use LEK and other methods to identify where horse mussel beds occur (or have occurred) in different regions of New Zealand (some information already exists from the ZBD200801 programme).
- Investigate the use of sidescan sonar and other remote sensing technologies to detect and map horse mussel beds, and map selected beds.
- Undertake fish-habitat surveys to quantify what is present, allowing for seasonal effects. As the potential spatial extent is rather large, careful planning will be required to target those components of horse mussel distribution that are most likely to have the highest values.
- Use modelling to predict more widely where horse mussel beds are likely to occur, and how these locations relate to bottom fished gears, sedimentation, and other factors deleterious to horse mussel survival.

Recommended measures

Given the potentially high value of horse mussel beds for supporting the juveniles of some fisheries species (e.g., snapper, trevally, and possibly others such as terakihi in more southern waters/on the continental shelf), their associated strong enhancement of biodiversity in many settings, their widespread occurrence around New Zealand, and their vulnerability to both direct (e.g. fishing) and indirect (e.g. sedimentation) stressors, more research and management effort should be directed towards this species. Ideally, this should include taking their role into account in spatially based fisheries management, along with other important biogenic habitats. In areas more affected by land-based sedimentation and other impacts (Morrison et al. 2009), this will need to include interactions with land use resource management agencies such as regional councils.

Infaunal bivalves (e.g. *Tawera spissa*, dog cockles, cockles, pipi)

Location

A range of infaunal (living in sediment) bivalve species occur in New Zealand's coastal zone at sufficiently high densities to dominate the seafloor, both as dense beds, and as dead shell surface deposits (Coen & Grizzle 2007's 2nd and 3rd shellfish habitat types). At these densities, they act as key species, providing functions including benthic-pelagic coupling, nutrient transfer, phytoplankton abundance regulation, carbon sequestration, and food provision. There is no evidence that they directly provide shelter for fish, aside from some small cryptic forms (e.g. cling-fish). Their dead shells tend to form dense, closely packed drifts, with little three-dimensional elevation, or associated small crevices and nooks, in areas of sufficiently low energy to allow dead shell to accumulate. Examples well known to New Zealanders include dense cockle (*Chione stutchburyi*) and pipi (*Paphies australis*) beds in estuaries. In deeper coastal areas, other bed forming bivalve species appear such as *Tawera spissa* (morning glory shell). This species is found around New Zealand, ranging in abundance from low density components of general invertebrate sandy/shell grit habitat assemblages, through to high density mono-specific beds which can extend over relatively large areas, and completely dominate the seafloor as live animals and dead shell. For example, a Greater Omaha Bay, Hauraki Gulf bed in 18–28 m water depth covered 1.5 km², with an average density of 907 individuals per m² (maximum 3476), and about 1.4 billion population size (Taylor & Morrison 2008). A larger infaunal bivalve in shallow coastal areas is the dog cockle *Tucetona laticostata*, which forms extensive beds with shell drifts at some locations where current speeds are high and the bottom sediments coarse (there is also a smaller bodied, less 'massive-shelled' species, *Glycymeris modesta*). In more sheltered, or deeper open coast environments, the heavy and thick nature of shells may

produce more complex shell drifts than smaller bivalve species, providing higher structural complexity (Figure 22). Beds are probably common around New Zealand; being recorded from Cape Reinga to North Cape (Keane 1986, Cryer et al. 2000), Northland (Mimiwhangata, Kerr & Grace 2005), Greater Omaha Bay (Taylor & Morrison 2008), Kawau Bay (Battershill et al. 1985, M.M., pers. obs.), Noises Islands and Tarakihi Island (inner Hauraki Gulf) (Dewas & O’Shea 2011, M.M., pers. obs., respectively), the inner South Taranaki Bight (Gillespie & Nelson 1996 – see Bryozoans), Tasman and Golden bays (Grange et al. 2003), Marlborough Sounds (Davidson et al. 2010), and Foveaux Strait (Michael 2007). McKnight (1969) also recorded them off the Manukau Harbour entrance, Hawkes Bay, Wanganui, Cape Farewell, Tasman Bay, Cape Palliser, Timaru, Oamuru, near Bligh Sound, and off the entrance to Doubtful Sound, Chalky Island.



Figure 22: Examples of dog cockle (*Tucetona laticostata*) habitat from the Noises Islands, inner Hauraki Gulf. a) surface of a dog cockle bed with dead shell, b) close-up of dead shell lying on sediment surface (note also presence of rhodoliths), c) mixture of dead dog cockles, and live scallop and horse mussel. (Source: S. Dewas, AUT University).

Value and Function

Dead shell accumulations (note that this includes epifaunal bivalves such as scallops and brachiopods), may provide structural complexity for other species on otherwise relatively featureless seafloor. For example, Auster et al. (1991), found significant associations between individual shells of ocean quahog (*Arctica islandica*), and young-of-the-year (0+ juveniles) of ocean pout (*Macrozoarces americanus*), at a 55 m water depth low relief outer continental shelf site, North America. Individuals were found under and alongside hinged and single valves, which were viewed as shelter. In Greater Omaha Bay, research dredge by-catch associated with dead hinged scallop shells included small octopus (Anderson 1997), and clingfish with egg masses (M.M., pers. obs.). In heavily fished epifaunal bivalve populations, dead shell densities may be significantly reduced, through physical removal of live animals as catch and incidental mortality, fewer shellfish growing to larger sizes, mechanical dead shell fragmentation, dispersal of bed shell while being returned as by-catch, and the loss of ‘cementing’ functions provided by associated biota (e.g. sponges and nesting mussels; see Cranfield et al. 1999 for Foveaux Strait examples). Dead shell from species such as *T. laticostata* can last over long time scales, with disarticulated valves collected from the Wanganui Shelf carbon dated at 9170 ± 210 years BP (Gillespie et al. 1998), and relict surface deposits shells from the Bay of Plenty dated at $35\,800 \pm 2250$ years (Beu 2004).

Dewas & O’Shea (2011) quantified dog cockle shell beds (“*large post-mortem deposits*”) around Otara Island (Noises Islands, inner Hauraki Gulf), as well as shell grit and rock gravel. Invertebrate diversities and densities were consistently higher in the dead shell beds over time. Three hundred and fifty one species (or Operational Taxonomic Units, OTUs) were recorded, of which 30% were found only in dead shell habitat, compared to 10.5% being in the shell and rock gravel habitats. Similarly,

Hewitt et al. (2005) sampled dead shell drifts in the Tonga Island Marine Reserve (Tasman Bay), finding significantly higher diversity than in adjacent bare substrates, and concluding that shell debris increased and maintained biodiversity. They emphasised the need to reduce disturbance regimes, and actively manage seafloor habitats in areas previously largely ignored.

Past and current status and threats

Little information is available, beyond the knowledge that direct and indirect fishing effects, and land-based impacts (Morrison et al. 2009) are important threats to many infaunal bivalves, depending on species and environmental context.

Information gaps

In the context of both where beds occur and their extents, and what fisheries values they may provide (beyond direct harvest), there is little data or knowledge available. Given this, where to target further research is open to debate. We suggest that initial research efforts be targeted at species which either directly provide elevated seafloor complexity (e.g., dog cockles), or which may provide an important substrate on which other biogenic habitat formers may grow (e.g. red algal meadows on *T. spissa* shell beds, *Ecklonia radiata* plants on paired dog cockle valves in some settings). Suggested research directions are similar to those for horse mussels.

Suggestions for new research are:

- Use LEK and other methods to identify where coastal infaunal bivalve beds (dog cockles and *T. spissa* beds are suggested candidates) occur in different regions of New Zealand.
- Investigate the use of sidescan sonar and other remote sensing technologies to detect and map beds.
- Undertake fish-habitat surveys to quantify what fisheries species associations are present, allowing for seasonal effects.
- Use modelling to predict more widely where beds are likely to occur, and how these locations relate to bottom fished gears, sedimentation, and other factors deleterious to bivalve bed survival.

Recommended measures

The role of dense infaunal shellfish beds in supporting fisheries species (aside from the shellfish themselves) in New Zealand is unknown. However, they are an important component of coastal habitat landscapes, and given their high biomass densities, are probably good indicators of high primary production areas. They also tend to occur in medium sands to coarser grit seafloor substrates (to which they contribute significant shell material), adding three dimensional complexity, which in turn appears to elevate biodiversity values (Hewitt et al. 2005, Dewas & O'Shea 2011), which may be important for fish foraging. They are known to be sensitive to land-based stressors such as sedimentation, and some species have declined in regions where human activities are dominant, such as the Greater Hauraki Gulf (e.g. pipi and cockles, Grant & Hay 2003, Hartill et al. 2004). Given these factors, and their likely contribution to food-webs supporting commercial finfish species, possible future research focuses in a similar context as that suggested for horse mussels – but with an additional emphasis on how they might contribute to trophic pathways culminating in fisheries species production.

3.6 Sponges (numerous species)

Location

Sponges occur around New Zealand, and are a central component of many rocky reef assemblages, especially below depths at which large algae are able to grow. They also occur across a range of soft sediment systems, where sufficient hard surfaces are available for initial attachment. The term ‘garden’ is used for situations where sponges grow in sufficient abundance and extent to form the dominant cover. In shallow north-eastern New Zealand, this is often on flat reef basements covered by a thin layer of coarse sediment, as well as on more topographically complex reef. Comparatively well studied examples include the “Sponge Garden” (Figure 23a) off Goat Island, Cape Rodney to Cape Okakari Marine Reserve (Battershill 1987), and Spirits Bay at the top of Northland (Figure 23b) (Cryer et al. 2000, Tuck & Hewitt 2011). A number of species are present; the dominant habitat-formers possess morphologies which provide three-dimensional structure off the seafloor, e.g., bowls, finger, tube, and mound forms. For example, Goat Island’s Sponge Garden (about 18–27 m depth, 33 species recorded) is defined by a high density of discrete branching and massive sponges, as well as encrusting sponges, e.g., *Polymastia granulosa*, *Aaptos aaptos*, *Raspailia topsenti*, *Axinella nsp.*, and *Cinachyra nsp.*, and algal species (Battershill 1987).

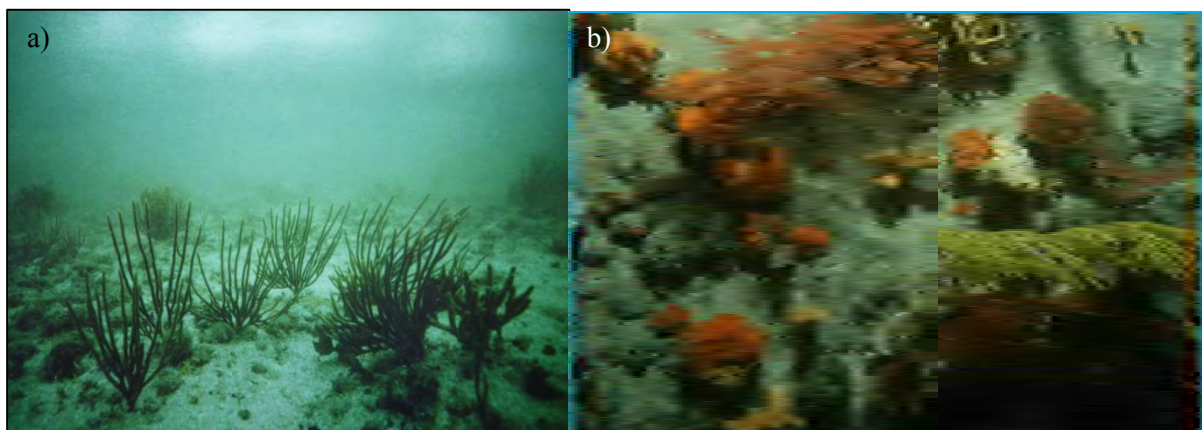


Figure 23: a) the ‘Sponge Garden’ (about 25 m depth) at the Cape Rodney to Cape Okakari Marine Reserve. (Source: Battershill 1987), b) deeper water sponge and gorgonian assemblage (about 70 m depth) off North Cape (Source: TAN1005 voyage).

Value and function

Battershill (1987) completed limited fish counts at Goat Island’s Sponge Garden in 1983 and 1986. Goatfish (*U. porosus*) dominated, but of particular note was the presence of snapper, (8.3 ± 2.3 (s.e.) per 500 m² in 1983, 27 ± 4 in 1986). The significant difference between years was due to an increase in 0+ snapper, with over 85% of fish in 1986 being juveniles (a density of more than 4.6 0+ snapper per 100 m²). It was stated that “*small fish persisted on the reef in large numbers throughout the year and observations made on similar reefs along Northland coasts suggests that these areas are important nursery grounds for a number of commercially important fish species*” (species not given). A further 20 Greater Hauraki Gulf similar sponge characterised reef sites known to the author were given which might also support juvenile snapper (figure 2.1, Battershill 1987).

Shears & Usmar (2003) assessed patch reef fish assemblages of a Cable Protection Zone (in theory a *de facto* marine reserve) in about 33–50 m water depth, west of Great Barrier Island (‘North-west

Reef?) using baited underwater video. Diving on the shallowest reef area, they reported a diverse encrusting invertebrate assemblage including the sponges *Ancorina elata*, *Stellata crater*, *Dendrilla rosea*, *Raspailia sp.* and *Aaptos aaptos*, which provided most of the biogenic structure component. Soft corals (*Alcyonium aurantiacum*) and hydroids (e.g. *Solanderia ericopsis*) also contributed. Twenty fish species were counted: the dominant species were blue cod, leatherjacket, scarlet wrasse, pigfish, snapper, tarakihi, golden snapper and carpet sharks. No snapper under 20 cm were counted, but juvenile blue cod (12–22 cm) were present.

Battershill & Page (1996) undertook a brief dive survey of Pariokariwa Reef, North Taranaki, and described it as having a unique and diverse sponge assemblage (55 species), with affinities with both warm-temperate and cool-temperate/sub-Antarctic faunas, and high biomass. Three main habitat types were noted, two dominated by numerous habitat-forming finger and massive sponge, as well as *E. radiata*. Fish numbers were described as ‘reasonable’ (no fish counts done), with many kingfish seen, and the reef fish assemblage dominated by wrasses (*Notolabrus celidotus*, *Notolabrus fusca*, *Notolabrus miles*), blue cod including juveniles, and red moki. Lost fishing gear including net and rope fragments was common.

Duffy (1992) diver surveyed Hawke Bay shallow rocky reef habitats, including some sponge gardens. At depths of more than 20 m, *E. radiata* cover was very low, and sponges (*Ancorina*, *Stellata*, *Callyspongia*, *Raspailia*), the hydroid *S. johnstoni*, and red algae dominated. Associated fish species included sea perch (*Helicolenus percooides*), half-banded perch (*Ellerkeldia huntii*) scarlet wrasse (*Pseudolabrus miles*), blue cod, large butterfly perch schools (*Caesioperca lepidoptera*) and sweep (*Scorpius lineolatus*). Further south, Cole (2000) mentions sponge gardens as being dominant in depths of more than 12 m on rocky reef sites north-east of Nelson, dominated by *Ancorina*, *Ircinia*, *Callyspongia*, *Crella*, and *Iophon*, as well as ascidians (*Cnemidocarpa*). Few fish were observed, but included some juvenile leatherjackets and tarakihi.

At greater water depths (more than 30 m) our very limited knowledge of sponge communities and associated fish assemblages declines to almost nothing. Off the eastern side of Rakitu Island, Great Barrier Island, Hauraki Gulf, limited camera surveys of the deeper reef systems (55–120 m) found them to be dominated by sponge species, including some larger habitat formers (Morrison et al. 2001, Sivaguru & Grace 2002). Substantial siltation was evident at some sites. Unrelated baited underwater video (BUV) work in the same general area recorded 32 fish species, including snapper and tarakihi (smallest size 22 cm) (Langlois et al. 2006). Trevally were the most common species, followed by golden snapper (*Centroberyx affinis*), sea perch (*Helicolenus percooides*), tarakihi (*Nemodactylus macropterus*), pink maomao, northern spiny dogfish (*Squalus griffini*), pigfish (*Bodianus unimaculatus*), butterfly perch, snapper, and leatherjackets. No other deeper continental shelf sponge garden information is available, although these habitats are likely to be common and widespread (e.g. OS2020 Bay of Islands programme, and ZBD20081 Biogenic Habitats unpubl. data).

New Zealand is not alone in its paucity of work on temperate sponge assemblages and potential fisheries functions. In a review of the functional role of sponges, Bell (2008) described a range of ecological functions in detail, but made no mention of their potential or known role in helping support fish or fisheries species. In the single study we could find (but see also Sainsbury 1988), work on New South Wales wrasse (labrid) reef assemblage quantified fish abundances and sizes across reef fringe habitats (3–7 m, patchy non-dominant algal species), urchin barrens (8–15 m), high sea urchin (*Centrostephanus rodgersii*) densities), and sponge gardens (15–22 m) (Morton & Gladstone 2011). The strongest and most consistent habitat associations were found with the sponge gardens, which

also had the most distinct fish assemblage, highest species richness, and highest individual densities. High seasonal abundances of Southern Maori wrasse (*Ophthalmolepis lineolatus*) recruits (50–99 mm) occurred in the sponge garden, while crimsonband wrasse (*Notolabrus gymnogenis*) and blue groper (*Achoerodus viridis*) selected fringe (algal) habitats. Larger individuals of these species occurred much more widely, indicating large ontogenetic habitat shifts subsequent to recruitment. Overall, it was concluded that sponge gardens were biodiverse areas, and as such deserved “*special consideration in the conservation of rocky-reef fishes*” (Gladstone 2007, cited in Morton & Gladstone 2011). An important additional point was that ontogenetic habitat use (connectivity) had largely been ignored in survey designs for temperate reef fish surveys, and was probably strongly under-represented in the scientific literature.

Past and current status and threats

There is little information available on threats to sponge gardens in New Zealand. In the Leigh Marine Reserve, Parsons et al. (2004) compared biological reef community habitat maps created in 1978 (from dive surveys, see Ayling 1978), against maps created in 2000. Over this 22 year period, sponge gardens (more than 12 m water depth) declined from 47% to 14% cover (66% decline), as did kelp forest (49 to 24%, 50% decline). Both were replaced by turfing algae, which increased from 2% to 52% (a 2600% increase). Turfing algae are more resistant to sedimentation than sponges and kelps, and this was the mechanism proposed to be driving these shifts, along with interactions with kelp (*E. radiata*) die-backs from disease. Bottom sediments in 2000 were composed of a mixture of size grades, with finer grades sitting within the turf (D. Parsons, pers. comm.). Inner Goat Island Bay often experiences fine silt plumes extending into the bay during heavy rain-fall events, which discolour the water brown, so land-based sediment inputs probably played a central role, although no direct evidence exists.

At a much broader spatial scale, sampling of the upper east Northland continental shelf (North Cape to Poor Knights) observed an apparent large-scale sedimentation gradient on deep reef systems (50–200 m) (os2020.org.nz, Morrison et al. 2010). No formal analyses are available, but video observations indicated that the more southerly reef systems were covered by fine silt layers, with putatively lower biodiversity, while the more northerly reef systems (Ranganui Bay and north) appeared to be relatively silt free, and with higher biodiversity. Similar observations along the lower East Coast of the North Island (Mahia Peninsula to Ranfurly Bank) in 2010 also suggested a large scale and substantial sedimentation gradient in that region’s deep reefs, with an inverse relationship between increasing epifaunal biodiversity, and decreasing fine sediment cover (Morrison & Jones, pers. obs.). As these patterns are at the hundreds of kilometres (bioregion) scale, they are concerning, and suggest that significant sedimentation impacts have and are occurring with little or no human awareness of them. No information exists on what has historically occurred, or is now occurring, in terms of land-based activities’ impacts on these communities (Morrison et al. 2009).

Fishing is the other key stressor on sponge assemblages (Figure 24), although assemblages on rougher ground have some natural protection from disturbance by actively towed gears. Little information is available in the New Zealand context, aside from in high profile areas such as Spirits Bay where dredging (and possibly trawling) has reduced high epifaunal biodiversity, including sponges, and the fishery has subsequently been closed in some areas (Tuck & Hewitt 2011).



Figure 24: Research trawl sponge by-catch off Cape Reinga (1980s). Associated fish species include structure associated species (sea perch and leatherjackets), as well as habitat generalists such as an eagle ray, school shark, and porcupine fish. (Source: Unknown).

Information gaps

New Zealand (non-taxonomy) sponge habitat studies have been small-scale, variable in methodology and taxonomic resolution, and not focussed on fisheries species associations, beyond broad descriptions of fish seen. Most research has also been at shallow water depths, given the limits of SCUBA diving, yet the great majority of sponge assemblages are found at depths greater than 30 metres. For example, very extensive areas of deeper continental shelf reefs occur off North Cape on the Reinga Shelf (Morrison & Jones 2011), along the East Northland coast (Morrison et al. 2010), and south of Stewart Island (unpubl. multibeam imagery, NIWA). Sponge gardens also occur on some soft sediment systems, such as the “Hay Paddock” sponge assemblage off Oamaru (about 70 m water depth) (Morrison & Jones 2011). Given this, large and fundamental information gaps exist.

Suggestions for new research are:

- Battershill (1987) suggested the existence of numerous sponge garden snapper nursery habitats in the Hauraki Gulf. Juvenile snapper respond to structural complexity in general, and so this is likely; we suspect that juveniles of other species such as trevally may also be found in association with sponges in higher current areas. Work should focus on the nature and extent of these sponge gardens, their fisheries species associations, and ideally (as with all other biogenic habitats), what proportion of snapper recruitment (or other species/functions) they contribute to fisheries production.
- The visual evidence of large scale degradation of continental shelf reefs in upper East Northland and along the lower east North Island is disturbing, and suggests fundamental human impacts which we are not yet aware of both there and elsewhere. These data need to be processed and analysed, along with any additional field measures required, and explored in terms of ‘is significant degradation occurring?, and if so, what management measures can be implemented?’.

- More broadly, investigate sponge assemblages in other regions of New Zealand in terms of what they are, and what fisheries species they may support. This needs to encompass both shallow coastal and deeper continental shelf environments, on both rock reefs and soft sediment seafloors. The Hay Paddock, as a possible unique biogenic habitat assemblage, should be further investigated, including seasonal sampling of its associated fish species to quantify if it is providing a suspected nursery function for species such as terakihi (Vooren 1975).

Recommended measures

Sponge assemblages (gardens) should be explicitly included in spatial fisheries management regimes, and their potential fisheries species linkages allowed for as they become known. That includes protection of high complexity sponge areas (gardens) from fisheries gear interactions, and mitigation of sedimentation and other land-based impacts as possible.

3.7 Bryozoan reefs and/or accumulations

Location

Bryozoans are colonial colony forming animals, with colony sizes ranging from very small (millimetre scale) to large (metre scale), depending on species; and a wide calcification; from very weakly calcified forms such as vittaticellid (catenicellidae) species (generally large, bushy, coloured and with inwardly curling morphologies) through to heavily calcified, massive forms, which may form biogenic reefs. Of the 903 identified bryozoan species of New Zealand (D. Gordon, pers. comm., in Batson & Probert 2000), a sub-set of larger sized bryozoan species are ‘frame-builders’ (Duncan 1957), with Wood et al. (2012) defining these as “*species that regularly grow to ≥ 50 mm in three dimensions*” (as in Batson & Probert (2000)). Of these, some are ‘habitat-formers’ (Turner et al. 1999, Bruno et al. 2003). Wood et al. (2012) defined the most relevant habitat-former scale as being “*those cases where frame-building bryozoans dominate (at least) square metres of seafloor and thereby contribute significantly to the habitat complexity of the locality*” (this includes at least 27 New Zealand species). As with many biogenic habitat-forming species, Wood et al. reported habitat-forming bryozoans as occurring in a range of assemblage dominance settings, including as single species (Cocito et al. 2000), as mixed bryozoan assemblages (Batson & Probert 2000, Harmelin & Capo 2001), and as a component of wider biogenic habitat assemblages including algae, sea-grasses, hydroids, sponges, gorgonians, bivalves, and ascidians (Stebbing 1971, Lindberg & Stanton 1988, Cranfield et al. 1999, Cryer et al. 2000, Morgado & Tanaka 2001, Lombardi et al. 2008) (Figure 25).

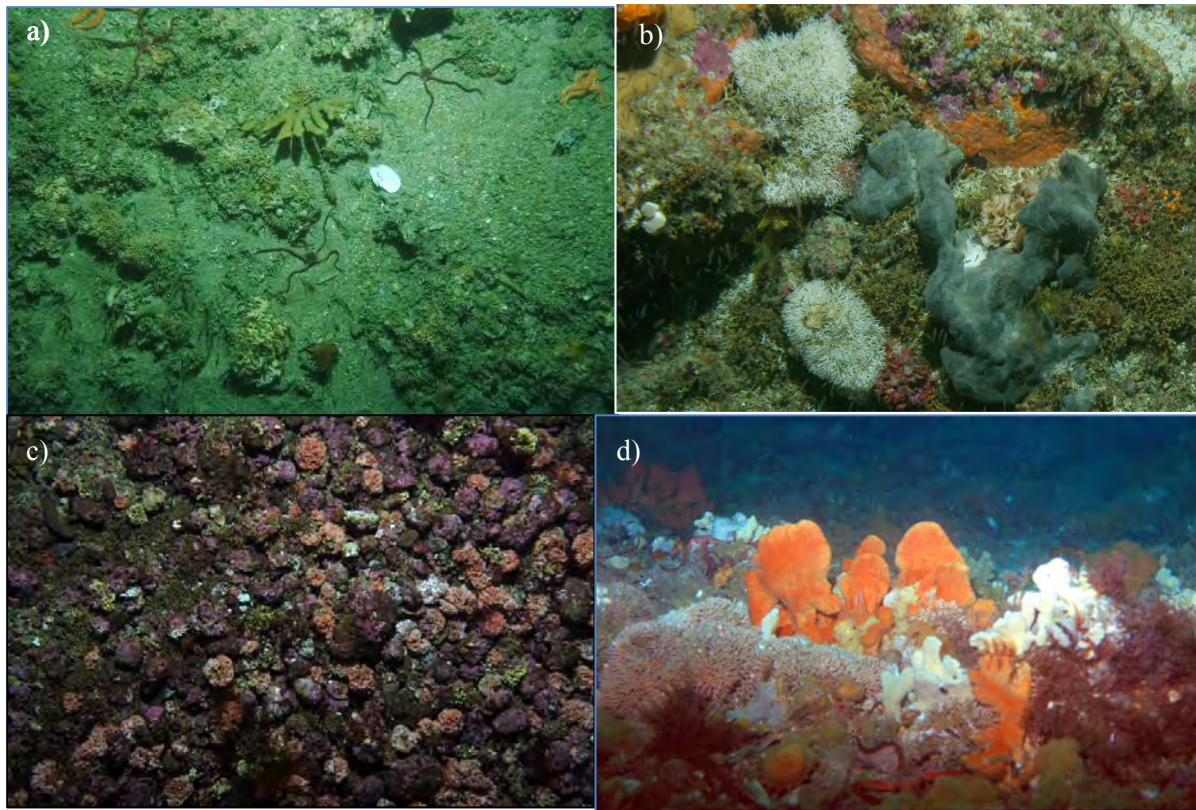


Figure 25: a) Otago Shelf bryozoan thickets, dominated by *Cintopora elegans* colonies, with juvenile sleeping blue cod, about 8 cm (centre of image) and quartz pebbles/gravel which may underpin colony development (Source: DTIS, TAN1108); b) Three Kings bryozoans, possibly a *Idmidronea* sp. (white), *Tetrocycloecia neozelanica* (brown), and *Reteporella* sp. (orange) (TAN1105); c) *Hippellozoon novaezelandiae* colonies at Three Kings Islands (TAN1005), d) Dense bryozoan colonies (*C. elegans*, central left), sponges, and red algae assemblage at 32 m water depth, in a high current area near the entrance to Paterson Inlet (Source: NIWA).

Batson & Probert (2000) reviewed the knowledge on New Zealand bryozoans and identified seven areas/regions which supported bryozoan species as a dominant seafloor habitat (Table 2). Most of these areas occurred on the continental shelf, across a range of water depths, including shallower coastal locations (Paterson Inlet/Foveaux Strait, Separation Point), the coastal shelf (Wanganui and Otago), and on shelf extensions from mainland New Zealand (South Maria Ridge, and Snares Platform). Taylor (2000) suggested that two key factors were associated with the successful colonisation of areas by bryozoans: suitable hard substrates such as rocks and shells; and a sufficient phytoplankton food supply. Adverse factors for colonisation were higher sedimentation and/or disturbance, and stagnant conditions. Batson & Probert (2000) listed the environmental parameters associated with New Zealand's main bryozoan areas, with all of them associated with biogenic carbonate sediments, strong tidal currents and/or high energy regimes, and apparently low sedimentation regimes. The one exception was Separation Point, where muddy seafloor sediments dominate. There is a suggestion that this location was historically much less sedimented, and the present-day bryozoan assemblages were established during conditions similar to those of the other bryozoan areas (see Separation Point section below). Wood et al. (2012) reported that in the New Zealand context, the larger bryozoan areas were associated with productive upwelling or mixing zones (Rowden et al. 2004): including a upwelling zone (Stanton 1973) in the Spirits and Tom Bowling Bays area (Cryer et al. 2000); and the constriction of the dominant Southland Current, with

associated current velocity increase, by the Otago Peninsula (Probert et al. 1979, Russell & Vennell 2009). On the South Taranaki Bight, off Wanganui, bryozoan beds are found in association with dog cockle beds, and occur across a range between sandier inshore sediments, and muddier offshore sediments (Figure 26), and cover about 2000 km².

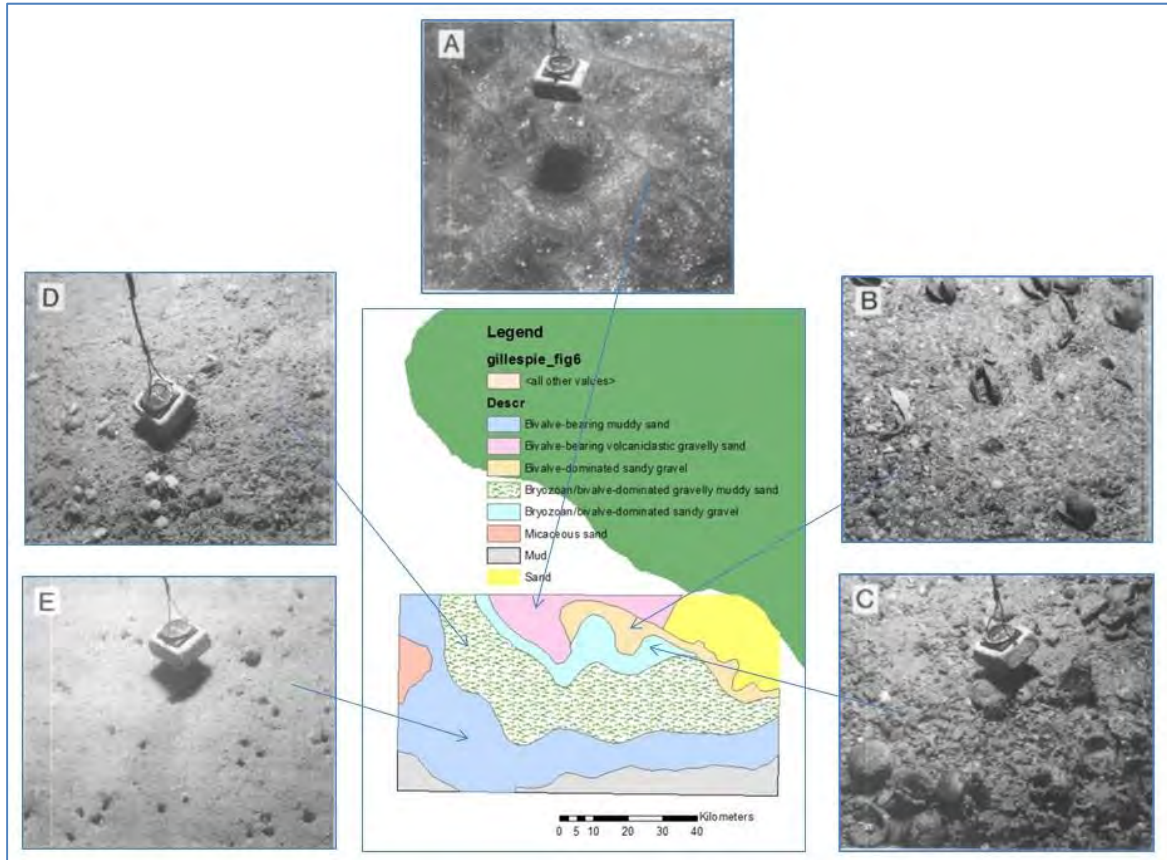


Figure 26: Seabed photographs of Wanganui Shelf seafloor (the compass is 8 cm across). A) Bottom type of rippled, terrigenous dominated shelly black sands; B) Bottom type of mainly dog cockle's *G. modesta* and *T. laticostata* shells and shell fragments; C) Bottom type of abundant living and dead *T. laticostata* provide a primary substrate for other organisms; D) Bottom type of bryozoans and scallop *Taochlamys gemmulata* occur in clumps on the muddy seafloor; E) Bottom 3 of sediments of mainly terrigenous muddy sands with only moderate skeletal material. Source: Gillespie & Nelson (1996).

Table 2: The location and relevant environmental parameters of seven New Zealand locations where bryozoan thickets or bryozoan-dominated sediments have been recorded as dominant seafloor habitat (modified from Batson & Probert 2000).

Location	Position and extent of bryozoan beds	Depth (m)	Hydraulic regime	Substratum	Dominant Bryozoa*	Associated fisheries species	References
South Maria Ridge	Off North Cape; 10 000 km ² (includes Three Kings Platform)	< 500	High energy, open shelf	CaCO ₃ gravels	<i>Steginoporella magnifica</i> , <i>Celleporina grandis</i> , <i>Celleporaria</i> sp, <i>Hippellozoon novaezelandiae</i> , <i>Iodictyum yaldwyni</i> , <i>Phidolopora avicularis</i> , <i>Galeopsis</i> spp, <i>Hornera robusta</i> , <i>Metroperiella mucronifera</i>		Nelson & Hancock (1984)
Tom Bowling / Spirits Bay	Across the top of the Northland Isthmus, >100 km ²	30–80	High energy open shelf, strong tidal flows	CaCO ₃ sediments, sands, gravels, reef	<i>Celleporaria agglutinans</i> , <i>Hornera</i> spp., <i>Diaperoecia purpurascens</i> , <i>Tetorcyloecia neozelanica</i> , <i>Calvetia</i> n. sp., <i>Galeopsis polyporus</i> , <i>Galeopsis porcellanicus</i> , <i>Celleporina sinuata</i> , <i>Spiritopora</i> n. sp., <i>Arachnopusia unicornus</i> , <i>Microporella</i> ordo	Scallops	Cryer et al. (2000)
Wanganui shelf	Wanganui mid-shelf; approx. 2 000 km ²	50–80	Variable	CaCO ₃ sandy gravels	<i>C. grandis</i> , <i>Adeonellopsis</i> spp	Leatherjackets	Gillespie & Nelson (1996)
Separation Point	Tasman Bay; <300 km ²	10–35	Strong tidal flows	Mud-rich, some gravel	<i>C. agglutinans</i> , <i>Hippomenella vellicata</i>	Tarakihi, snapper, John dory, red and blue cod	Bradstock & Gordon (1983)
Otago Shelf	Off Otago Peninsula; at least 100 km ²	70–120	High current velocities off Peninsula	CaCO ₃ gravels	<i>Cinctipora elegans</i> , <i>H. robusta</i> , <i>Adeonellopsis</i> spp, <i>C. grandis</i> , <i>C. agglutinans</i> , <i>Cellaria immersa</i> , fenestrate cheilostomes, <i>Otionellina</i> spp	Blue cod, red cod, southern pigfish	Probert et al. (1979), Batson (2000)
Foveaux Strait	Western Foveaux Strait; Historically bryozoan beds much larger	25–45	Strong tidal flows	Terrigenous/ CaCO ₃ gravels	<i>C. elegans</i> , <i>Hippomenella vellicata</i> , Catenicellids	Blue cod, oysters	Fleming (1952), Cranfield et al. (1999)
Paterson Inlet	Localised at inlet entrance; patchy thickets	<25	Moderate to strong tidal currents	Gravels	<i>C. elegans</i> , Cyclostomata		Willan (1981)
Snares Platform	South of Stewart Island; 50 000 km ²	< 250	High energy, open shelf	CaCO ₃ gravels	<i>C. elegans</i> , <i>D. purpurascens</i> , <i>Galeopsis</i> spp, <i>Foveolaria cyclops</i>		Nelson et al. (1988)

The Separation Point bryozoan beds are dominated by the large frame builder *C. agglutinans*, which forms large mounds which cover some 55 km² of seafloor (as of 2003, Grange et al. 2003) (Figure 27). These are protected within a larger 156 km² zone, where all power-fishing methods have been banned since 1980 (Mace 1981). Approximately an additional 300 km² of foliaceous colonies of *Hippomenella vellicata* ('paper coral') at Torrent Bay were eliminated by fishing by the end of the 1960s (estimated from figure in Saxton 1980b, in Wood et al. 2012), and are thought not to have recovered (Grange et al. 2003). In 1982, limited diving observations at Separation point reported *C. agglutinans* covering up to 50% of the seafloor, with colonies to 50 cm high. The area was very turbid, with low levels of light penetration and considerable tidal currents (Bradstock & Gordon 1983). In 2002, the full extent of the protected area was mapped using side-scan sonar, and ground-truthed using a remote operated vehicle (ROV) (Grange et al. 2003). Bryozoan mound cover was estimated at 55 km², covering 38% of the protected area. There was also the suggestion of bryozoan mounds occurring outside the protected area.

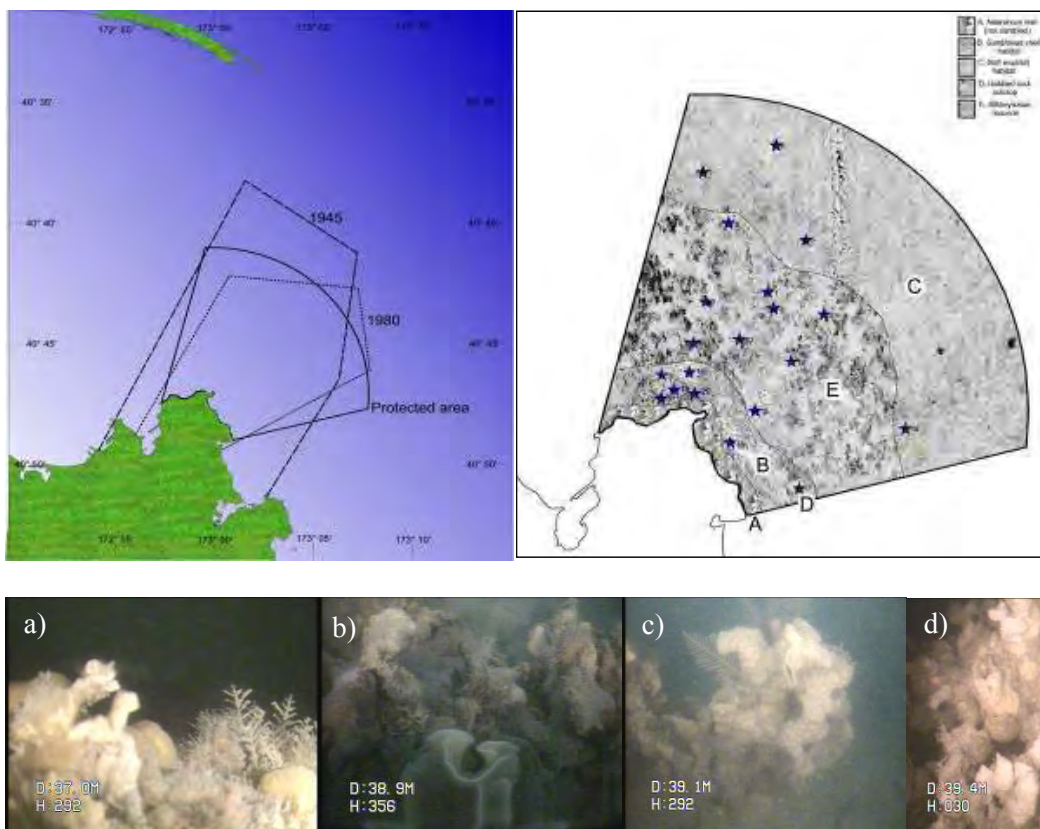


Figure 27: top) Separation Point bryozoan bed protected area, and extent of the beds themselves (1945, 1980, based on fisher observations), and present day bed extent (habitat 'E', determined by sidescan sonar: Separation Point bryozoan mounds; a) hydroids and sponges, b) bryozoan (*Hippomenella*) and encrusting fauna, c) bryozoan (*Celleporaria*) and hydroids, d) bryozoan colony (*Celleporaria*) (Source: K. Grange, NIWA.).

The Otago bryozoan beds occur where the dominant Southland current accelerates as it passes northwards around the constriction of the peninsula, with surface currents of up to 26 cm s⁻¹ (Carter et al. 1985). The mid-shelf is dominated by gravels mainly composed of iron-stained quartz pebbles, thought to be relic terrigenous gravel from rivers once emptying material into this area (Carter et al. 1985), and which forms a hard substrate for bryozoan colonies. Batson & Probert (2000) found high bryozoan abundance to be restricted to a relatively narrow 75 to 110 m depth range band. The seven frame-builders mostly overlapped in their distribution, although two species (*C. grandis* and

Adeonellopsis spp.) extended slightly deeper (to 110–120 m) than the other five species. Colonies were patchily distributed, and abundances often changed markedly.

In Paterson Inlet, Willan (1981) described a number of species assemblages, including coarse material (in particular shell gravel) accumulations in areas of moderate to strong currents often colonised by bryozoans (especially *C. elegans*), growing in large mounds up to 15 cm tall and 50 cm across (Figure 25d). Associated species included ascidians, sponges and tubicolous polychaetes, along with nesting bivalves, chitons and brachiopods in the clump interstices. Willan (1981) also noted that *C. elegans* was dominant on the mid Otago Shelf (Probert et al. 1979), and that recent (with respect to 1981) NZOI cruises had also collected it on the Mernoo and Veryan Banks (Chatham Rise).

No information is available for the Snares Plateau.

Value and function

The role of bryozoan reefs in supporting fisheries function has often been proposed, but solid empirical evidence is scant, aside from some work on blue cod in Foveaux Strait (e.g. Carbines & Cole 2009). At Spirits Bay, Tuck & Hewitt (2011) suggested that the diverse three-dimensional epifauna (including bryozoans) could potentially be providing important settlement surfaces for scallop spat, based on observations elsewhere. However, while the specific area sampled by Cryer et al. (2000) supported high biomass scallop harvests for several years following its discovery, by the time of first sampling in January 1999, few adult scallops were found, and no scallop spat. Possible fisheries functions for the Wangaunu Shelf beds are unknown, though most of New Zealand commercial leatherjacket catch comes from the South Taranaki Bight, and this species is strongly associated with biogenic habitats.

The Separation Point beds have been very widely cited as a key example of the role of bryozoans in providing juvenile fish nurseries, in particular for snapper and tarakihi. Fishers reported catching large number of small fish such as snapper and tarakihi here (small is not defined specifically) and following concerns of habitat damage (or rather over-fishing of small fish) Separation Point was closed to power fishing in 1980. Vooren (1975) reviewed available information on where juvenile tarakihi grounds might occur around New Zealand, and reported that the Golden / Tasman Bay area was an important nursery ground (based on higher juvenile abundances) (Figure 28). Vooren stated “*the Tasman Bay nursery ground coincides with an area known among the local fishermen as "the coral", containing an extremely rich benthic epifauna of sponges and small corals... In the north-eastern part of Tasman Bay, where a minor concentration of young tarakihi was found in 1970, a small area of "coral" is also said to exist. The trawl net of James Cook [research vessel] brought up large quantities of this material at most stations where young tarakihi were abundant, especially in the centre of the nursery ground. The young tarakihi in Tasman Bay are evidently closely associated with areas of a rich benthic epifauna of the type mentioned. ... The author was not competent in this field, and no samples of the epifauna were taken during the present study. Research on this important aspect of the nursery remains a task for the future*”. In the 1970 trawl survey of the area, tarakihi, red gurnard, leather jacket, and snapper dominated the catch (kg per hour), while red cod and blue cod were small and common (Vooren 1975). He concluded that young tarakihi (under 27 cm) were found almost exclusively in 20–45 m water depth, in a zone extending from Farewell Spit to the south-eastern shore of Tasman Bay (Figure 28). He called this zone the ‘nursery ground’, estimated to be between 18 and 33 km wide and about 75 km long, with a total area of about 2000 km² (however, examination of his figure (Figure 28) suggests the actual area to be much smaller, based on where

high juvenile abundances were caught). Most of the juvenile catch also came from outside of Separation Point stations, with little sampling of the Separation Point area. Vooren (1975) and fisher accounts in Saxton (1980a, b) are the two data sources on which the fisheries nursery importance of Separation Point are based. Neither would meet the empirical data standards required today to show a nursery function. The 2002 Separation Point ROV survey sighted barracouta (*Thyrstites atun*), tarakihi, blue cod, and leatherjackets (Grange et al. 2003). Bryozoan mounds included many bryozoan species, as well as brachiopods (*Liothyrella neozelanica*), sponges (e.g., *Callyspongia*), hydroids, and horse mussels (see lower row, Figure 27).

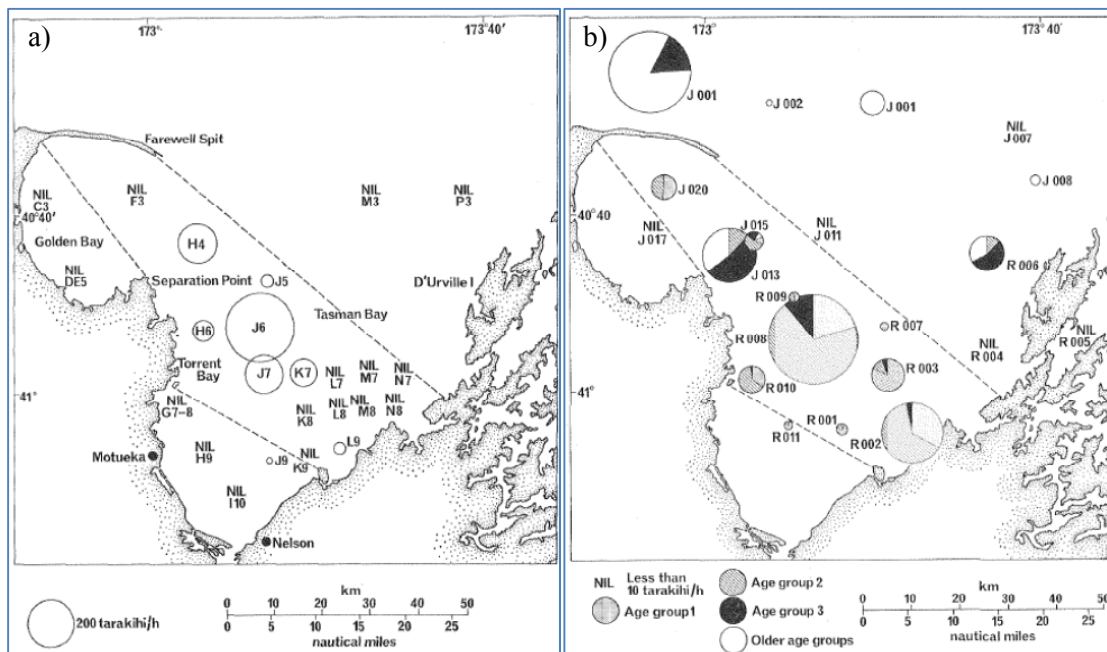


Figure 28: Catch rates of tarakihi from Tasman Bay trawl surveys, a) 1963, b) 1970). The broken lines denote the estimated nursery area extent. (Source: Vooren 1975).

On the Otago Shelf, Batson & Probert (2000) noted that numerous hydroids, ascidians, brachiopods, barnacles, serpulid tubeworms, and sponges colonised large bryozoan colonies, while larger *H. vellicata* colonies often held mobile megabenthos, such as ophiuroids, gastropods, bivalves, octopus, crabs, shrimps (including the abundant galatheoid *Munida gregaria*), and small fish (Batson 2000). Fish included juvenile blue cod and red cod (*Pseudophycis bachus*) as captured by dredge and underwater photographs (Batson 2000). Seafloor images showed reasonably discrete patches of bryozoans (referred to as thickets) and associated mega-fauna (e.g., sponges, hydroids, ascidians, and horse mussels) separated by open gravel (Batson 2000). Jones (2006) estimated a mean thicket cover of 4% through the central area, with up to 56% cover at some places. The same spatial arrangement was also seen in the Biogenic Habitats TAN1108 voyage, which found numbers of juvenile blue cod (e.g. Figure 25a) along with slightly lower numbers of juvenile southern pigfish (*Congiopodus leucopaecilus*). Batson & Probert (2000) noted that in the United Kingdom, juvenile queen scallops preferentially settled on genus *Cellaria* bryozoans (Mason 1983), and while settlement had not been observed, *Cellaria immersa* and *Cellaria tenuirostris* were abundant off the Otago Peninsula, as were queen scallops (*Zygochlamys delicatula*).

Foveaux Strait biogenic reefs support several fisheries species, most notably blue cod and oysters. Jiang & Carbines (2002) assessed blue cod diet at fished and unfished biogenic reefs (two locations,

each with a fished and unfished site). Blue cod from the disturbed sites consumed larger proportions of crustaceans, while those from undisturbed sites had a more diverse diet; with the conclusion that fishing reduced prey choices, and that the protection of biogenic reefs should be undertaken to protect the productivity of the blue cod fishery. However, no empirical evidence was given to link prey diversity to blue cod productivity. Carbines (2004a) aged some of these fish, and found no significant growth differences at one paired site location, but significant differences at the other (for both males and females). Paired t-tests by age class found differences to be “*biologically significant*” for only the the youngest blue cod sampled (3 years), with fish at the undisturbed site being on average 20% larger in length. This was attributed to oyster dredging effects, although a lack of effect at the other paired site location remained unexplained, as did an absence of growth effect in older age classes at the significant location.

Carbines & Cole (2009) assessed the demersal fish assemblages of two adjacent sites, putatively differing only in fishing disturbance: one not fished for seven years, the other recently dredged. Overall fish densities were 32.5 times higher on the recovering site in summer; reducing to 4.9 times by autumn; driven by a five-fold increase in dogfish (*Squalus acanthias*). Excluding this species, the autumn difference was 31.8 times higher. Seven fish species were present on the recovering site in summer (172 fish, mean density 5.20 ± 0.91 per 100 m², 81% blue cod), with only dogfish on the dredged site (5 fish, 0.16 ± 0.03 per 100 m²). In autumn, four demersal fish species were seen on the recovering site (153 fish, 3.78 ± 0.91 per 100 m², 80% blue cod) and three on the dredged site (27 fish, 0.76 ± 0.21 per 100 m², 89% dogfish). Habitat effects were significant for brown phase, blue phase, total blue cod, and leatherjacket. Season effects were significant for dogfish, while for all other species (tarakihi, blue moki, scarlet wrasse *Pseudolabrus miles*, and sea-perch) there were no significant effects. Sponge and macro-algal cover, topographic complexity and general epifaunal cover were orders of magnitude greater at the recovering site, while tunicate and ophiuroid were higher in the dredged area. Fish and habitat variable comparisons found sponge cover to be significantly positively correlated with blue cod densities (all classes), leatherjackets and scarlet wrasse. Topographic complexity, general epifauna cover, and macro-algae cover also correlated significantly with brown and blue phase blue cod, and leatherjackets. Carbines & Cole (2009) acknowledged study design limitations (unable to control fishing effort), but argued that the two sites were chosen to be as similar to each other in all aspects, apart from their fishing history. They concluded that “*this un-replicated “natural” experiment without pre-dredging observations in the treatments clearly implies that on-going disturbance and reduction of complexity of seabed habitat by oyster dredging drastically reduces the diversity and abundances of demersal fishes in that area.*” Predation was suggested as the underlying mechanism (Connell & Jones 1991, Gotceitas et al. 1995a, b, Tupper & Boutilier 1995, Lindholm et al., 1999; Johnson 2006).

Past and current status and threats

No information is available for the Three Kings/South Maria Ridge area, although a seafloor trough between there and mainland New Zealand is thought to minimise land-derived sediment inputs. The biodiverse Spirits Bay area is now closed to all mobile fishing gears, although recovery potentials are unknown.

On the Wanganui Shelf, Gillespie & Nelson (1996) concluded that the bryozoan/dog-cockle beds were present as “*small lenses within predominantly terrigenous [sediment] systems (Mount 1984, Nelson 1988)*”, and that eventually sediment inputs would reach a level that exceeded their tolerances, and they would ‘drown’ (e.g., Simone & Carannante 1988, cited by Gillespie & Nelson 1996). It was

argued that physical processes helped maintain the carbonate producing zone (bryozoans/bivalves), but also restricted its distribution, with high energy shallower waters preventing the survival of delicate organisms such as branching bryozoan colonies (found at 50–80 m depth zone); while at deeper depths mud accumulation prevented biogenic species from establishing. The biogenic habitat itself provided positive facilitation by providing recruitment surfaces, while high nutrient levels provided by the D’Urville Current enhanced growth. However, Gillespie & Nelson noted that the carbonate zone was slowly being encroached upon and covered by both inshore and offshore sediments based on piston sediment core samples. Recent impact assessment studies on potential iron sand extraction have also noted probable fishing damage to the bryozoan beds, in terms of reduced community structure and smaller colony sizes than might be expected (T. Anderson, NIWA, pers. comm.).

At Separation Point and Torrent Bay, the presence of bryozoans was first noticed by commercial fishers in the 1940s. As fishing technologies improved, these habitats were opened up to trawling. Targeted fishing of the Torrent Bay bed/s, dominated by the more brittle *H. vellicata* (‘paper coral’), reduced both bryozoan abundance, and the proportions of juvenile fish (snapper and tarakihi) in the catch (Saxton 1980a). These beds could not be located in 2011 using multibeam sonar and DTIS (TAN1108 voyage), and are presumed to have never recovered from the fishing impacts, with Grange et al. (2003) suggesting the mechanism being a lack of hard settlement surfaces. At Separation Point, the more robust *C. agglutinans* dominated community helped to protect this area from fishing until 1972–74, when the introduction of pair trawling enabled fishers to fly their nets over the area (Grange et al. 2003). Significant damage commenced, and by 1979 there was concern among fishers that these beds would be destroyed (along with their important fish nursery functions), as they observed reductions in the numbers of juvenile snapper and tarakihi being caught (Saxton 1980a). In 1980 the Separation Point area was closed to power fishing.

Survey work in 2003 (23 years later) observed many bryozoan colonies to be covered by a silt film and growing only from the distal tips, suggesting sedimentation stress (Grange et al. 2003). Bryozoan mounds are generally rare in silty environments (Batson & Probert 2000, Wood et al. 2012), yet the Separation Point seafloor is dominated by soft muds and silts. One hypothesis is that coarser surface sediments were once present which allowed bryozoan settlement, before heavy sedimentation arrived following human forest clearances. A Tasman/Golden Bays hydrographic model (with suspended sediment loads) has shown that with the right combination of river flows and wind, the Motueka River can influence western Tasman Bay, and during flood conditions extend around Separation Point into Golden Bay (Tuckey et al. 2006). This suggests that adverse land-based impacts from sedimentation may be significant (Grange et al. 2003), despite full protection from power fishing methods. It is highly likely that the historical fisheries functions of Tasman and Golden Bay bryozoan beds have declined heavily into the present day.

For the Otago Shelf, Batson & Probert (2000) interviewed local fishers to assess possible interactions between local fisheries and the bryozoan thicket grounds, and to generate a fishing history of the area. Dredge and trawl fisheries date back to the late 1800s (Brett 1999), when bottom trawling of the shelf was undertaken by up to three vessels (mainly targeting barracouta (*Thyrsites atun*) and red cod). Fishing of the bryozoan grounds was probably of low intensity, given the easily damaged natural fibre nets. Fishing pressure increased from the 1960s, with parts of the bryozoan grounds being trawled for red cod, tarakihi, silver warehou (*Seriola punctata*), and rig (*Mustelus lenticulatus*). Some fishers still avoided some parts of the bryozoan grounds to avoid gear damage. Intensity and extent of this fishing could not be quantified, but occasional large catches of ‘cornflakes’ (bryozoans) were made in

water depths of 70–100 m. It was reported that few fish were taken in such shots, and fishers would subsequently move to other areas. Bryozoans were also reported as being very patchy in their distribution. Joint venture vessels have also fished in the general area since the 1960/70s, using steel bobbins and synthetic nets. The Otago shelf queen scallop fishery operates in deeper water (110–150 m) further out on the shelf, and is hence spatially removed from the main bryozoan area. However, occasional large catches of bryozoans are still occasionally made, in particular in an area south of Hoopers Canyon, in 90–110 m water depth. Such patches are actively avoided where possible (Batson & Probert 2000). Since 2002 a voluntary closed area of about 110 km² has been established, but no monitoring of fishing, or mapping of the extent and health of the bryozoan thickets, has taken place. The voluntary closed area is not publicly listed by the New Zealand Ministry for Primary Industries (T. Brett, pers. comm., in Wood et al., 2012).

Arguably the best studied biogenic New Zealand habitats in terms of scale and complexity are the bryozoan reef complexes of Foveaux Strait (Figure 29), which have been dredged for oysters for more than 130 years. Cranfield et al. (1999) used a range of information sources and observations to create a comprehensive history of fishing and associated changes for Foveaux Strait. Before fishing commenced, the Foveaux Strait seafloor was thought to be extensively covered by epifaunal biogenic reefs, composed of tidally-orientated linear aggregations of individual patch reefs. The principal reef component was the bryozoan *C. elegans*, heavily cemented together with other encrusting bryozoan species, ascidians, sponges, and polychaete worms. Bivalves in particular characterised these reefs, especially dredge oysters and several mussel species. Fishers targeted the oysters associated with these reefs, which only occurred at commercial densities in association with the biogenic reefs. Local groups of reefs were exploited (with each group being clearly named). As the biogenic material was removed by fishing, dredge efficiencies improved, so that eventually only oysters remained. Fishing continued until oyster densities declined to commercial extinction, at which time fishers moved onto the next group of reefs (Cranfield et al. 1999). Disease also played a significant role in oyster declines. Cranfield et al. (1999) inferred that the presence of epifaunal reefs may have given oyster populations some resistance to disease, perhaps through some chemical mechanism. Cranfield et al. (1999) also observed that fishers noted lower numbers of recruiting oysters attached to adults in the oyster beds without epifaunal reefs as opposed to those that still contained them, and that maximum oyster sizes were also less in the non-epifaunal reef beds, suggesting growth interactions. In 1999, it was estimated that 58 million m³ of coarse biogenic sediment was held within a large dune system in southwest Foveaux Strait, transported from the southern Strait as a result of reef destruction. Overall, it was stated that if the percentage of finer sediments found in present day reefs was taken into account, then the total volume of sediment likely to have been lost by fishing was likely to be in the order of hundreds of millions of tons since fishing began 135 years ago (Cranfield et al. 2003). Cranfield et al. (2004) suggested a successional habitats model that described the interactions between oysters, bryozoans, and other associated species.

However, Michael (2007) had a strong and fundamentally opposed view to the dynamics between oysters, blue cod, and bryozoans, and disagreed with most of the work published by Cranfield, Carbones, and others. The arguments are too detailed and complicated to include here, but the unpublished report is available from MPI Wellington.

No information was available for Paterson Inlet, or the Snares Plateau.

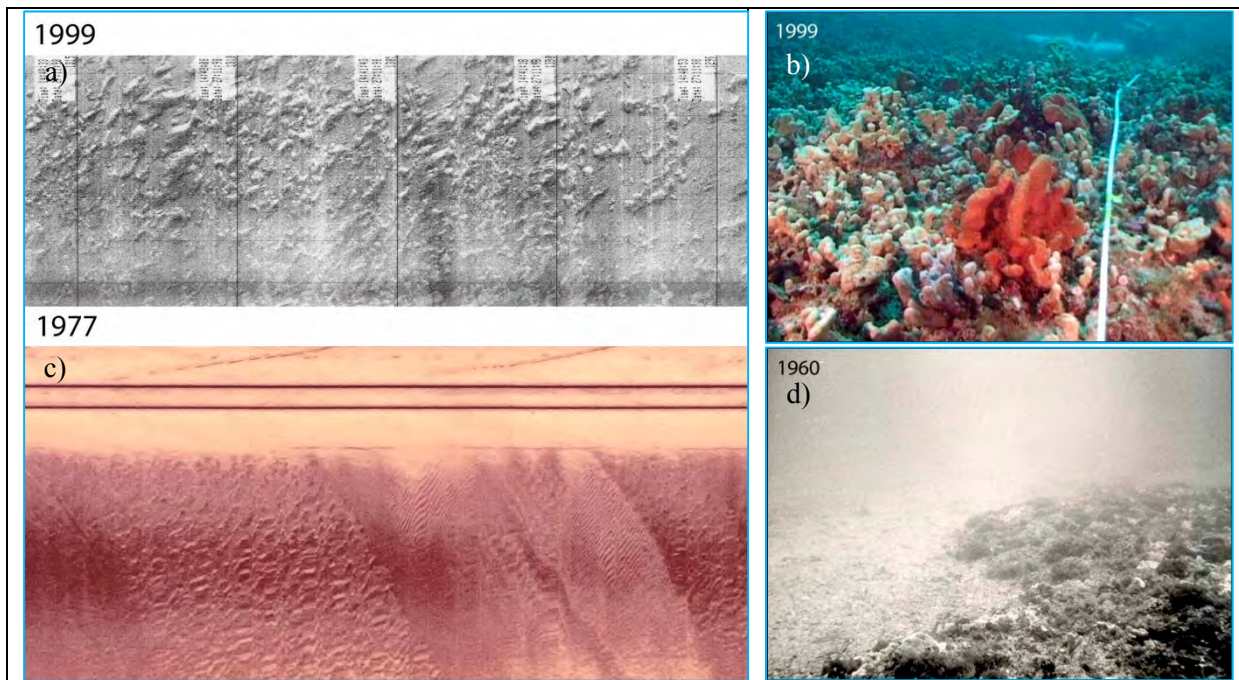


Figure 29: Bryozoan biogenic reefs in Foveaux Strait, as seen on side-scan sonar images from a) 1999, and c) 1977, and as photographed by divers, b) 1999, d) 1960 (Source: K. Michael, NIWA).

Information gaps

While the main areas of bryozoan beds appear to be known, knowledge on their species associations, and the functions which they provide to fisheries species, are largely unknown. Foveaux Strait is the most studied area, with a focus on the links and interactions with oysters and blue cod. Separation Point is explicitly closed as a habitat area for nursery fish (especially terakihi and snapper), but empirical data showing its role for this and other species is absent. The Otago Shelf bryozoan beds elevate biodiversity values, and support juvenile fish such as blue cod, red cod, southern pigfish and perhaps others (Probert et al. 1979, Batson & Probert 2000, Wood 2005, Jones 2006, Wood et al., 2012, M.M. and E.J. unpubl. data). Potential fisheries species roles for Spirits Bay/Three Kings/South Maria Ridge, the Wanganui Shelf, and Snares Shelf bryozoans are unknown.

Suggestions for new research are:

- Separation Point is in effect a marine reserve for juvenile fish and their associated bryozoan habitat. Established in 1980, aside from Grange et al. (2003), no research has been directed at the bryozoan's extent and ecological role, nor their potential fish nursery contribution to fisheries productivity. There is evidence of land-based sedimentation degradation and decline. High definition mapping (preferably multibeam sonar) and quantification of associated fisheries species such as juvenile terakihi, snapper, and blue cod using video or other means, would define what the Separation Point area actually supports. Potential sedimentation impacts could be quantified with field measures and experiment, and sedimentation history assessed using sediment cores. Given these data, and additional approaches, work could then focus on what proportion of fisheries production might be supported by Separation Point's bryozoan's fish nursery functions, and if additional management actions might be warranted.
- More accurate definitions of the extent of other bryozoan beds using appropriate remote sensing technologies. The Otago Shelf beds would be the ideal start given their proximity to

land, and limited extent based on point samples. Fisheries species work as described for Separation Point above would then be the next logical step.

Recommended measures

Formal protection of the Separation Point bryozoan beds from power from power fishing has been in place since 1980, and an informal protection of some of the Otago Shelf since 2002. These restrictions show that the value of bryozoan beds is already recognised by management agencies and marine end-users to some extent. It would be logical to extend these protections to other key areas, or at least high quality locations within these areas. However, both marine and land-based threats may be operating, depending on environmental setting, and for some locations such as Separation Point, coordinated cross-agency collaborations may be warranted.

3.8 Tubeworms

Location

A range of species create tubes, with some reaching sufficient sizes and/or densities to provide biogenic habitat for fisheries species. Two larger bodied tubeworm species have received some scientific attention in New Zealand. *Phyllochaetopterus socialis* (known as wire-weed or tarakihi weed by fishers) lives in a thin wiry tube some 8–10 cm in length. Its occurrence ranges from isolated individuals within mixed epifaunal assemblages, through to extensive dense mono-specific meadows at the tens of kilometres scale. In the Marlborough Sounds, a survey recorded it as being present at 14 out of 43 sites (42%), with all 14 sites being outer Sounds muddy seafloors (Escourt 1967); Davidson et al. (2010) also recorded it. Out on the North Otago Shelf off Oamaru, Batham (1969) described “a vast meadow of so-called tarakihi weed” (55–88 m water depth), known locally as the Hay Paddock. The on-going existence of the Hay Paddock was confirmed through Local Ecological Knowledge (LEK) interviews in 2010 (ZBD200801). Sampling in 2011 showed a seafloor covered by extensive low relief sponge cover (mainly finger forms) and *P. socialis* (Figure 30a). Beam trawl samples suggested that the sponges were growing over *P. socialis* tubes. The Hay Paddock extends over more than 140 km² (LEK polygons) with about 7 km² mapped and sampled through ZBD200801. The LEK interviews also reported extensive ‘wire-weed’ (*P. socialis*) further north off North Canterbury. The TAN1108 voyage found extensive meadows in 70–110 m water depth (Figures 30b). About 90 km² was enclosed by the area identified by multibeam sonar, with the meadow continuing off to the north and west. Further inshore (50–70 m water depth) only small wire-weed areas were found in the largest of the LEK wire-weed polygons, with the occasional patches encountered appearing to be of lower quality (shorter and smaller tubes), and associated with muddier sediments.

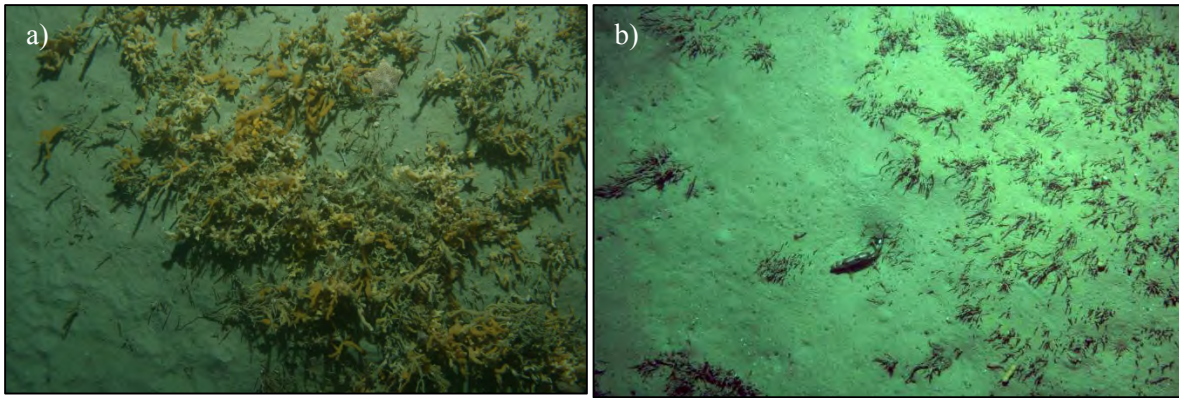


Figure 30: a) the Hay Paddock, with *P. socialis* and substantial sponge assemblage; b) *P. socialis* ('wireweed') meadow off North Canterbury, with sleeping tarakihi. (Source: TAN1108).

Another tubeworm habitat former, which occurs in shallower water, is *Galeolaria hystrix*. This species secretes calcareous tubes, with collectively can form three-dimensional mounds more than a metre high and several metres in diameter (Figure 31). As with *P. socialis*, densities range from scattered individuals, through to dense three-dimensional mounds. In New Zealand, its range extends from the Taranaki Coast down to Stewart Island (Hare 1992, Morton 2004, Smith et al. 2005, Davidson et al. 2010), as well as New South Wales and South Australia (Day & Hutchings 1979). Mounds have been found at two shallow water sheltered locations in New Zealand: on rocks/cobbles at Port Underwood, Marlborough Sounds (Davidson et al. 2010); and in Big Glory Bay, Stewart Island (Smith et al. 2005). In the Marlborough Sounds, Davidson et al. (2010) described tubeworm mounds dominated by *G. hystrix* as widespread in sheltered areas, but most often found as individual tubes attached to hard substrates. Mound densities were described as “usually sparse or occasional” at most locations where they occurred, but at some locations they became “relatively common or abundant”, covering up to 100% of the seafloor. Mounds occurred on both soft and hard seafloor, but appeared to need some hard structure on which to initially establish; including dead shell in soft sediment systems. Three mound locations were found: Perano Shoal, 6–30 m water depth, 38 000 m², in Queen Charlotte Sound; and the ‘Knobbies’, 3–12 m depth, 34 000 m², and Whataroa Point, 3–14 m, 9000 m², in Port Underwood (Davidson et al. 2010).

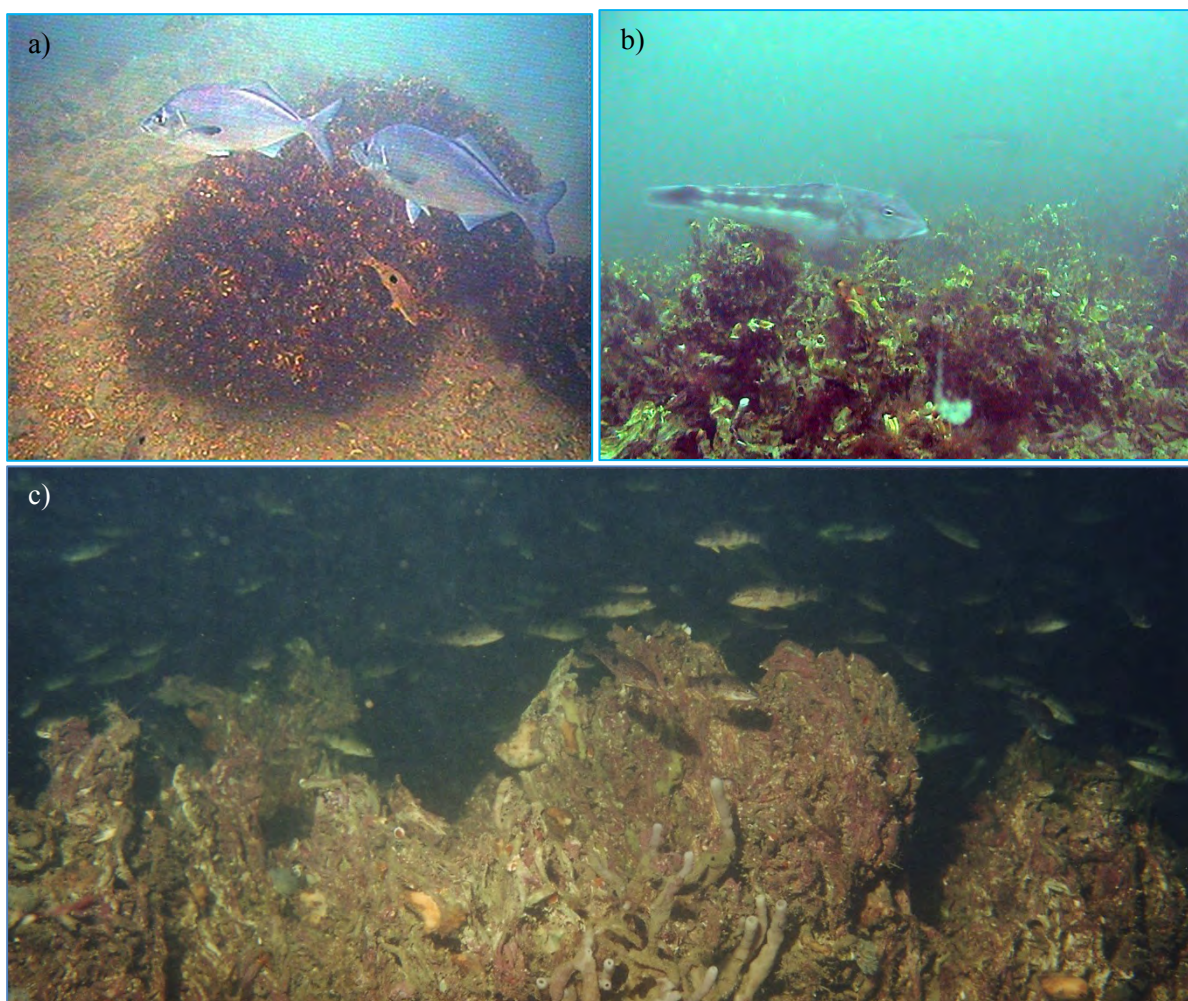


Figure 31: *Galeolaria hystrix* mounds, a) discrete mounds in Port Underwood, with associated blue moki and spotties, b) continuous *G. hystrix* mounds at Perano Shoal, Queen Charlotte Sound, with adult blue cod (Source: R. Davidson, Davidson Environmental Ltd), c) top of *G. hystrix* mound at Big Glory Bay, Paterson Inlet, with spotties, sponges, and ascidians (Source: A. Smith, University of Otago).

Further south, mounds occur in Big Glory Bay, Paterson Inlet, Stewart Island (Figure 31c), in 9–16 m water depth (Smith et al. 2005). These authors surveyed sites identified by sidescan sonar, and found 114 reefs (mounds) within a survey extent of 28 000 m², using visual diver transects. Reefs were patchy and clumped in their distribution, with an overall reef density of 0.004 reefs per m². Most reefs were 1–5 m in diameter, up to 1.5 m high. Sixty-four per cent of reefs were in a whole state and alive, with the remaining 36% broken or dead. The habitats surrounding the reefs were a mixture of mud and red algal meadows (see Algae: *Adamsiella chauvinii* section). A particularly large *G. hystrix* reef, in “*excellent condition*”, was found south of Bravo Island, being 1 m high and 6 m in diameter, and “*with many fish in abundance*”. An even larger (but dead) reef was found just east of Groper Island, almost 100 m in diameter.

Davidson et al. (2010) also reported two other polychaete biogenic habitats from the Marlborough Sounds; low-lying *Owenia petersena* mounds covering up to 90% of the seafloor at Gannet Point on sand at 10–12 m water depth, over an area of 36 000 m² (Morrisey et al. 2009a, b); and a dense sabellid tubeworm (*Bispira bispira* ‘A’) mat at Bob’s Bay at 3–6 m water depth, of 29 000 m². This

species has also been recorded from Northland (Houhora and Whangarei harbours), the Bay of Plenty (Mount Manganui) and Wellington Harbour (Davidson et al. 2010).

There are a number of invasive / non-indigenous species (NIS) of tubeworm species that may also provide habitat for fisheries species. For example, the parchment worm *Chaetopterus* sp. (Figure 32a) has at times occurred widely across the Hauraki Gulf, causing problems for scallop dredge fishers, and concerns about the exclusion of other benthic species (Tricklebank et al. 2001). However, it has also been reported by fishers as being a favoured dietary item for adult snapper, and the tubes themselves might conceivably provide shelter for small fish. Similarly, the recently arrived Mediterranean fan-worm *Sabella spallanzanii* (Figure 32b) (Morrisey et al. 2013), while regarded as a major threat to coastal ecosystems, may also provide some benefits to fisheries species. In Port Phillip Bay, Australia, work on demersal fish assemblages noted that abundances of the little rock whiting (*Neodax balteatus*) were higher in areas of fan-worm (Parry et al. 1996, Hobday et al. 1999)

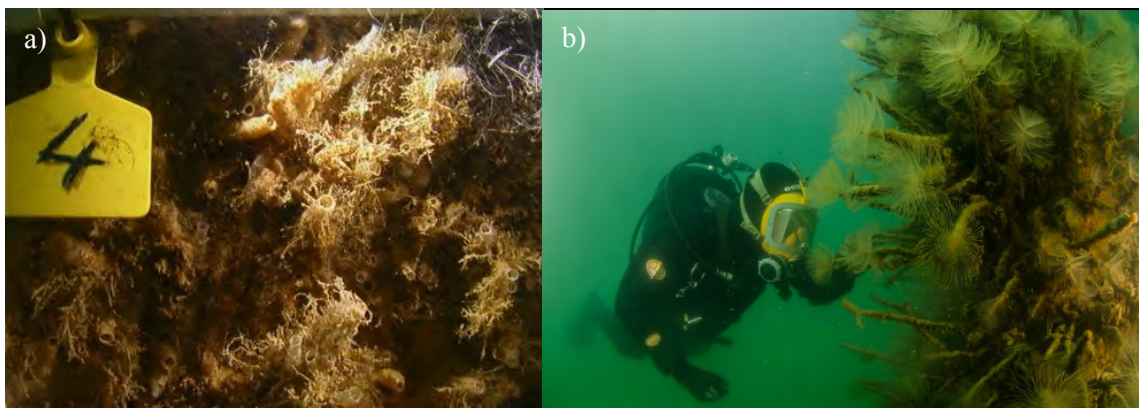


Figure 32: a) parchment worm *Chaetopterus* sp. tubes (Source: G. Inglis, NIWA); b) Mediterranean fan-worm (*Sabella spallanzanii*) growing on wharf structures, Viaduct, Auckland (Source: C. Middleton, NIWA).

Value and function

From around New Zealand, virtually nothing is known about the potential role of tubeworms in fish and other fished species life histories, although low relief worm tube meadows similar to those described by Stoner et al. (2007) (see following) are widespread in many areas. Overseas workers have shown that even ‘low-relief’ tubeworm beds can be correlated with increases in fish densities. Stoner et al. (2007) used a towed video sled to quantify habitat use of 0+ northern rock sole (*Lepidopsetta polyxystra*) at five soft sediment near-shore nursery sites around Kodiak Island, Alaska. One of the dominant seafloor habitats involved was ampharetid polychaete tubeworm beds, which were less than 2 cm in height. Fish density was modelled on habitat variables. At the broadest regional scale, a model combining sediment composition, surface bed-form, temperature, and the density of worm tubes best explained rock sole density. At the site scale, within-nursery fish density variations were best explained by depth, habitat structural complexity created by emergent fauna and macro-algae, and worm tube density. At the finest spatial scale, under 1 m, there was little evidence of fish being in direct contact with objects such as shells and macro-algae, instead they were loosely associated with these objects at the tens of metres scale. High densities of 0+ rock sole were found in low to medium density tubeworm beds, but not in high density tubeworm beds, whose effect on sole densities was negative. While worms are an important food source for sole, Stoner et al. argued that the key function of low to moderate tubeworm densities was to provide refuge from predation, via

camouflaged burial within areas of high structural complexity. Such burial was not possible within continuous dense tubeworm habitats, and so they were avoided by 0+ sole (an example of habitat quality effects).

The Hay Paddock and wire-weed habitats of the east Canterbury continental shelf were found to have a range of associated species, especially invertebrates, with the wireweed meadows holding large numbers of small sea perch (TAN1105 voyage). However, their value as fisheries habitats, in particular nursery functions for species such as terakihi, remains unknown. Davidson et al (2010) noted the presence of blue moki, blue cod, tarakihi and other fish with the *G. hystrix* mounds (Figure 31a, b). In Big Glory Bay, fish were described as being abundant around mounds, including blue cod, spotted wrasse, pigfish, red cod, butterfly perch and triple fins. Skate (*Raja nasuta*) and shark egg cases were also commonly found attached to the reefs (Smith et al. 2005).

No quantitative information on the value of tubeworm habitats to fisheries productivity is available.

Past and current threats and status

For the east Canterbury continental shelf wireweed meadows, commercial fishing was observed in the 90 km² area of wire-weed encompassed by multibeam mapping, and bobbin marks were observed on some video footage. Information from the LEK interviews suggests that these meadows may be slowly reducing in extent as fishing around their edges physically removes structure, although some meadow areas cannot be fished due to the undulating seafloor. Fishing trawl intensity footprints suggests that these habitats are being actively targeted by coastal trawlers. The shallower land-ward wireweed areas may also be being adversely affected by sedimentation, with some circumstantial video evidence. These *P. socialis* habitats may therefore be being adversely affected by at least two stressors, sedimentation and commercial fishing.

For the Big Glory Bay *G. hystrix* mounds, reefs on the southern side (n=32) were in much better condition than those on the northern side, (n=37), while those of inner Big Glory Bay (n=14) were almost all in excellent condition. However, it was observed that these latter reefs also had a lot of sediment sitting on them, and ascidians and sponges were largely absent. Greatest species diversity and abundance (algae, invertebrates, and fish) was associated with those reefs where worm tube occupancy rates were highest (Elliot 1995), i.e., the healthiest reefs. It was not known whether low worm tube occupancy rates were of concern for the longer term survival of reefs (Smith et al. 2005). Physically damaged reefs were thought to be a result of anchor and equipment (aquaculture operations) disturbance, with fishers actively targetting these reefs for their associated fish species. Earlier work by Elliot (1995) also noted that the *G. hystrix* reef heads often grew away from the seafloor in an “irregularly lobate shape”, increasing their vulnerability to impacts which could break the reef off near the base, such as anchors with associated chains and rope.

Information gaps

For most of the above tubeworm species currently known to form biogenic habitats in New Zealand’s coastal zone, observations suggest that fish diversity and abundances are higher in such habitats, relative to adjacent ‘unstructured’ areas. However, quantitative work is yet to be undertaken on what those fish-habitat relationships actually are; and what it means relative to the wider context of fisheries production (in the sense of Beck et al. 2001 or Dahlgren et al. 2006). It is also likely that other tubeworm species, such as low mat formers (Stoner et al. 2007), also generate biogenic habitats which may support fisheries values. Species such as flatfish and red gurnard might conceivably use

such comparatively low-relief biogenic structure at the juvenile stage. Based on overseas knowledge, the importance of such fine scale biogenic habitats should not be overlooked.

Suggestions for new research are:

- Following ZBD200801 analysis of the Hay Paddock and *P. socialis* (wire-weed) beds, undertake fish-habitat sampling with appropriate seasonality to assess what fisheries functions these habitat types may provide. Assess threats (fishing and sedimentation), and provide information to resource managers on how these threats might be managed. As with other biogenic habitats, work towards assessing what proportion of fisheries productivity they might support.
- Undertake similar work for the *G. hystrix* mounds, focusing on Paterson Inlet and Port Underwood.
- For less visually obvious mat forming tubeworm species, investigate the role that they might play for fisheries species (in the sense of Stoner et al. 2007). This might include scallops in sandy habitats, as scallop spat have been noted attached to such tubes (M.M., pers. obs.).
- NIS species such as Mediterranean fan-worm and the parchment worm *Chaetopterus* sp. may also be providing biogenic habitat functions. Basic surveys of what organisms are associated with these species would provide a first look at what sort of habitat roles they might play.

Recommended measures

Protection of the highly three-dimensional *G. hystrix* mounds from relevant threats, in particular fishing, seems a priority, although more knowledge will be required of where they occur. The Hay Paddock and *P. socialis* (wire-weed) meadows of the East Canterbury coast are also worthy of more directed spatial management of fisheries impacts, and possibly sedimentation, depending on what is found from the suggested research above. As all three of these biogenic habitats also appear to be relatively rare and support higher biodiversity values, their management is also of relevance to other agencies such as DOC and regional councils.

3.9 Coastal (less than 200 m water depth) gorgonians, red and black corals, hydroids, ascidians, brachiopods, sea-pens, sea-whips and other species

Location

For a range of biogenic habitat formers, relatively little information could be found in the literature on their occurrence and possible roles. Gorgonians occur both on rocky reefs and soft sediment locations where sufficient patches of harder substrate are available for attachment. They were part of the biogenic habitat forming species mix identified at Spirits Bay by Cryer et al. (2000), and gorgonian ‘fields’ were also encountered during the TAN1105 voyages in a relatively extensive area north of North Cape (approximately 90–140 m water depth) (Figure 33a) and on the north-western side of Ranfurly Bank, East Cape (TAN1108) (Figure 33b).

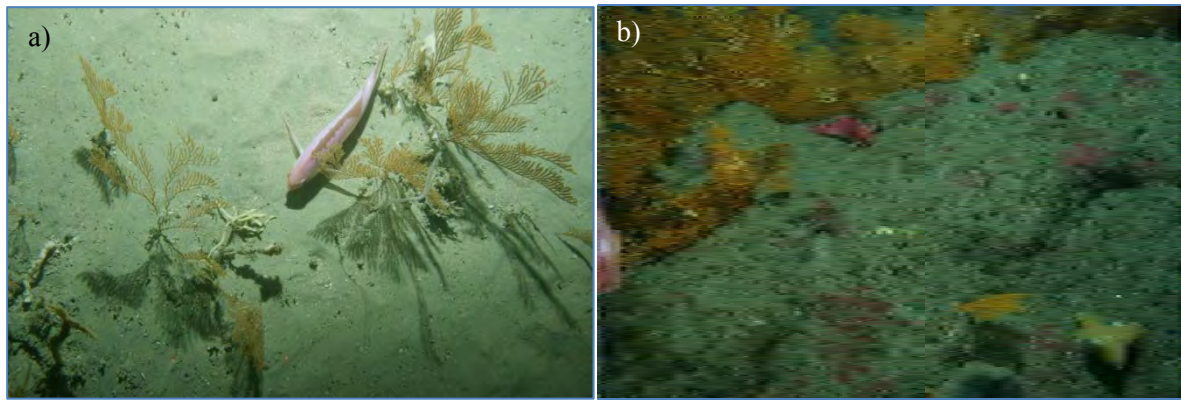


Figure 33: Examples of gorgonian ‘fields’, a) north of North Cape, and b) north-western Ranfurly Bank, East Cape. The fish are sleeping pink maomao about 30 cm in size (Source: DTIS, TAN1105 and TAN1108).

Black corals are also relatively wide-spread on deeper reef systems (not all species are habitat forming). In Fiordland, they occur within diving depths, due to ‘deep-water’ emergence through highly tannin laden waters reducing light penetration levels. Grange (1985) surveyed the rock walls down to 35 m, and found an average 0.25 colonies per m² (one colony every 4 m²), mainly at 15–35 m depth, through there was strong site and fiord variability. Ninety per cent of colonies were less than 50 cm tall, with rowth rates estimated at 3.9 cm yr⁻¹, based on size frequencies (Grange & Singleton 1981).

For red coral (*Errina novaezelandiae*) (Figure 34b), only one New Zealand study was found, conducted in Doubtful Sound, Fiordland. Small colonies were found to be most abundant. Larger corals (over 20 cm) were estimated to be in excess of 30 years old, and genetics indicated limited larval dispersal among neighbouring populations. Population densities were found to be patchy, with average densities of 7–10.9 colonies per minute searched by divers (Miller et al. 2004).

No substantive information could be found on hydroids, brachiopods, ascidians (e.g. sea tulips/ kāeo, *Pyura pachydermatina*), sea-pens, and sea-whips, in terms of their possible habitat-former role in the New Zealand context.

Willis et al. (2010) assessed the “China Shops” in Fiordland, a term used by local fishers and divers to describe sites where diverse assemblages of delicate three-dimensional epifaunal invertebrate species were growing on the rock walls (Figure 34). Some of these have been protected with Marine Reserve status. However, Willis et al. (2010) surveyed 20 China Shop sites, and found that the features (species and biodiversity) used by local marine environment users to identify these as ‘China Shops’, were not always significant site characterisers in formal numerical analyses (the notable exception being the ‘Strawberry Fields’, orange ascidians Figure 33a). This was attributed to spatial mismatches over small extents, as well as the formal surveys assessing whole assemblages, while the China Shops were implemented on an ad hoc basis, “based on the observations of only one or a few people, and the features that may have stood out in a person’s memory may constitute a very minor part of the whole assemblage” (Willis et al. 2010). Species “considered to be iconic Fiordland species (e.g. black coral, cup sponges, large tube anemones)” did not generally make a significant contribution to the characterisation of sites. Willis et al. (2010) suggested that to meet the requirements of managers, a classification system based on coarse habitat types was needed, similar to that developed by Shears et al. (2004) for rocky reefs in north-eastern New Zealand.

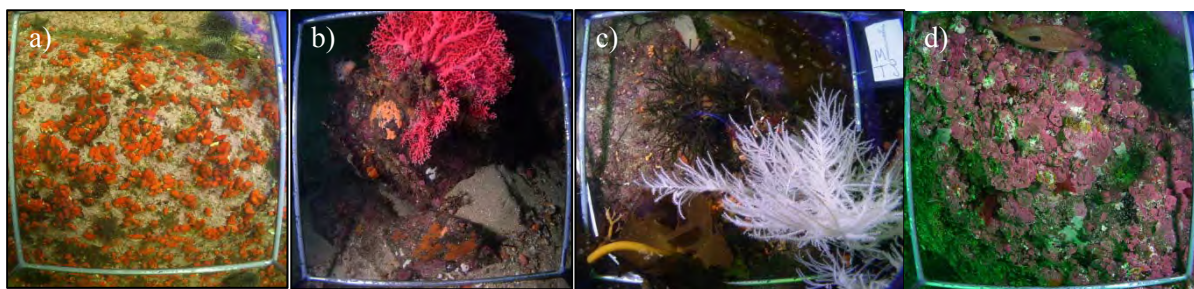


Figure 34: 50 cm photo quadrats; a) ascidians (*Ocnus brevidentis*) at the The Narrows (“Strawberry Fields”), b) red coral (*Errina novaezelandiae*) at Charles Fanny Island, c) black coral and *Codium* sp., at Isthmus Sound sill d) plate corallines, at Breaksea wall (Source: T. Willis, NIWA).

Value and function

Unknown.

Past and current status and threats

Largely unknown.

Miller et al. (2004) assessed red coral population vulnerability to recreational diver impacts in Fiordland. Small colonies were found to be most abundant. Damage was up to eight times higher in dived versus un-dived locations, with larger colonies showing the greatest damage rates.

Information gaps

There is insufficient information on which to make detailed suggestions for work to address information gaps. A generic start would be to assemble data and unpublished material together to see where these habitats occur and in what densities. Presence/absence data is likely to be useful at only the largest spatial scale in identifying species ranges, as it is the habitat values of these species that are of interest.

Recommended measures

Insufficient information is available.

BURROWS AS BIOGENIC HABITAT

Infaunal burrows provide important biogenic habitats in marine soft sediment environments. Burrow systems vary in size and complexity, depending on the burrowing organism, and range from shallow and small burrows (millimetres to centimetres) to extensive structures that greatly extend laterally and to sediment depth (decimetres to metres) (Swinbanks & Murray 1981, Reichelt 1991). Infaunal burrows are frequently the only physical structure in intertidal and subtidal sediments (Figure 35), and provide habitat and refuge for burrow inhabitants and associated fauna (Karplus 1987, Warren 1990, Griffis & Suchanek 1991). In addition, burrow construction and maintenance often result in considerable sediment disturbance (bioturbation), and the latter is particularly relevant for burrowing organisms that also process sediment for food (deposit-feeding). Bioturbation is a ubiquitous feature in marine sedimentary environments and occurs to different degrees in estuarine and coastal areas and in deep-sea sediments (Meadows & Meadows 1991). The presence of burrows and bioturbation by

burrowing organisms can have a profound impact on the associated ecosystem, affecting physical properties (e.g., sediment porosity, water and oxygen content, resuspension rates) and biogeochemical processes (e.g., nitrification-denitrification, nutrient fluxes) with indirect and direct repercussions for associated biota and ecosystem productivity (de Wilde 1991, Levinton 1995, Sandnes et al. 2000). Recognition of the functional importance of bioturbators has prompted warnings that their broad-scale loss could impair marine ecosystem functions (Lohrer et al. 2005).

The effects of bioturbation are often species-specific, depending on the burrowing and feeding activities and burrow shape or size (Meadows & Tait 1989, Jones & Jago 1993). Owing to their prodigious sediment processing rates, burrowing crustaceans, i.e., decapod crabs and shrimps have been identified as important bioturbators in sedimentary habitats (Suchanek et al. 1986, Botto & Iribarne 1999). They are common components of tropical and temperate ecosystems, where they frequently occur at high densities (Montague 1982, Iribarne et al. 1997, Roberts et al. 1981, Wynberg & Branch 1991). Burrowing crabs occur in intertidal and shallow subtidal habitats and can reach population densities of several hundred individuals/m² (Krebs & Valiela 1978, Jones & Simons 1983). They create permanent/semi-permanent burrows (that in intertidal habitats usually extend to the water table) and a number of species also process sediment for food, resulting in substantial reworking of sediment (Botto et al. 2006). Burrowing (thalassinidean) shrimps, also referred to as ghost or mud shrimps, have long been recognised as important infaunal bioturbators with potentially the greatest impact over the largest depth range (Swift 1993, Cadée 2001). Burrowing shrimps are present in intertidal and subtidal sediments, where they create relatively deep burrows (more than 2 m burrow depth) (Pemberton et al. 1976, Witbaard & Duineveld 1989, Dworschak & Ott 1993, Bird & Poore 1999); furthermore, a number of species (i.e., callianassids) are deposit-feeders, and their burrowing and feeding activities are reflected in prolific sediment turnover rates (see review in Rowden & Jones 1993, Berkenbusch & Rowden 1999). Owing to their ecological significance, callianassid shrimps have been formally identified as “ecosystem engineers” (Berkenbusch & Rowden 2003), a term coined to describe organisms that have a disproportional influence on the environment in which they live via habitat modification and impacts on resource flows (Jones et al. 1994). Although generally in lower density than thalassinids, larger crustaceans (scampi species, some Goneplacid crabs) are known to form large burrows in deep waters, and some of these species are known from the New Zealand region (Tuck & Spong 2013).

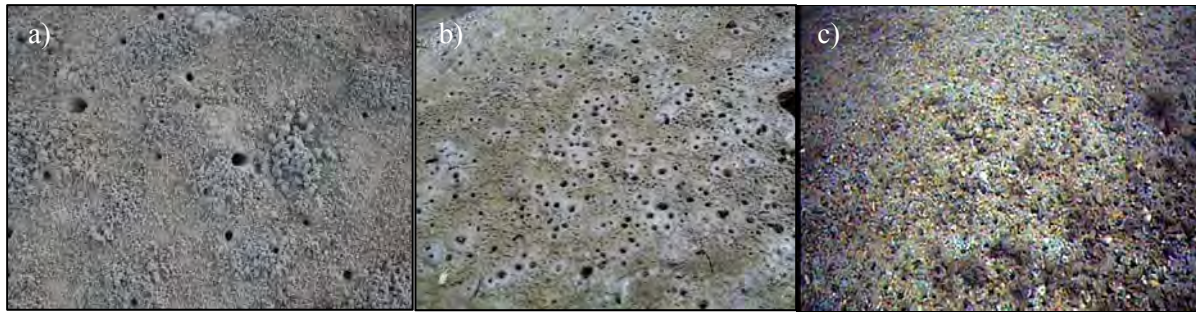


Figure 35: Examples of burrow features in the intertidal and subtidal, a) burrow holes of the tunnelling mud crab *Austrohelice crassa*, with excavated sediment adjacent to the burrow openings, b) burrowing ghost shrimp *Neotrypaea californiensis* burrow openings at the sediment surface of an intertidal mudflat in Oregon, United States. Ghost shrimp burrows are complex systems that extend to considerable sediment depth and are connected to the overlying water column by multiple openings. c) subtidal burrows (probably ghost shrimp) in Pelorus Sound, in zone between cobble banks, and the silt and fine sand that dominates the Sound's seafloor (Source: a, b, K. Berkenbusch, University of Otago; c, Rob Davidson, Davidson Environmental Ltd).

A number of burrowing crustaceans are important prey items for fish (including commercial species) (McLay 1988, Posey 1986a, Warren 1990) and, therefore, reflect a direct trophic link between sedimentary habitats and fishery productivity. Although few reports establish a direct, non-trophic link between burrowing crustaceans and fisheries species (but see Mouritsen 2004), a large number of studies document the ecological significance of burrows and burrowing crustaceans (e.g., Bortolus & Iribarne 1999, Webb & Eyre 2004). Through their influence on nutrient dynamics and primary productivity, bioturbators impact on higher trophic levels within sediments and the overlying water column, such as filter-feeding bivalves (Pillay et al. 2007), and their biogenic structures and activities play a central role in determining soft sediment community structure and diversity (Posey 1986b, Widdicombe et al. 2000, Berkenbusch et al. 2007). By influencing the abundance and distribution of benthic meio- and macrofauna, which constitute an essential food source for a diverse range of fish species, including commercially important flatfish (Edgar & Shaw 1995, Meng et al. 2001), bioturbators affect food web dynamics, with potential consequences for fisheries productivity.

New Zealand's intertidal sedimentary habitats support a number of burrowing crustaceans, including crabs and thalassinidean shrimps (Figures 36, 37) (Morton & Miller 1973, McLay 1988). The two most conspicuous burrowing crab species are *Helice crassa* and *Macrophthalmus hirtipes*, which are both common in soft sediments throughout New Zealand, where they occur at different tidal levels (Jones 1976, McLay 1988). *Helice crassa* is present in high intertidal areas, where it can reach high densities (more than 400 individuals/m², Jones & Simons 1983); *Macrophthalmus hirtipes* burrows in soft sediments close to mean low water and also occurs in shallow subtidal habitats, usually at densities of approximately 30 individuals/m² (Beer 1959). Thalassinidean shrimps endemic to New Zealand include *Callianassa filholi* and *Upogebia danai*; the former species is a deposit-feeder and present in intertidal and subtidal sediments throughout New Zealand (Berkenbusch & Rowden 1998); as is the latter, a New Zealand endemic. The biology and ecology of *Callianassa filholi* has been the focus of a number of studies (e.g., Devine 1966, Berkenbusch & Rowden 1998, Berkenbusch et al. 2000) and this species has been identified as a significant bioturbator (Berkenbusch & Rowden 2003, 2007).

Less research has focussed on subtidal burrowers, but work associated with photographic surveys of scampi in key New Zealand fishery areas has identified a number of species that are likely to excavate

their own burrows, or use burrows created by other species (Tuck & Spong 2013). Scampi (*Metanephrops challengeri*) are likely to form the largest (diameter) burrows, although the Goneplacid crab *Neommatocarcinus huttoni* is likely to also form burrows, given its body shape. On the basis of overseas studies, these burrows are likely to extend 30–40 cm into the seabed (Rice & Chapman 1971, Tuck et al. 1994). Predatory and scavenging isopods form high densities of small shallow vertical shafts, while burrows of thalassinids and echiuran worms are generally narrow, but may extend over a metre into the seabed.

The following section reviews existing information on the importance of crustacean (crab and shrimp) burrows as biogenic habitats to fisheries production in New Zealand's marine environment. As burrowing and bioturbation are often intrinsically linked, i.e. for deposit-feeding crustaceans, information on the functional importance of bioturbation was also considered. Direct trophic interactions between burrowing crustaceans and lower/higher trophic levels are not included, although they contribute to the ecological role of burrowing crustaceans.



Figure 36: Examples of burrow making animals, a) stalk-eyed mud crab *Macrophthalmus hirtipes* at the sediment surface. This species is common on intertidal mudflats throughout New Zealand, where it lives in burrows in mid- to low-intertidal areas, b) New Zealand's tunnelling mud crab *Austrohelice crassa* with a burrow opening in the background, Papanui Inlet, Otago. (Source: K. Berkenbusch, University of Otago/Dragonfly Ltd).

4.1 Impact on geotechnical sediment properties

Burrowing and deposit-feeding organisms modify the habitat in which they live by altering geophysical and geotechnical properties of marine sediments, thereby controlling erosional and depositional processes, sediment stability, and diagenesis (Meadows & Meadows 1991). By influencing sediment properties (e.g., grain size, sedimentation rate, penetrability, shear strength, critical erosion velocity), bioturbators have a disproportionately large impact on the suitability of habitats for other species, and burrowing crustaceans in particular have been identified as important habitat modifiers in tropical and temperate regions (Roberts et al. 1981, Warren & Underwood 1986, Berkenbusch & Rowden 2003). Their influence on sediment properties is intensified when sediment is also processed for food, and the burrowing and deposit-feeding activities of a number of shrimp and crab species are reflected in prodigious sediment turnover rates (Berkenbusch & Rowden 1999, Botto et al. 2006). In addition, burrowing crustaceans are often present at high densities (Jones & Simons 1983, Posey 1986b), further augmenting their impact on soft sediment ecosystems.

Physical habitat modifications by burrowing crustaceans are evident in changes in water content, penetrability (firmness), and sediment grain size, well below the sediment surface (Rowden et al. 1998a, Tamaki et al. 1992). While surface deposit-feeding species had similar effects on the surface layers (increased porosity and particle mixing), the effects caused by burrowers extended somewhat deeper (Katrak & Bird 2003).

The presence of crab species has been linked to physical habitat changes in different sedimentary habitats. Fiddler crab (predominantly *Uca pugnax*) burrows elevate soil hardness and increase surficial permeability (water percolation rate through the substrate) and water drainage in salt marsh sediments (Bertness 1985, Bortolus & Iribarne 1999, Botto & Iribarne 2000). On sediment dominated by fine sand or silt, burrowing and feeding activities loosen the sediment matrix and decrease sediment firmness to the respective burrow depth (20 cm for *Uca uruguayensis*, 35 cm for *Chasmagnathus granulata*). Fiddler crabs exhibit high sediment reworking rates and impact sediment grain size distribution, sediment erodability and bedload transport, but specific effects vary between species. By depositing clay particles on the sediment surface, *Chasmagnathus granulata* increased the cohesiveness of surface sediment and improved sediment stability, which was evident in low sediment bedload transport rates associated with its burrow beds. In contrast, *U. uruguayensis* pelletised sediment at the surface, which increased surface roughness and concomitantly erosion by decreasing shear strength, resulting in elevated sediment transport rates where this species was present (Botto & Iribarne 2000). In mangrove ecosystems, bioturbation by crabs has also been shown to change surface topography, particle size distribution, and degree of aeration (Warren & Underwood 1986, Lee 1998).

Changes in sediment grain size and sediment sorting frequently result in layers of coarse particles at the bottom of the bioturbated zone, with finer material deposited at the sediment surface, either in the form of fine particles or incorporated into faecal material (Meadows & Meadows 1991). The activity of burrowing crabs is also evident in high sediment turnover rates, which vary depending on the species and habitat. Average daily sediment turnover rates have been recorded between 5.9 kg.m⁻² and 2.6 kg.m⁻² sediment wet weight for Fiddler crabs (Iribarne et al. 1997). Turnover rates also vary seasonally, related to crab activity and burrow collapse, and re-excavation (Takeda & Kurihara 1987).

Significant sediment turnover rates have also been documented for callianassid shrimps and reveal, particularly for the one New Zealand species studied, that prodigious amounts of sediment are processed as the shrimps constantly rework sediment for burrow construction/maintenance and feeding. Sediment turnover by the New Zealand species, *Callianassa filholi* (Figure 36a) on an intertidal sandflat in Otago Harbour resulted in an estimated annual rate of 96 kg.m⁻² (dry) sediment weight (Berkenbusch & Rowden 1999), and the annual sediment turnover rate by its subtidal Northern Hemisphere counterpart *C. subterranea* was about 11–15 kg.m⁻² (dry) sediment (Stamhuis et al. 1997, Rowden et al. 1998b). In tropical ecosystems, sediment turnover by callianassids has been estimated to reach up about 3.4 kg.m⁻² (dry) sediment per day (Roberts et al. 1981).

As unwanted sediment is ejected from the burrows, it forms mounds at the sediment surface, and ecosystems inhabited by burrowing crustaceans are often characterised by a large number of sediment mounds (Dworschak 1983, Suchanek et al. 1986, Warren & Underwood 1986, Botto & Iribarne 2000). The latter modify the surface topography and increase roughness, which in turn decreases shear strength and increases erosion (sediment resuspension) (Rowden et al. 1998b). As unconsolidated sediment mounds are susceptible to resuspension by currents, burrowing crustaceans contribute significant amounts of sediment to the water column, resulting in high turbidity with

potentially adverse effects for associated biota (Suchanek 1983, Aller & Dodge 1974, Pillay et al. 2007).

4.2 Impact on geochemical sediment properties

Burrowing organisms (e.g., Figure 37) also play a central role in regulating benthic biogeochemical processes, with direct effects on sediment-dwelling organisms (i.e., microorganisms) and ecosystem productivity (Aller et al. 1983, Andersen & Kristensen 1991, Mchenga et al. 2007). The sediment surface is crucial for the uptake of oxygen from overlying water and is the metabolically most active site in sediments (Koike & Mukai 1983). Burrow walls provide a substantial increase in surface area across which oxygen enters the sediment matrix, and burrow inhabitants further enhance the supply of oxygen by actively irrigating their burrows (bioirrigation) (Forster & Graf 1992, Ziebis et al. 1996b). By accelerating the exchange of burrow/interstitial with overlying water, burrowing organisms provide a markedly more efficient transport of oxygen and oxidised compounds deep into the sediment matrix than passive, molecular diffusion driven by pore water concentration gradients (Kristensen 2000, Ziebis et al. 1996a).

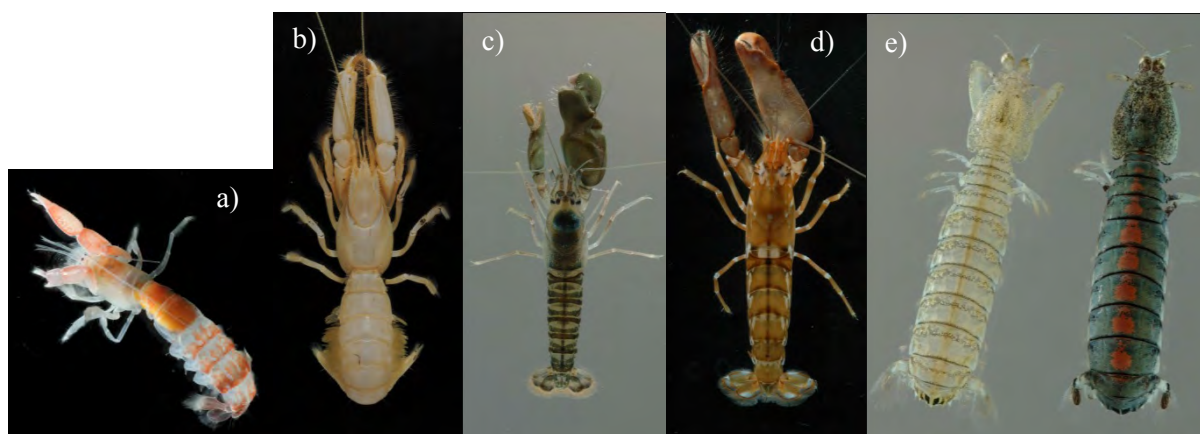


Figure 37: Various burrowing shrimp species collected from the Leigh area, a) *Callianassa filholi*, b) *Acetigebia danai*, c) *Alpheus euphrosyne richardsoni*, d) *Alpeus* sp., e) *Heterosquilla tricarinata*, male and female (NB: image scales are not equal) (Source: R. Taylor, Leigh Marine Laboratory).

The availability of oxygen is essential for microbial activities involved in organic matter mineralisation (aerobic respiration) and chemical and bacterial oxidation of reduced products from anaerobic mineralisation (Ziebis et al. 1996a). As a number of burrowing animals line their burrows to stabilise them, burrow walls are often enriched in organic matter, but the linings can also reduce the transport between ambient sediments and the burrow lumen (Aller et al. 1983). In addition, bioirrigation is usually intermittent, so that oxygen conditions in the burrow wall are highly variable, and the presence of labile organic matter, steep chemical gradients and narrow redox zonation significantly impacts on the chemical and biological composition of burrow environments (Kristensen 1988). By providing aerobic and anaerobic micro-niches in the burrow wall and associated sediment, burrowing organisms determine the distribution and abundance of microorganisms (Yingst & Rhoads 1980, Kristensen 2000) and control biological and chemical processes, including mineral cycling and nutrient release (benthic-pelagic coupling) (Koike & Mukai 1983, Waslenchuk et al. 1983). An increase in oxygen coupled with the increase in the aerobic-anaerobic interface stimulates oxidation processes, such as nitrification (and thereby anaerobic denitrification), and sulphite and pyrite oxidation (Malcolm & Sivyver 1997). Mineralisation rates and coupled nitrification-denitrification are further enhanced by the increase of organic matter in burrowed sediments (e.g., through passive

accumulation, faecal material, burrow linings), thereby fuelling sediment metabolism and nutrient recycling (Henriksen et al. 1983, Kristensen 1985). Organic matter decomposition is particularly important in estuaries and coastal environments, where organic detritus is one of the most important food sources and a large proportion of the energy flow is via detrital pathways (McLusky & Elliott 2006); in estuaries, high concentrations of organic detritus have been linked to high fish production (Day et al. 1989). Moreover, the active exchange of burrow water greatly increases the flux of solutes into the water column, including toxic metabolic substances and products of organic matter decomposition, such as ammonium, which is critical in marine waters as they are usually nitrogen-limited (Pelegrí et al. 1994, Lohrer et al. 2004). As a consequence, the activity of burrowing organisms constitutes an important link for porewater-seawater exchange (Gust & Harrison 1981, Waslenchuk et al. 1983).

4.3 Burrow irrigation

The significant increase in sediment surface and associated oxygenation of sediment through crustacean burrows has been confirmed in a number of studies, which report a range of values depending on the species and ecosystem involved. For example, high densities of *Callianassa subterranea* (20–50 individuals.m⁻²) in the North Sea result in 1.2–1.5 m² of internal surface below every square metre of sediment surface (Witbaard & Duineveld 1989, Forster & Graf 1992), and *Callianassa* [*Pestarella*] *truncata* burrows increase the sediment-water interface by approximately 400% and supply oxygen to 60–80 cm sediment depth in the Mediterranean Sea (Ziebis et al. 1996b). As oxygen from the burrow interior diffuses into ambient sediment, it produces more oxidised conditions (positive redox potential), and examination of oxygen patterns in relation to *Callianassa subterranea* burrows showed the presence of oxidised sediment at about 3 mm thickness around irrigated burrows (Forster & Graf 1992). At the same time, oxygen appeared to be transported across internal surfaces into the sediment at a similar rate to that across the pelagic sediment-water interface (Forster & Graf 1992).

In addition to active burrow irrigation and molecular diffusion transporting oxygen into the sediment, the uneven topography at the sediment surface associated with burrows and bioturbation promotes advective oxygen transport (Ziebis et al. 1996a). Sediments inhabited by burrowing crustaceans are frequently characterised by sediment mounds at the sediment surface (Suchanek et al. 1986, Warren & Underwood 1986, Botto & Iribarne 2000), which result in an uneven microtopography and greatly increase sediment roughness (Rowden et al. 1998b). As boundary layer flows encounter roughness at the sediment surface, the small-scale flow regime changes, resulting in localised pressure differences that drive advective pore-water flow (Vogel 1994, Ziebis et al. 1996a), including increased oxygen penetration depths in permeable sediments (Ziebis et al. 1996a). As many coastal habitats and a large proportion of the continental shelf (40%) are characterised by permeable sediments that are exposed to boundary layer flows and populated by infaunal organisms, advective transport processes expand the oxic sediment volume greatly beyond the zone supplied by diffusion (Ziebis et al. 1996a).

4.4 Geochemistry of burrow environments

Oxygen is used by burrow inhabitants (many species groups) for aerobic decomposition processes, and oxygen consumption rates are indicative of organic matter decomposition in the sediment (Koike & Mukai 1983, Kristensen 2000). For example, measurements of dissolved oxygen and nitrogen compounds in the burrows of two thalassinidean shrimp species, *Callianassa japonica* and *Upogebia major* in Japan revealed dissolved oxygen concentrations that were 12–45% lower in *Callianassa japonica* and 30–41% in *Upogebia major* burrows than in overlying water (Koike & Mukai 1983).

The authors attributed the main proportion of oxygen consumption to respiration of microorganisms and chemical oxidation, a notion supported by markedly higher ammonium and nitrate (plus nitrite) concentrations in the burrow water, reflecting prolific organic matter decomposition. Oxygen consumption and ammonium production rates were similar to those at the sediment surface, confirming the high productivity of the burrow systems (Koike & Mukai 1983).

The biogeochemical significance of burrows has been highlighted for burrowing crustaceans that stabilise their burrows by lining the walls (deVaugelas & Buscail 1990, Felder & Griffis 1994) and/or incorporate plant or algae material into the burrows (Dworschak 2001, Abed-Navandi & Dworschak 2005). Burrow walls are lined by using compacted, fine sediment, detrital material and sediment-binding mucous excretions (mucopolysaccharides), and the presence of reactive organic material and heterogenous redox conditions in the burrow wall promote the growth and production of diverse microbial populations (Dobbs & Guckert 1988, Papaspyrou et al. 2005).

Similar to burrowing shrimps, crabs and their burrows have been documented to have a considerable impact on physical and biogeochemical sediment properties. Intertidal sediments with crab burrows are characterised by higher organic matter and water content than sediments devoid of burrows (Bortulus & Iribarne 1999, Botto & Iribarne 2000, Mchenga et al. 2007) and aeration of sediment increases the availability of nutrients and reduces toxic solute concentrations (Smith et al. 1991).

Several studies have documented that burrows reflect unique microhabitats for benthic microorganisms, often supporting high concentrations of chlorophyll and high densities of bacteria and microphytobenthos (microbes and unicellular algae, commonly diatoms). Burrow linings of intertidal *Callianassa* [*Sergio*] *trilobata* contained equally high chlorophyll *a* concentrations as the sediment surface, and fatty acid analysis revealed markedly higher (over four times) microbial biomass in burrow linings than in ambient subsurface sediment, with a diversity of aerobic and anaerobic microbes present (Dobbs & Guckert 1988). In the Aegean Sea (Greece), chemical properties in *Pestarella tyrrhena* burrows were distinctly different to those of the sediment surface and ambient anoxic sediment, with significantly higher values for total organic carbon, carbohydrates, proteins and lipids in the burrow walls, resulting in a 10-fold increase in bacterial abundance (Papaspyrou et al. 2005). Chlorophyll *a* values were similar in the burrows and at the sediment surface, possibly owing to the burial of microphytobenthos, the transport of microalgae from overlying water and the passive and active accumulation of seagrass detritus. Molecular analysis of bacterial communities determined that the bacterial composition of the burrow wall was more similar to ambient anoxic sediment than the sediment surface, which the authors considered indicative of a stable burrow environment (Papaspyrou et al. 2005).

Two studies from Australia confirm the importance of shrimp burrows in relation to benthic biogeochemical processes (Bird et al. 2000, Webb & Eyre 2004). Bird et al. (2000) examined burrows of the thalassinidean shrimp *Biffarius arenosus* and showed that physicochemical and microbial properties of the burrow wall were more similar to the sediment surface than to surrounding subsurface sediments. As microbial activity was higher in the walls than in surrounding sediments, the authors suggested that periodic ventilation of the burrow system causes fluctuating oxygen conditions in different parts of the burrow, resulting in a mosaic of microenvironments, conducive to a diverse and productive microbial community, including aerobic (nitrifying) and anaerobic (denitrifying and sulphate reducing) bacteria (Bird et al. 2000). A subsequent study examined oxygen consumption and nutrient fluxes in subtidal *Trypaea australiensis* burrows and showed a 5-fold increase in the total rate of sediment porewater exchange/irrigation in sediment containing shrimp compared with sediments

without them (Webb & Eyre 2004). Burrows represented a 76–108% increase in reactive sediment surface area, corresponding with an 81% increase in oxygen demand in shrimp-inhabited sediment, of which 85% was used for oxidation processes and microbial respiration and the remainder for respiration by the shrimp. The high metabolic activity in sediment containing shrimp burrows was reflected in elevated denitrification rates which were four times higher in sediments where shrimp were present, representing 76% of the total denitrification at the study site. Sediment organic content was 13% higher where shrimp were present, confirming the shrimp's influence on the accumulation of organic matter. Ammonium (NH_4^+) efflux from burrow sediment was also higher with a concomitant lower efflux of nitrate (NO_3^-) and nitrite (NO_2^-), which the authors considered indicative of a close coupling of nitrification-denitrification in shrimp-inhabited sediment (i.e. increased ammonium mineralisation enhanced denitrification). These data indicate that the shrimp contributed considerably to the net sediment nitrogen efflux at the subtropical estuarine study site and as there was also an efflux of phosphate PO_4^{3-} from sediments containing shrimp, the presence of *Trypaea australiensis* probably contributes nutrients to primary productivity in the water column (Webb & Eyre 2004).

The presence of crab burrows has also been linked to enhanced productivity as they determine nutrient dynamics and growth of associated plants. Stable isotope analysis of accumulated organic matter across four different estuaries in South America revealed that sediments where crab (*Chasmagnathus granulatus*) were present were particularly enriched in nitrogen, and nitrogen enrichment may have been owing to increased denitrification rates stimulated by the crab burrows (Botto et al. 2005). The authors suggested that the crabs enhance sediment denitrification rates, so that the supply of nitrates to the water column decreases, and these nutrient dynamics suggest bottom-up effects of *Chasmagnathus granulatus* in these ecosystems (Botto et al. 2005). In a mangrove setting in Australia, the removal of crabs (predominantly *Sesarma messa* and *S. semperi longicristatum*) resulted in an increase in sediment sulphide and ammonium concentrations concurrent with a reduction in mangrove growth and reproductive output (Smith et al. 1991). The authors suggested that the removal of crabs reduced sediment aeration, which lead to elevated solute concentrations in the sediment as mangrove plants were unable to access the nutrients, resulting in the observed lower productivity (Smith et al. 1991).

In a southern United States saltmarsh, fiddler crab *Uca* spp. burrows affect the production, respiration and biogeochemistry of the associated habitat (Montague 1982). The presence of burrows was linked to an increase of carbon dioxide efflux accounting for 20–90% of the sediment respiration and burrow water was distinctly different from interstitial water. Burrow water was lower in salinity, but higher in concentrations of phosphate and ammonium than interstitial water, while burrow walls were oxidised by the burrowing activity of the crabs. In the vicinity of burrows, *Spartina alterniflora* standing stock increased by 23% owing to enhanced nutrient availability and sediment permeability. By providing nutrients and oxygenating the sediments, fiddler crabs influenced the subsurface metabolism of the salt marsh, resulting in higher *Spartina alterniflora* production (Montague 1980).

The positive impact of burrowing crabs on salt marsh productivity, nutrient cycling, and energy flow has also been reported by Bertness (1985) and Taylor & Allanson (1993). In a New England salt marsh, *Uca pugnax* burrows increased soil drainage, substrate redox potential and the decomposition of below-ground plant material, which differentially affected *Spartina alterniflora* production at different tidal heights (Bertness 1985). Experimental reduction of crab densities showed little effect in the lower intertidal zone, but resulted in a 47% decrease in above-ground plant biomass and a 35% increase in root biomass at intermediate tidal levels over a single growing season. As fiddler crabs are

abundant in salt marshes along the east coast of the United States, they appear to play a major role in generating and maintaining high productivity and probably mediate rates of marsh accretion and succession (Bertness 1985).

In addition to actively maintained burrows, abandoned burrow structures have also been shown to influence sedimentary habitats in the absence of burrow inhabitants (Ray & Aller 1985, Aller & Aller 1986). Relict burrows are abundant in deep-sea areas where they persist for long periods of time owing to low disturbance and low sedimentation rates (Weaver & Schultheiss 1983). Laboratory measurements of physical induced irrigation in burrow mimics (similar to shrimp burrows) showed similar flow rates through the burrows to those induced by active irrigation by burrow inhabitants (Ray & Aller 1985). Even at mean low velocities, irrigation driven by pressure gradients of overlying water currents was sufficient to produce similar solute concentrations in the burrow water to those in the overlying water. As physically induced irrigation was comparable to biological irrigation, uninhabited burrow structures appeared functionally equivalent to their inhabited counterparts and equally able to modify the sedimentary ecosystem albeit in the absence of burrow inhabitants (Ray & Aller 1985). A study of relict burrows in deep water (about 4800 m depth) on the Nova Scotian Rise/Canada confirmed that these biogenic structures trap highly reactive organic matter and are sites of enhanced biological activity and decomposition in otherwise organic-poor sediments (Aller & Aller 1986). Different types of abandoned burrows (including polychaete tubes and unidentified structures similar to shrimp burrows) containing surface derived organic matter, and mucus-enriched burrow walls supported significantly higher bacterial and meiofaunal densities than ambient sediment. As relict burrows are common in the study region, they may impact on as much as 34% of the sediment in this area by providing considerable food sources in a food-limited environment (Aller & Aller 1986).

4.5 Influence on associated biota

The functional importance of infaunal burrows is directly linked to the creation of habitat and refuge for other species, and biogenic structures in the form of burrows, mounds, and pits are sources of spatial and/or structural heterogeneity that can greatly affect the distribution and abundance of meio- and macrofauna (Bell et al. 1980, Posey 1986b, Widdicombe & Austen 2003). As burrows provide physical structure in an otherwise unstable environment, extend the sediment-water interface and oxygenate deeper sediment, they provide microhabitats in sedimentary environments that contain few protective structures. Burrows extend the available living space and enable associated organisms to persist at sediment depth (Bromley 1996), and therefore ameliorate pressure from predation and competition. In intertidal areas, burrows retain water at low tide and represent a buffer from environmental extremes such as oxygen deficiency and temperature changes. Inquilines (burrow inhabitants) also benefit from the provision of food by their host, e.g., through the excavation of sediment during burrow maintenance and burrow ventilation (Karplus 1987, Nara et al. 2008).

At the same time, the presence and activity of burrowing crustaceans have a profound impact on associated species and assemblages and ecological repercussion include both beneficial and adverse effects on animals and plants (Suchanek 1983, Dittmann 1996, Berkenbusch et al. 2000). Few studies report direct interactions between burrowing crustaceans and commercial species (fisheries or aquaculture) (but see Feldman et al. 2000, Dumbauld et al. 2001, Mouritsen 2004), but the impact on benthic assemblages has potentially significant consequences for fisheries productivity via trophic interactions. As benthic meio- and macrofauna are important food sources for fish (Edgar & Shaw 1995, Meng et al. 2001), influences determining their distribution and abundance are likely to impact

on associated fish species.

4.6 Burrows as habitats for other species

A range of different taxonomic groups, including crustaceans, bivalves, polychaete worms and fish, have been reported to share burrows with a crustacean host in a commensal association. The latter include ectosymbiotic relationships, with the commensal attached to the host's body, but also organisms that live freely within the burrow environment. The association between *Neotrypaea californiensis* and *Clevelandia ios* was the subject of a field and laboratory study in Oregon/United States, where the goby temporarily uses intertidal ghost shrimp burrows as a refuge during spring and summer, possibly to avoid predators, such as migrating shore birds and fish (Hoffman 1981). The blind goby *Typhlogobius californiensis* [*Othonops eos*] lives permanently in pairs in *Callianassa affinis* [*Neotrypaea bifari*] burrows (Wittenberger & Tilson 1980) and obligate mutualistic gobiid-alpheiid (snapping shrimp) associations are well recognised for a number of different species combinations, particularly in the tropics and subtropics (Yanagisawa 1984, Karplus et al. 1974, Karplus 1987, 1992). Karplus (1987) reviewed the associations between 13 different species of snapping shrimps and gobies, which occur in a range of sediment types from silty mud to coral rubble, and extend from the intertidal zone to over 50 m water depth. In these associations, the snapping shrimp provide the burrows, whereas the goby partner provides a predator warning system, alerting the shrimp to approaching potential predators (Karplus 1987). In addition to shelter, the goby may also benefit from an increased food supply in the form of small invertebrates that become available in excavated sediment during burrow construction and maintenance (Karplus 1987). Snapping shrimps have also been shown to share burrows constructed by other crustacean species, including stomatopods (Froggia & Atkinson 1998), upogebiid and callianassid shrimps (e.g., Schembri & Jaccarini 1978, Dworschak & Coelho 1999, Dworschak et al. 2000, Anker et al. 2001) and xanthoid crabs (Silliman et al. 2003).

The presence of small bivalves in the burrows of thalassinidean shrimp species has been documented for several different species combinations including ectosymbiotic bivalves living on the host's body (Kato & Itani 1995, 2000), and species living freely in the burrow environment (MacGinitie 1934, 1935, Kerr & Corfield 1998, Itani & Kato 2002, Nara et al. 2008). The clam *Cryptomya californica* occurs at considerable depth (up to 50 cm) in *Neotrypaea californiensis* burrows (MacGinitie 1935, Swinbanks 1981, Lawry 1987), where it is situated in the wall and extends its siphons into the burrow lumen (Griffen et al. 2004). Its Japanese congener *Cryptomya truncata* lives commensally with the burrowing shrimps *Nihonotrypaea japonica*, *Upogebia major* and *U. yokoyai* (Itani & Kato 2002, Nara et al. 2008), and similar to *Cryptomya californica*, its posterior edge protrudes into the burrow system (Nara et al. 2008). As these bivalve species are suspension-feeders with extremely short siphons, they require access to the sediment surface, and the burrows allow *Cryptomya* to stay at the sediment-water interface at depth and burrow ventilation by the shrimp provides food from overlying water (MacGinitie 1935, Griffen et al. 2004, Nara et al. 2008).

A different form of commensalism appears in the interaction between burrowing *Neotrypaea californiensis* and a small spionid polychaete (Bromley 1996). The polychaete *Spio* sp. is only present at sites that are continuously covered by water and the uneven microtopography caused by ghost shrimp bioturbation provides a suitable habitat for this species as it retains water at the sediment surface (Bromley 1996).

4.7 Influence on meiofauna

In a *Spartina alterniflora* saltmarsh in the United States, the top fraction of sediment (0.5 cm) immediately surrounding burrows of the fiddler crab *Uca pugnax* supported higher densities of total meiofauna and nematodes than sediment between burrows, but copepods were present at lower abundances (Bell et al. 1980). Nematodes were also significantly more abundant in the lower sediment fraction (0.5–3 cm depth) in sediment where crab burrows were present when compared with the lower fraction of sediment without burrows. The authors suggested that nematodes may have benefited from an increase in food supply linked to the crabs' faecal pellets and associated microbial activity around the burrows, resulting in higher nematode densities (Bell et al. 1980).

In contrast, Hoffman et al. (1984) documented negative effects of fiddler crab *Uca pugnax* on associated meiofauna in a saltmarsh habitat. Experimental removal of the crab resulted in a ten-fold increase in the abundance of nematodes and meiofaunal crustaceans and a four-fold increase in annelid worm density. As *Uca pugnax* is a deposit-feeder and has been shown to ingest meiofauna, the detrimental impact may be related to direct predation by the crab and not to its influence on sediment properties. These authors concluded that the negative effect of predation by the crabs outweighed the potential positive effects of the presence of burrows, resulting in an overall decline in meiofaunal abundance (Hoffmann et al. 1984).

The notion of direct predation reducing meiofaunal densities was supported by an Australian study of foraging soldier crab *Mictyris longicarpus* (Dittmann 1993), but the negative impact of its congener *Mictyris platycheles* on meiofauna in a Tasmanian estuary was linked to disturbance and not predation (Warwick et al. 1990). The latter study examined natural occurring differences in *Mictyris platycheles* densities to examine the ecological effects of the intense disturbance caused by the feeding and burrowing activities of *Mictyris platycheles*. Although total abundances were not affected, nematodes showed significantly reduced species richness, species diversity and evenness in areas disturbed by the soldier crab. In addition, assemblage compositions of nematodes and copepods were also distinctly different between sediment with and without crabs, owing to differences in relative abundances of common species and not changes in abundance of a few dominant ones (Warwick et al. 1990).

Other studies have shown elevated levels of potential food such as benthic microphytobenthos and bacterial numbers in shrimp burrows, but reduced meiofaunal densities (Branch & Pringle 1987, Dobbs & Guckert 1988). Although bacterial numbers were markedly elevated (30–100%) in the presence of *Callianassa kraussi*, i.e., in the burrow linings, meiofaunal densities were reduced in sediments that contained the shrimp, and the authors were unable to explain this inconsistency (Branch & Pringle 1987). Similarly, Dobbs & Guckert (1988) reported lower meiobenthic densities, particularly nematodes, in *Callianassa* [*Sergio*] *trilobata* burrows, with concomitant high chlorophyll *a* concentrations and highly abundant microbial communities, i.e., in the burrow linings; as their sampling design discriminated towards meiofaunal species with shells, the authors speculated that their findings may have been related to this sampling bias (Dobbs & Guckert 1988). Nevertheless, low nematode diversity and population densities were also evident in a tropical reef lagoon, Great Barrier Reef, Australia, where a burrowing ghost shrimp (*Callianassa* sp.) dominated the subtidal, sedimentary environment (Alongi 1986).

4.8 Influence on macrofauna

The impact of burrowing crustaceans on benthic macrofauna has been recognised in a number of studies conducted in New Zealand and overseas, which have revealed positive and negative effects on associated species. At a subtidal site in Otago Harbour (Dunedin), Thrush (1988) investigated macrobenthic recolonisation patterns at different distances to *Macrophthalmus hirtipes* burrows following a simulated storm. Although the same taxa were present, total number of taxa, total number of individuals, and abundance of some of the common polychaete taxa were significantly lower at the burrow entrance than at a distance over 1m from the burrow. The patterns persisted 30 days after the simulated storm and were attributed to physical disturbance by the crabs walking in and out of their burrows (Thrush 1988). Also in Otago Harbour, significant bioturbation by the ghost shrimp *Callianassa filholi* determined the macrofaunal assemblage composition at an intertidal site, with distinct differences in assemblage composition evident between areas of low and high ghost shrimp densities (Berkenbusch et al. 2000). The differences were related to lower abundances of common taxa (i.e., the amphipod *Paracorophium excavatum*, and the small bivalve *Perrierina turneri*) at high-density ghost shrimp sites, and although bioturbation activity varied throughout the year (Berkenbusch & Rowden 1999), differences in assemblage composition were evident even at times of low sediment turnover activity (Berkenbusch et al. 2000). A subsequent study of intertidal macrofaunal assemblages across three Otago inlets (including Otago Harbour) and three estuaries in Oregon/United States confirmed the universal importance of ghost shrimp (*Callianassa filholi* in New Zealand; *Neotrypaea californiensis* in the United States) in structuring benthic communities (Berkenbusch & Rowden 2007). The ghost shrimps consistently imposed assemblage patterns over small spatial scales within each inlet/estuary and exerted their influence through changes to sediment grain size (Berkenbusch & Rowden 2007). In addition, experimental recruitment of ghost shrimp to previous non-bioturbated areas in a single inlet in each respective biogeographical region resulted in a distinct shift in assemblage composition (Berkenbusch et al. 2007).

Mouritsen (2004) investigated the impact of this ghost shrimp species on little-neck clam *Austrovenus stutchburyi* populations in Otago Harbour, where both species exhibit complementary distributions. Bioturbation by *Callianassa filholi* prompted the clam to emigrate from areas containing ghost shrimp, possibly to avoid unconsolidated sediment. As the clam spent considerable time crawling at the sediment surface, they became susceptible to sublethal predation (foot cropping) by benthic-feeding fish, which in turn impeded the clam's ability to bury in the sediment for several weeks. The resultant prolonged exposure at the sediment surface led to a 5 to 6 fold increase in lethal predation pressure from shorebirds and predatory whelk, *Cominella glandiformis*. This study highlights the broad ecological effects of interspecific interactions between burrowing ghost shrimp and clams – whilst *Callianassa filholi* bioturbation had negative effects on the resident *Austrovenus stutchburyi* population, it was beneficial to benthic-feeding fish and epifaunal predators. In addition, as this bivalve species supports recreational and commercial fisheries in the Otago region (Ministry of Fisheries 2007), the impact of *Callianassa filholi* has direct consequences for the population distribution and abundance of a fisheries species.

Adverse effects of *Callianassa* [*Neotrypaea*] *californiensis* on a filter-feeding bivalve were also reported from intertidal areas in southern California/United States, where the ghost shrimp seem to inhibit recruitment by *Sanguinolaria nuttallii* (Peterson 1976). Experimental removal of the ghost shrimp resulted in high bivalve recruitment, whereas bivalves did not recruit to sediment containing shrimp (Peterson 1976). The same ghost shrimp species controlled an introduced bivalve population in another Californian lagoon system, where it exerted its influence via sediment disturbance (Murphy

1985). Although densities of introduced *Mercenaria mercenaria* were high in one area, the species was absent in a neighbouring lagoon where the ghost shrimp was present at relatively high abundances. At the same time, growth and survival of the bivalve were strongly negatively correlated with suspended particulate matter, and laboratory experiments showed that turbidity and sediment destabilisation caused by the ghost shrimp were sufficiently high to have a detrimental impact on *Mercenaria mercenaria* (Murphy 1985).

The adverse effect of *Neotrypaea californiensis* and *Upogebia pugettensis* on introduced and native oyster species (*Crassostrea gigas*, *Ostrea lurida*) has also been documented in Washington/United States estuaries, where pesticides are used to control shrimp populations and enable benthic oyster culture (Feldman et al. 2000, Dumbauld et al. 2001). As high densities of burrowing shrimp increase sedimentation rates and destabilise sediment, they limit oyster production by smothering oysters or causing them to sink into the sediment (Dumbauld et al. 2001). Both shrimp species are also regarded as pests for the aquaculture of Manila clam *Ruditapes philippinarum* in Washington, as they affect the survival of small clams (Toba et al. 1992).

In a tropical lagoon in Jamaica, ghost shrimp (*Callianassa* sp.) caused substantial sediment reworking and bottom instability, and infaunal diversity was decreased in areas dominated by the shrimp (Aller & Dodge 1974). The absence of most epi- and infaunal bivalve species, i.e., suspension-feeding ones from ghost shrimp areas, was attributed to the sediment instability and elevated sediment resuspension promoted by ghost shrimp activities (Aller & Dodge 1974). Biogenic disturbance by *Callianassa* spp. was also considered community limiting in a coral reef lagoon in Australia, where bioturbation by the shrimp negatively affected infaunal abundances (Riddle et al. 1990). Infaunal densities were significantly negatively correlated with relative height of shrimp mounds, with highest values recorded in the valleys between mounds, indicating that disturbance by bioturbation restricted the infaunal community (Riddle et al. 1990). The significance of sediment modification by shrimp was also evident following the disturbance by a tropical cyclone (Riddle 1988). Changes in microtopography and sediment grain size imposed by the cyclone at a *Callianassa*-dominated site led to a significant shift in infaunal species, with infauna dominated by species attracted to coarse sediment. However, after six weeks, ghost shrimp bioturbation returned the sediment to pre-cyclone grain size properties, with a resultant shift to pre-disturbance infaunal composition (Riddle 1988).

Long-term observations on an intertidal sandflat in western Kyushu, Japan describe changes in the distribution of individual macrofaunal species associated with the population expansion of *Callianassa* [*Nihonotrypaea*] *japonica* (Tamaki & Suzukawa 1991, Tamaki et al. 1992, Tamaki 1994). The burrowing shrimp population was initially restricted to the upper zone of the intertidal sandflat, but expanded its distribution range considerably to almost the entire sandflat in 1983, resulting in beneficial and adverse effects on associated species (Tamaki & Suzukawa 1991, Tamaki et al. 1992, Tamaki 1994). The isopod *Eurydice nipponica* was predominantly present in areas occupied by the shrimp, and when the latter species extended its range, the distribution of the isopod population expanded concurrently, with a concomitant 10-fold increase in population density (Tamaki & Suzukawa 1991). As the isopod usually occurs on exposed sandy beaches and subtidal areas that contain well oxygenated sand, it is possible that bioturbation by the shrimp sufficiently changed the sediment properties of the sandflat to provide suitable habitat for *Eurydice nipponica* (Tamaki & Suzukawa 1991). Habitat amelioration via shrimp bioturbation also explained the significant increase in snake eel *Pisodonophis cancrivorus* populations at this site (Tamaki et al. 1992). The increase in softness and sediment water content of the sediment through the shrimp's burrowing activities enabled the snake eel to bury easily and the increase in available habitat seemed to promote adult

migration from other areas. As *Nihonotrypaea japonica* is also an important prey species of the snake eel, the trophic significance of the shrimp contributed to the beneficial effects of its sediment disturbance for the snake eel population (Tamaki et al. 1992). In contrast to species benefiting from the increase in shrimp distribution, the filter-feeding gastropod *Umbonium (Suchium) moniliferum* became locally extinct at this site following the shrimp's expansion (Tamaki 1994). The possible impact of the shrimp may have been owing to its bioturbation activity, leading to the burial of newly-settled *Umbonium* juveniles and preventing feeding at the sediment surface. Species directly associated with the gastropod, including predators, ectoparasites and hermit crabs (that use the empty shells) disappeared subsequently, indicating the wider-ranging ecological consequences of the shrimp's population expansion (Tamaki 1994).

A recent study of an intertidal sand flat in Ariake Sound, Japan examined the distribution patterns of four dominant species, two thalassinidean shrimp (*Nihonotrypaea japonica*, *Upogebia major*) and two bivalve species (*Ruditapes philipinarum*, *Macraa veneriformis*) (Tamaki et al. 2008). The Manila clam *Ruditapes philippinarum* dominated the entire sand flat in the late 1970s, where it occurred at high densities and supported a productive commercial fishery (maximum annual yield 3830 tonnes), while the other three species were present, but only at low densities. In the 1980s, the abundance of *Ruditapes philippinarum* declined (annual yield less than 680 tonnes since 1990), whereas the populations of *Nihonotrypaea japonica*, *Upogebia major* and *Macraa veneriformis* expanded considerably; by 2004, populations of each species dominated different parts of the sand flat, with *Ruditapes philippinarum* restricted to the lowest quarter of the shore. As all four species exclusively use phytoplankton as their food source, the authors speculated that a reduction in planktonic diatom abundance coupled with sediment disturbance by the shrimp may have caused the adverse effect on *Ruditapes philippinarum*, resulting in the shift of dominant species in Ariake Sound (Tamaki et al. 2008).

Tamaki et al. (1992) describe a correlative study between ghost shrimp and snake eel populations and inferred that bioturbation-induced changes in sediment properties influenced the distribution of snake eels. Although there have been no causative studies that examined the influence of bioturbation on fish distribution, it is worth noting that the distribution of flatfish, which support commercially valuable fisheries, is greatly affected by sediment grain size properties. A number of North American studies established a strong link between sediment grain size and the distribution of a range of flatfish species, including Pacific halibut (*Hippoglossus stenolepis*), northern rock sole (*Lepidopsetta polyxystra*), winter flounder (*Pseudopleuronectes americanus*), and yellowfin sole (*Pleuronectes asper*), some of which support very valuable commercial fisheries (Moles & Norcross 1995, Phelan et al. 2001, Stoner & Abookire 2002, Stoner & Ottmar 2003). The preference for different sediment grain sizes varied with the size of fish and seemed to be related to their ability to bury, identifying sediment grain size as a critical factor for the fine-scale distribution of flatfish (Stoner & Abookire 2002). Substantial changes to sediment grain size, as have been attributed to biogenic disturbance, are therefore likely to affect the distribution of flatfish.

4.9 Influence on aquatic plants

Ghost shrimp can also exert their influence on benthic assemblages by controlling the distribution of seagrasses in tropical and temperate sedimentary habitats (Roberts et al. 1981, Suchanek 1983, Berkenbusch et al. 2007). Seagrass (predominantly *Thalassia testudinum*) abundance in a shallow Caribbean lagoon was negatively correlated with the mound density of ghost shrimp (*Callinassa* spp.) and experimental transplantation of seagrass into high-density ghost shrimp areas resulted in a

drastic deterioration of seagrass within weeks of transplantation (Roberts et al. 1981, Suchanek 1983). In a southern New Zealand inlet, bioturbation by the ghost shrimp *Callinassa filholi* impeded the experimental establishment of *Zostera capricorni* [*muelleri*] (Berkenbusch et al. 2007). The negative impact of ghost shrimp on seagrasses has been attributed to physical displacement and burial of seagrass plants, seeds and/or seedlings by sediment disturbance (Suchanek 1983, Duarte et al. 1997). In addition, indirect adverse effects associated with ghost shrimp bioturbation include the impediment of photosynthetic processes through increased sedimentation and resuspension of fine particles reducing light levels and covering of seagrass blades in fine sediment particles (Suchanek 1983).

As seagrasses play a crucial role in the functioning of inshore ecosystems, the adverse effects of ghost shrimp bioturbation on seagrass distribution has flow-on effects for associated species, including fish and lobster. Seagrass habitats support distinct macroinvertebrate assemblages and a shift in their distribution concomitantly changes the infaunal assemblage composition (Berkenbusch & Rowden 2007). Moreover, seagrass beds are considered important habitats for fish (see Seagrass section) and other fauna (e.g., lobster) (Jackson et al. 2001, Selgrath et al. 2007), and bioturbation effects on seagrasses are therefore likely to have flow-on effects for other species, including commercial ones.

4.10 Threats to burrows and burrowing organisms

The most obvious threat to biogenic structures and bioturbators are large-scale disturbances to the benthic habitat. Although some burrowing crustaceans have shown remarkable resilience to substantial anthropogenic and natural disturbances (Riddle 1988, Norkko et al. 2002), their ability to withstand adverse effects is greatly dependent on the extent and frequency of the disturbance. Natural disturbances, such as storms, can significantly affect coastal and offshore sedimentary habitats (Riddle 1988, Posey et al. 1996) and can cause a marked decline in bioturbator densities (Tamaki et al. 2008). Although callianassid shrimp seemed relatively unaffected by a tropical cyclone that disturbed the sedimentary habitat in Australia (Riddle 1988), population densities of *Upogebia major* were markedly reduced following a typhoon in Japan (Tamaki et al. 2008). In New Zealand, the burrowing crab *Helice crassa* was the only macroinvertebrate that was relatively unaffected by a one-off catastrophic sedimentation event; furthermore, bioturbation by this species remobilised thick clay deposits and mixed them into the underlying sediment, significantly improving the habitat for other colonising macroinvertebrates (Norkko et al. 2002).

Bioturbators are also directly threatened by fishing (e.g., bottom trawling) and aquaculture activities that inadvertently or deliberately remove and/or kill them (Widdicombe et al. 2004; Feldman et al. 2000). Scampi (*Metanephrops challengeri*) is the target of a dedicated fishery in a number of deepwater areas (main fisheries in the Bay of Plenty, Hawkes Bay/Wairarapa, Auckland Islands and the Mernoo bank area of the Chatham Rise). Bottom trawling also impacts other bioturbators with other megafauna and causes repeated disturbance to the seafloor (Jennings et al. 2001) and the application of pesticides is targeted to remove burrowing shrimps from intertidal oyster growing areas (Feldman et al. 2000, note: not New Zealand). In view of the functional importance of burrowing and bioturbating organisms, their removal is likely to have profound impacts on the overall ecology and functioning of sedimentary ecosystems.

THE DEEP SEA (MORE THAN 200 M WATER DEPTH)

For this review, we define ‘deep sea’ as being greater than 200 m water depth (Gage & Taylor 1991). With water depths well beyond the photic zone, animals assume the dominant role as biogenic habitat

formers. Generally speaking, our (limited) knowledge of how biogenic habitat may contribute to fisheries productivity rapidly declines with increasing water depth, due in no small part to the increasing logistical and financial costs of researching such environments. Most research has tended to focus within the range of scuba diving, generally less than 30 m (more often less than 10 m). Particular focus has been on saltmarsh, mangroves, seagrass (see previous sections), and coral reefs (tropics only), often with fisheries support being only a peripheral component of the work. Stock assessments of both coastal and deep water fisheries largely ignore the role of habitat in production, although it is slowly being recognised that to support viable stocks with appropriate harvest limits, sustainable fisheries require appropriate habitat in which fish can forage, take refuge, grow and reproduce (Auster & Langton 1999, Andrews et al. 2002, Rice 2006). Deeper water fish generally have lower levels of productivity; they are slow growing and long lived compared to continental shelf species, have low natural mortality rates, and are vulnerable to overfishing with slow recovery rates (Clark et al. 2001). The issue of whether these fisheries are sustainable is still debated (see Clark et al. 2001) and potentially central to this issue for many species is a better understanding of the role of habitat. Morato & Clark (2007) discuss the fact that seamount fish often occupy a range of habitats and that is important to understand what drives habitat selection, in order to sustainably manage fisheries and the surrounding ecosystem. In addition to fishing, other activities such as oil extraction and sea bed mining are continuing to expand into deeper water environments, such as proposed phosphate mining on the Chatham Rise, and (in coastal waters), the proposal to mine iron sands from the Whanganui Shelf in the South Taranaki Bight.

As the majority of deep-sea fisheries in New Zealand which might impact on biogenic fauna occur on, or around, seamounts, this review largely focuses on seamount biogenic fauna. The role of biogenic habitat in the deep-sea, in particular of corals, has only recently emerged as an area of ecological, economic and conservation interest (Auster 2005). Until recently, New Zealand research mostly focussed on fish and fisheries (see Probert et al. 1979, Clark 1999, Clark & O'Driscoll 2003, Tracey et al. 2004). While New Zealand studies have suggested links between the physical characteristics of seamounts and fish communities, quantitative information is lacking on any relationship between fish and benthic invertebrates (Clark & Field 1998, Tracey & Fenaughty 1997, Clark et al. 2001, Tracey et al. 2004).

While marine habitats are increasingly being tied to parts of the life cycle of commercially important species (Armstrong & Falk-Petersen 2008), despite focussed research there is still little information on how habitat loss may affect fisheries, and whether fishing activities are damaging to the fisheries themselves in terms of reduced production (Armstrong & Falk-Petersen 2008). This knowledge gap is even more acute in deep-sea environments. Given this, this section of the review is based largely on international studies, with the limited information from New Zealand included where available.

5.1 New Zealand's deep-water fish and fisheries

In New Zealand and South Eastern Australia, major aggregations of mid-slope demersal fish are known to be associated with topographic features including seamounts (Koslow et al. 1994) but it remains unknown if there are benthic-fishery interactions. As distinct geological features, seamounts can provide a focal point for both fish and fisheries (Clark 1999), and it is unsurprising that New Zealand seamounts are the location of important commercial fisheries, targeting large associated fish aggregations (Clark & O'Driscoll 2003). Seamounts are important meso-scale habitats for deep-water fish species in New Zealand (Clark & O'Driscoll 2003) and declines in catch levels and/or quotas as well as improved

technologies have changed the focus of deep-sea fisheries from the flat to seamounts where aggregations of fish occur for spawning or feeding (Clark & O’Driscoll 2003). There are major fisheries for orange roughy (*Hoplostethus atlanticus*) (Figure 38), black oreo (*Allocyttus niger*), smooth oreo (*Pseudocyttus maculatus*), black cardinal fish (*Epigonus telescopus*), alfonsino (*Beryx splendens*), bluenose (*Hyperoglyphe antarctica*) and rubyfish (*Plagiogeneion rubiginosum*) on and around New Zealand seamounts (Clark & O’Driscoll 2003). Of these seamounts, nearly 80% in the 500–1000 m depth range have been fished. Because of the often small size of seamounts, fishing efforts can be highly concentrated, and hence strongly impact on the extent of biogenic habitat. The New Zealand orange roughy fishery has been the biggest and most persistent deep-sea fishery, established in New Zealand for 20–30 years with an increasing seamount focus (Clark & O’Driscoll 2003). Despite this, there have been very few studies specifically examining the habitat of seamount fishes, or attempts to make comparisons with neighbouring areas. The authors reported only one species (black oreo *A. niger*) being more frequent on the seamount compared to the slope, while orange roughy were found on all sampled seamounts, but were also common on the slope, and hence are not obligate on seamounts (Figure 38). Orange roughy are observed to spawn over seamounts (migrating towards seamounts at certain times of year) but do not feed during spawning (Morato & Clark 2007). Clark & Tracey (1994) suggested that orange roughy populations may have different components – some residing on seamounts all year, and others migrating to the seamounts for spawning. Outside of spawning, orange roughy seemingly disperse over wide areas of slope. This mixture of movement behaviours, known as partial migration, is widely found in many other animal groups such as birds and mammals, and is recognised as common in marine fishes also, including many fisheries species (for an excellent review and example, see Kerr et al. 2009).

Dunn et al. (2009) used research trawl data (12 541 bottom trawls and 713 mid-water trawls) to assess where the nursery grounds of orange roughy might be. Juveniles were initially caught on the seabed, near known spawning grounds, and towards the shallower end of the species’ distribution. They were absent from mid-water, and the shallower and deeper bottom tows. Densities were greatest at 850–900 m. As juveniles grew in size, their spatial and depth distribution expanded to include both shallower and deeper areas, with a skew towards deeper water, so that by the time of maturation onset, densities were relatively high in 850–1300 m of water. The early nursery grounds were in relatively warm water, but on the south Chatham Rise appeared to be bounded by the presence of a cold-water front. No information on bottom habitats was included beyond depth, and whether they were sampled on flats or hills. There was also discussion of whether small juveniles (under 10 cm) were in fact meso-pelagic (living in the water column), with no evidence of them doing so from meso-pelagic trawl tows. As an interesting additional note, they also commented that a mid-water trawl survey was completed in 1992 on the south Chatham Rise and areas of the Sub-Antarctic, searching for mesopelagic juveniles of black and smooth oreo (*A. niger* and *P. maculatus*). Both species are suspected to have a mesopelagic juvenile phase, but the survey did not record a single specimen from 64 stations. The only juveniles recorded in New Zealand have come from bottom trawls, but juvenile oreos are rare in bottom trawls until about 20 cm in length (in contrast to orange roughy juveniles which are encountered on the seabed often at these and smaller sizes, Dunn et al. 2009). As a general rule, the ecology of the juvenile life history phases of deep-sea fisheries species is very poorly known.

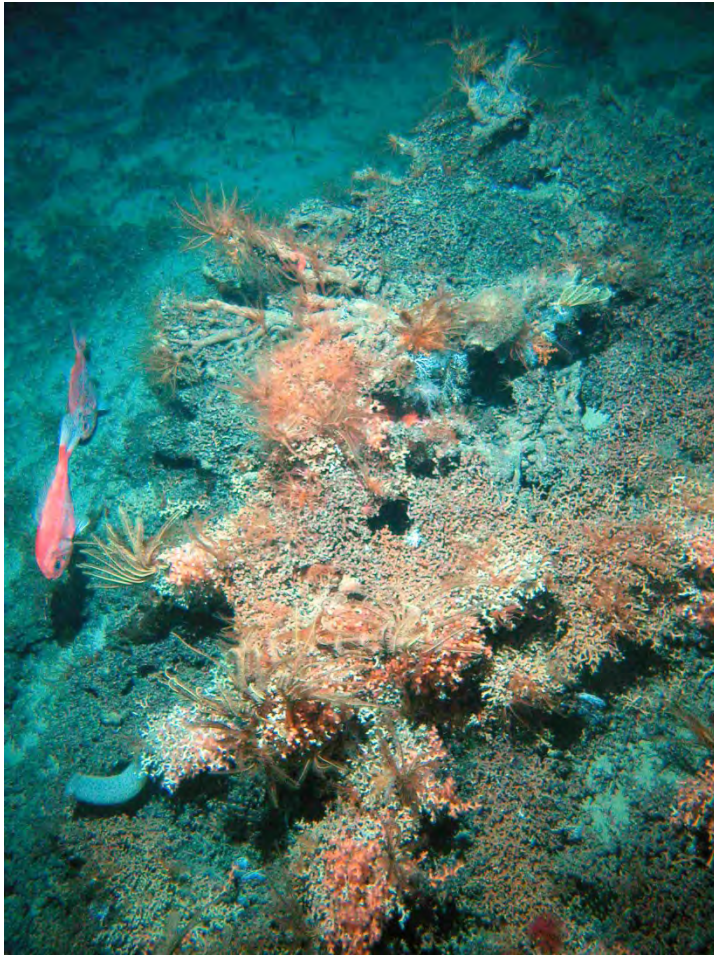


Figure 38: Adult orange roughy adjacent to deep-water coral and associated crinoids. Note that orange roughy do not show any special associations with deep-water corals, being found on seamounts where all of the coral cover has been (putatively) removed by fishing (Source: DTIS).

Tracey et al. (2004) looked at fish faunal differences between slope and seamounts. Species richness was higher on the slope compared to seamounts. Total species richness was similar in all seamount regions, but mean species richness was higher in southern areas. For all areas, orange roughy or smooth oreo were dominant (probably due to survey timing). A total of 70 fish species were found, other very abundant species included Baxter's lantern dogfish (*Etmopterus baxteri*), Plunket's shark (*Centroscymnus plunketi*), seal shark (*Dalatias licha*), longnose velvet dogfish (*Centroscymnus crepidater*), shovelnose spiny dogfish (*Deania calcea*), leafscale gulper shark (*Centrophorus squamosus*), spiky oreo (*Neocyttus rhomboidalis*), black oreo (*A. niger*), ribaldo (*Mora moro*), black cardinalfish (*Epigonus telescopus*), four-rayed rattail (*Coryphaenoides subserrulatus*), unicorn rattail and white rattail (*Trachyrincus* spp.), Johnson's cod (*Halargyreus johnsonii*), and warty squid (*Moroteuthis* spp.). Orange roughy were the only fish found in all of the 10 areas. There were strong similarities between fish species on the four Chatham rise seamount areas and the Puyseger Bank area, which differed from the other areas investigated (Mercury Knoll, Challenger Plateau, and East Cape). These latter areas differed from each other. Depth, longitude, latitude, sediment type, bottom temperature, and current convergence zones were all found to be important influences on structuring fish assemblages (Tracey et al. 2004 and references therein) and the depth, height and diameter of seamount, as well as impact on local current regimes, were also considered as potential explanations (Tracey et al. 2004). No information was included on the potential role of biogenic habitats.

Leathwick et al. (2006) used research trawl data to predict fish species richness at the national scale, and found the highest richness to occur along the northern flanks of the Chatham Rise and around the northern end of the Solander Trough. High richness was also predicted for Tasman Bay, and a strip of water around the continental slope off the coast of Westland, Otago, and from Kaikoura north along the east coast of New Zealand to the Bay of Plenty. Moderately high species richness was predicted for large areas with depths between 500–1000 m on the Chatham Rise and Challenger Plateau. In these areas, richness was predicted to decrease with progression to greater depths. So-called “cold spots” were located in the Challenger Plateau (McClatchie et al. 1997 as cited in Leathwick et al. 2006). Leathwick et al. (2006) determined depth to be the single most important environmental predictor of variation in fish species richness. Highest richness was observed 900–1000 m (moderately high richness observed between 400–1100 m) and in waters with high surface chlorophyll a and in zones where different water bodies mix. Lower species richness was observed in waters that were cooler than would be expected (given their depth). As with Tracey et al. (2004), no information on biogenic habitat influences were available for inclusion in these analyses.

5.2 Corals

Location

Globally two thirds of all known coral species are found in the deep-sea (Roberts & Hirshfield 2003), and cold-water coral ecosystems occur extensively in deep waters on continental shelves, slopes, seamounts and ridges around the world (Roberts et al. 2006, Ross & Quattrini 2007). In New Zealand’s deep-sea the major biogenic taxa are the scleractinian (stony) corals, and to a lesser degree, octocorals (which include gorgonians). The New Zealand region possesses one of the world’s most diverse deep-sea coral faunas (Rowden et al. 2008). Cnidarians can comprise some of the most visible fauna on seamounts - including Scleractinia (stony corals), Antipatharia (black corals), Zoanthidea (zoanthids), Octocorallia (gorgonians, sea fans, soft corals) and Stylasteridae (hydrocorals). The corals *Solenosmilia variabilis* and *Madrepora oculata/Madrepora vitiae* are the species most commonly observed to form ‘reefs’ or ‘thickets’, most often on seamounts. In the New Zealand region there are good quality coral and sponge presence records but as most seamounts have not been biologically sampled there are no wide-spread presence/absence records of habitat-forming species in general (Rowden et al. 2008). *Solenosmilia variabilis* is one of the major reef forming corals and builds extensive reefs on seamounts, alongside the secondary reef formers *Madrepora oculata* and *Desmophyllum dianthus* (Koslow et al. 2001, Clark & O’Driscoll 2003).

There is little published information on the occurrence of biogenic corals in the New Zealand region. Tracey et al. (2011) used a range of information sources to model the distributions of five habitat-forming coral species: *Madrepora oculata*, *Solenosmilia variabilis* (Figure 39), *Goniocorella dumosa*, *Enallopsammia rostrata* and *Oculina virgosa*. Using boosted regression trees, they described the distribution (presence) of these species in terms of depth, geographic distribution, and geomorphic habitat associations, using eleven environmental input variables (depth, bottom water temperature (corrected for depth), slope, seamount, sea surface current velocity, orbital current velocity, tidal current speed, sea surface temperature gradient, surface water primary productivity, dissolved organic matter and particulate organic carbon flux). They found that the importance of these environmental variables differed greatly between species, but depth and seamount occurrence were consistently important factors for describing observed coral species distribution. *M. oculata*, *S. variabilis*, and *E. rostrata* occurred in deep waters (more than 1000 m) where seabed slopes were steep, tidal current

and orbital velocities were slow, sea surface primary productivity was low, and where seamounts were generally present. By contrast, *G. dumosa* and *O. virgosa* were found in relatively shallower waters, where sea surface primary productivity was high and tidal current speeds were generally fast. Spatial predictions were consistent with the recorded observations and identified that all species (except *O. virgosa*), were distributed throughout the region and were found primarily between about 200 and 2000 m.

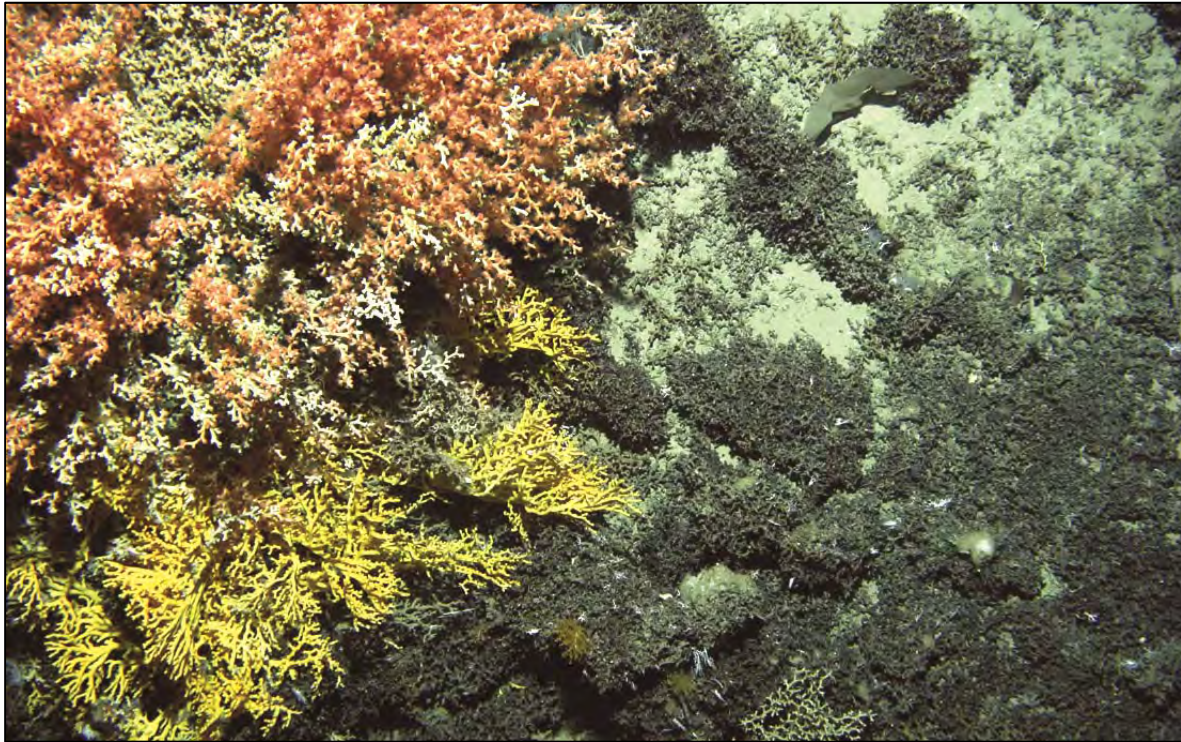


Figure 39: Sea floor dominated by habitat-forming stony corals *Solenosmilia variabilis* (upper left) and *Madrepora oculata* (lower left) on a seamount off New Zealand. (Source: Tracey et al. 2011).

Value and function

By offering a suite of potential habitats biogenic fauna may enhance the survivability of deep-sea fish (Costello et al. 2005). Cold-water corals act as ecosystem engineers and are “*arguably the most three-dimensionally complex habitat in the deep-sea*” (Roberts et al. 2006) and can provide habitat for numerous invertebrates and fish (Rowden et al. 2008) yet few quantitative studies have been made, with most findings relating to fish-invertebrate habitat associations being anecdotal or qualitative. One of the central issues relevant to corals, and all structure forming invertebrates, is how much these fauna contribute to the overall functioning of the ecosystem, as well as the life histories and productivity of economically important fishes (Auster et al. 2005, Tissot et al. 2005). Etnoyer & Morgan (2005) define habitat-forming deep-sea corals as “*those families of octocorals (e.g. Coralliidae, Isididae, Paragorgiidae and Primnoidae), hexacorals (Antipathidae, Oculinidae, and Caryophyllidae), and stylasterids (Stylasteridae) with species that live deeper than 200 m, with a majority of species exhibiting complex branching morphology and a sufficient size to provide substrata or refugia to associated species*”. Etnoyer & Morgan (2005) did not consider scleractinian solitary corals to be habitat forming.

These ecosystems are recognised as biodiversity hot spots, important habitats, and as repositories of past-climatic conditions. For the coral *Lophelia*, at thousands of years old, the scale of such reefs (and associated carbonate mounds) can exceed several kilometres in length and occur at heights of up to 300 m (Roberts et al. 2006). As with many other biogenic habitats, corals occur in a variety of density settings; including as individual colonies, in beds, and as biogenic reefs proper. All of these forms potentially provide habitat for a wide range of other animals, including other corals, sponges, echinoderms, and fish. Deep-sea coral habitats offer a large surface area for invertebrate colonisation, as well as a matrix within which small fish can shelter. Consequently, competition and predation may be reduced in deep-sea reefs (and other complex biogenic habitat) with greater availability of foods and shelter (Roberts et al. 2006). Sub-habitats within coral-based habitats include coral rubble, sediment clogged coral frameworks, and dead coral frames (Rogers et al. 2007) which further increases habitat availability and associated biodiversity (Jensen & Frederiksen 1992, Mortensen et al. 2004b, in Rogers et al. 2007, Rogers et al. 2007). Possible roles of these habitats in supporting deep sea fisheries include shelter, spawning and foraging functions. In general, the number of macrofaunal and megafaunal species and the density of organisms tend to be higher on cold-water coral reefs relative to surrounding unstructured habitats (Husebø et al. 2002, Jonsson et al. 2004, and Roberts et al. 2006). However, effectively all studies are observational in nature, and are often not specifically focussed on fisheries species. Relatively few studies have addressed the role of deep-sea invertebrate fauna in providing habitat for fish and other fauna.

Tissot et al. (2005) examined deep bank habitats off southern California, and found that only 1.8% of sessile invertebrate individuals (sponges, black corals, and gorgonians) had other organisms attached or lying on them. These associated species included crinoids, sponges, crabs, basket stars, brittle stars, sea-stars, anemones and salps, with fewer than 1% of the observations being of fish. Of the 108 fish species observed, only 6 were found more often adjacent to invertebrate colonies, than predicted by chance. Furthermore the median distances between fishes and invertebrates (1–5.5 m) indicated little actual physical contact between the two groups, bringing into question whether any functional relationship was operating (but note scale issues in this argument). Parrish (2004) (PhD thesis: as cited in Tissot et al. 2006) also determined that there was no evidence of black corals serving to aggregate fish, but nevertheless concluded that they co-occurred. However, Tissot et al. (2006) did consider that their observations of a lack of commensals might be unique to their study region on shelf communities off southern California.

Ross & Quattrini (2007) documented fish species abundance on and around deep coral banks (*L. pertusa*, *Enallopsammia profunda*, *Leiopathes* spp., *Keratoisis* spp.) (356–910 m) off South Carolina, United States. Characterising three broad habitat classes, “prime reef”, “transition reef”, and “off reef”, the authors investigated the distribution of fish species. Different fish species had specificity to both prime and off reef habitats, while transition reefs had a mixture of species found on either prime reef or off reef habitat. Prime reef was characterized by the morid cod *Laemonema melanurum* (21% of total), rough-tip grenadier *Nezumia sclerorhynchus* (17%), alfonsino *Beryx decadactylus* (14%), and the blackbelly rosefish (scorpinfish) *Helicolenus dactylopterus* (10%). Off reef areas were dominated by Pluto skate *Fenestraja plutonia* (19%), shortbeard codling *Laemonema barbatulum* (18%), hagfish *Myxine glutinosa* (8%), and shortnose greeneye *Chlorophthalmus agassizi* (7%). On transition reef, *N. sclerorhynchus* was the most abundant (25%) followed by *L. barbatulum* (16%) and *L. melanurum* (14%). Ross & Quattrini (2007) observed that swallowtail bass *Anthias woodsi*, *B. decadactylus*, American conger *Conger oceanicus*, and cutthroat eel *Dysommia rugosa* were specific to deep-reef habitats, whereas species including *C. agassizi*, blind torpedo ray *Benthobatis marcida*, *F. plutonia*, and longfin hake *Phycis chesteri* were more common away from reefs. Overall more

species were observed on reef than off. Of particular interest was that in contrast to shallow coastal complex structure habitats (reef, vegetation, anthropogenic) which serve as nursery habitats for juvenile fish, on the deep coral banks they rarely observed or collected small juveniles of most fish species. While allowing for possible seasonal effects, they felt that they would have encountered juveniles if present. This absence was consistent with a similar reported lack of juvenile fishes from *Lophelia* reefs, which was attributed to cryptic behaviour (Costello et al. 2005). However, frequent rotenone station collections by Ross & Quattrini (2007) on the deep coral reefs did not flush out potentially hiding juvenile fishes. In fact, these authors noted that juveniles of most species were largely lacking from shelf edge reefs in the region. It was suggested that ontogenetic habitat shifts might be in play, with the juveniles of many species being found elsewhere. Examples included juveniles of several deep-water species (e.g., *P. americanus*, *N. bairdii*) which occupied surface or mesopelagic environments (references in Ross & Quattrini (2007), as well it being possible that juvenile fishes were utilising open, soft bottom habitats away from deep reefs, where predation might be less severe. Juveniles of a few species (roughly *Hoplostethus* spp., *L. barbatulum*, and *Nezumia* spp.) were collected by the authors in otter trawl surveys away from the reef habitats.

The majority of cold-water coral reefs have been found in the northeast Atlantic Ocean, and are usually dominated by *Lophelia pertusa*. Narratives of some of the first observations of *L. pertusa* reefs in 1982 described many fish and crustaceans swimming in and out of the corals (Hovland et al. 2002). More than 1300 species of fish and invertebrates were reported living on *L. pertusa* reefs in the north-eastern Atlantic (Roberts et al. 2006). Many fish species associated with *Lophelia* reefs are commercially fished (Hall-Spencer et al. 2002; Husebø et al. 2002). In the continental break off south-western Norway, Furevik et al. (1990; Norwegian publication as reported in Husebø et al. 2002) observed faunal differences between *L. pertusa* and non-coral substrate from an ROV. Associated with the major coral habitat were sponges, gorgonians, soft corals, squat lobsters, crabs, sea urchins and ophiuroids with the fish fauna dominated by redfish (*Sebastes marinus*), tusk (*Brosme brosme*), and saithe (*Pollachius virens*). Redfish were observed to swim in groups (3–7 fish) very close to the top of the coral colony, or lying in between. The behaviours of tusk and saithe were different – with fish swimming actively around the branches but occurring as solitary individuals. Sponges and sea-pens were the most visible macrofauna on the soft bottom, with fish including cod, haddock, saithe, greater fork-beard, skate and ratfish.

Following on from the work of Furevik et al. (1990; Norwegian publication), Husebø et al. (2002) investigated the occurrence of redfish, ling (*Molva molva*), and tusk, on and off *L. pertusa* reefs on the continental shelf off south-western Norway (150–330 m). Based on experimental long-lining, *Lophelia* reefs were observed to support significantly more redfish than non-coral habitat; this species is commercially important (e.g. in the Faroes, Norway). Ling and tusk were also reported to be more numerous in coral habitat, although this difference was not significant statistically. Wolf fish (*Anarhichas minor*), haddock (*Melanogrammus aeglefinus*) and greater fork-beard (*Ohycis blennoides*) were mainly caught in coral habitat; in contrast spurdog (*Squalus acanthias*) as well as skates (*Rajidae*) and rays (*Torpedinidae*) were numerous in non-coral areas (complementing the observations of Furevik et al. 1990). Cod, saithe and Atlantic halibut were caught in both habitats in small numbers. Husebø et al. (2002) observed larger redfish, tusk and ling over coral compared to non-coral habitat, but could not hypothesise on the reasons e.g., enhanced feeding, or larger fish seeking out reef habitat. *L. pertusa* was however hypothesised to fill different functional needs for each species in general, e.g., feeding location for tusk, whereas for the planktivorous redfish their affinity for the reef was attributed to the physical structure of the reef.

Costello et al. (2005) found greater fish abundance (80% higher) and species richness (92% higher) on *Lophelia* reef than seabed, and concluded that *Lophelia* reefs provide a very important fish habitat functioning role in deep-water ecosystems. Furthermore, the authors found that 68% of fish species associated with *Lophelia* reefs were commercially fished, and cumulatively comprised 82% of the abundance of fish associated with *Lophelia* reefs. In total, the 17 commercial fish species identified as showing associations with reefs make up 90% of the total tonnage of fish landed in the North Atlantic (ICES 2003, as cited in Costello et al. 2005). It was noted however that the greatest diversity of fish were recorded in the transitional habitats between the reefs proper and surrounding habitats, and that these species were not confined solely to reef habitats, suggesting that reefs act as centres of fish species richness and abundance (Costello et al. 2005).

Oculina varicosa is a facultative zooxanthellate coral (i.e., it possesses algal symbionts in shallow water) and has been compared to *Lophelia* reefs in terms of both structure and development. Found down to 100 m along the eastern Florida shelf of the United States, *Oculina* may serve as a proxy for deep-water coral reefs. Its equivalent in New Zealand waters is *Oculina virgosa*, which has been recorded from 29 to 792 m, with a median depth of 105 m (Tracey et al. 2011). The invertebrate biodiversity of the *Oculina* reefs is considered to equal shallow tropical reefs (Reed 2002) and it is believed that the dense invertebrate community in turn supports dense and diverse fish populations (G. Gilmore pers. comm., in Reed 2002). Deep *O. varicosa* reefs are breeding grounds for commercially important fish such as gag (*Mycteroperca micolepsis*) and scamp (*Mycteroperca phenax*) groupers (Reed 2002) These fish inhabit a variety of depths, but favour water depths greater than 70 m during spawning activities. *O. varicosa* reefs on the continental shelf edge may also form part of the migration routes for king mackerel (*Scomber omoruscavalla*), Spanish mackerel (*S. maculatus*), and wahoo (*Acanthocybium solandri*). Deep-water *Oculina* reefs have also been implicated in the courtship and mating of some species (Reed 2002) and large populations of the commercially important squid *Illex oxygonius* have been observed spawning on the banks (NOAA, 1982 as cited in Reed 2002). Historically (1970s), Reed et al. (2002) reports that *Oculina* reefs were observed to hold abundant fish populations, and to support extensive breeding and feeding grounds for commercially important populations of grouper and snapper, with large spawning aggregations of scamp and gag grouper common above individual *Oculina* reefs. Such spawning aggregations were specifically targeted by fishing. By the 1990s, after 20 years of fishing effort, both *Oculina* habitat and associated fish abundances were greatly reduced. In response to these issues, in 1984, 315 km² was designated as the ‘*Oculina* Habitat of Particular Concern’ (OHAPC) and trawling, dredging, bottom long-lines and anchoring were prohibited; establishing the first “deep-sea” coral marine protected area in the world. This *Oculina* Marine Protected Area (MPA) was further expanded to 1029 km² in 2000. However, illegal trawling has continued, and manned submersible and ROV observations between 1995 and 2003 indicated that portions of the coral habitat within the MPA had been reduced to rubble, and grouper spawning aggregations were likely to be absent.

Growing as single or multiple trees, colonies of the gorgonian *Primnoa* can be greater than 2 m in height and be up to 7 m wide, depending on species (Krieger & Wing 2002). These slow growing colonies may be several hundred years old (Risk et al. 2002 as cited in Andrews et al. 2002). In the eastern Gulf of Alaska, Krieger & Wing (2002) observed *in situ* (from a manned submersible) six rockfish species beneath, among, or above *Primnoa* spp., and concluded from this that these corals held some attraction for rockfish. Below depths of 300 m, almost all suspension feeders (including sponges, crinoids, basket stars, anemones) present were associated with the coral. *Primnoa* itself was predated on by sea stars, nudibranchs and snails (Krieger & Wing 2002). Species included the commercially valuable rockfishes (rough-eye *Sebastes aleutianus*, short-raker *Sebastes borealis*, and yelloweye *Sebastes ruberrimus*). Krieger & Wing (2002) suggested that *S. ruberrimus* may use *Primnoa* as a viewing point to capture

prey. Generally *Sebastes* species seem to have a dependence on regions with a hard bottom and substantial relief (Brodeur 2001 and references therein) though they have also been associated with flat bottoms (Krieger 1992, as cited in Brodeur 2001). In the Pribilof Canyon (Bering Sea), Brodeur (2001) reported an association of rockfish with pennatulaceans, with the night time phenomenon of hundreds of rockfish (*Sebastes alutus*) resting in sea whip (*Halipteris willemoesi*) forests, swimming out during the daytime to feed on dense euphausiid swarms. Brodeur (2001) recorded fewer rockfish in areas with damaged sea whips, and no rockfish in areas without sea whips, and conclude that in an otherwise featureless environment sea whips may represent important structural habitat for rockfish.

Gorgonians can also form dense stands, which have been recorded in the North Pacific, throughout Hawaii, along the Aleutian Island Chain, and in the Gulf of Alaska and the Bering Sea (Stone 2006). Redfish (*Sebastes* spp.) as well as shrimp, galatheids, and other crustaceans have been found to be abundant in these habitats, as well as attached suspension feeders including other corals, crinoids, basket stars, and sponges (Parrish & Baco in press, as reported in Rogers et al. 2007). Tissot et al. (2005) and Etnoyer & Morgan (2005) also observed fish egg cases attached to vase sponges and gorgonians respectively.

In the Gulf of Mexico, gorgonians (*Callogorgia* spp) colonies are widespread and considered to be habitat forming (Etnoyer & Warrenchuk 2007). During survey work in 2003, egg cases of an unknown species of scyliorhinid catshark were found in abundance on a low-relief mound at 533 m depth in a large field of gorgonians (family Primnoidae) in the Mississippi Canyon, Gulf of Mexico. Gorgonian colonies were spaced one to two metres apart, and were heavily silted, with no hard bottom substrate being evident. These colonies were 25–50 cm tall, with a total of 296 egg cases, attached to 117 colonies (11% of the colonies observed). The highest number seen on a single colony was 17, with a mode of one egg case per colony. Octocorals with eggs were described as being “somewhat clustered”. The egg case dimensions ranged from 48–57 mm in length, and 18–22 mm in width, consistent with those of the chain cat-shark (*Scyliorhinus retifer*). Submersible observations in the mid-Atlantic Bight have also documented egg cases of this species attached to soft corals, hydroids, and derelict fishing gear (Able & Flescher 1991). Etnoyer & Warrenchuk (2007) concluded that large (over 1 km) monotypic fields of gorgonian octocorals on low relief mounds could provide nursery habitat to fish species in the Gulf of Mexico. They also noted that deep scleractinian thickets were rare in the Gulf, and therefore gorgonians might provide essential habitat for cat-sharks simply due to a lack of alternatives. It was suggested that widespread and local anthropogenic impacts to gorgonian communities, such as bottom trawling, longlining, and ocean dumping, posed inadvertent threats to deep water nursery habitats for cat-shark populations.

Past and current status and threats

In New Zealand, our knowledge is largely limited to species presence/absence range modelling (Tracey et al. 2011). One of the key goals of such modelling is to provide information relevant to the development of management strategies that could provide protection and conservation of these vulnerable and at-risk taxa (Clark & Tittensor 2010). However, in terms of predicting functional fisheries habitats, it does not address the issue of where such species occur in sufficiently dense aggregations to provide actual habitat values. Knowledge of threats is limited, although fishing of seamounts has had a strong impact.

Watling & Norse (1998) (in-)famously compared the effect of trawling the seabed to forest clear cutting, the action both reducing structural biodiversity, and the dependant biota. Removing biogenic

habitat in the deep-sea puts recovery at a scale of decades (if not more) and the changes may be such that the environment may never return to a similar state. It is widely agreed that trawling can significantly alter marine benthic habitats and communities (see Koslow et al. 2001 and references therein) which may in turn yield “secondary” or “indirect” impacts on the community e.g. juvenile or adult fishes which utilise biogenic structures (Sainsbury 1988, Koslow et al. 2001). It is also thought that damage to habitat forming corals can affect local hydrodynamic and sedimentary conditions (Rogers 1999) and can have profound implications for the entire ecosystem e.g., a shift from a diverse reef community to a reduced species/biomass “disturbance” community (Koslow & Gowlett-Holmes 1998). The effects of trawl gear have long been known and in the one to two decades there has been growing political and public awareness on this issue (Clark & O’Driscoll 2003). There is little dispute that destructive fishing gear is a major cause of habitat deterioration removing both biogenic and sedimentary structures, as well as the organisms themselves (Armstrong & Falk-Petersen 2008).

Rogers et al. (2007) state that there may be a direct link between commercial fish species and benthic habitat forming organisms, with fishing not only removing the fish but the habitat essential to support these communities. Fosså et al. (2000), based on the observations of Norwegian long-line fishermen, reported that there has been a marked decline in ling and tusk catches in continental shelf areas where corals had been removed e.g. due to trawling (reported in Husebø et al. 2002). However, Koslow et al. (2001) observed no secondary ecological impacts on the deep water fisheries off southern Tasmania resulting from the loss of coral habitat, and attributed this to the natural absence of juvenile orange roughy and oreosomatid fishes (i.e. juveniles do not use coral as habitat), and also taking into account the fact that the dominant benthopelagic fishes mostly feed on water column prey (Bulman & Koslow 1992). However, Koslow et al. (2001) did consider that the removal of *Solenosmilia variabilis* might affect the numerous invertebrates and several fishes which were associated with coral substrate, and noted that many could be endemic to the region. Overall Koslow et al. (2001), considered observations of seamount reefs to be too limited to form definitive conclusions pertaining to the roles of such biogenic habitats in the deep-sea.

Information gaps

Collectively, deep-water studies of biogenic habitat and associated fisheries species are at a very early stage, and largely revolve around observations of what is present, either through remote camera systems, or through direct observation by submersibles. Very little work could be found that made an attempt to link fisheries production to deep-sea biogenic habitats, and for most finfish fisheries species little information was even available on where juvenile life stages were to be found. The high relative abundance of biogenic habitats on seamounts was particularly noticeable (Rogers 1999). Two areas of research are suggested.

Suggestions for new research are:

- Review and analyse existing video and other samples to assess whether fish associations (especially of juveniles) occur with deep-sea biogenic habitats. A proposal has already been put to BRAG and is currently on the 2014 short list (BRAG documentation).
- Continue to focus effort on where the juveniles of species such as orange roughy, oreos, and others occur, as a common comment from the studies reviewed is that the location of juveniles is usually unknown, and in fact some species may have ontogenetic habitat shifts from other (potentially pelagic and/or non-biogenic) habitats to biogenic habitats as they grow (which would differ greatly from shallower coral and other systems).

Recommended measures

It is not possible with the present state of knowledge to make any definitive conclusions on possible links between deep-sea biogenic habitats and fisheries production. However, the vulnerability of biogenic habitat species such as deep-sea corals, which are fragile, sessile, slow growing, long-lived, have a low natural mortality rate, may have limited larval dispersal, and are restricted to certain habitats (e.g. seamounts) which are the focus of commercial fisheries; makes it prudent to take a conservative approach in protecting them from undue losses (Roberts & Hawkins 1999). Deep-sea corals are also at risk from other threats e.g. increased atmospheric CO₂ (drop in ocean alkalinity). Andrews et al. (2002) cited a number of authors in saying that “*many species of deep-sea corals provide high relief habitat for a number of ecologically important species of invertebrates and fishes*” and made the recommendation that biogenic habitats be better studied, especially against a backdrop of fisheries declines.

In the United States, the Sustainable Fisheries Act of 1996 moved towards protecting “Essential Fish Habitat” under the premise that sustainable fisheries are dependent upon healthy fish habitat (Andrews et al. 2002). The North Pacific Fishery Management Council identified Habitat Areas of Particular Concern (HAPC) and corals and sponges were amongst those types recognised (Andrews et al. 2002). Furthermore, Witherell & Coon (2002 conference proceedings; as cited in Andrews et al. 2002) recognised red tree coral as essential fish habitat. The essential fish habitat programme was started, stemming from the 1996 Sustainable Fisheries Act (USA), to promote the protection of this habitat (Andrews et al. 2002). Conservation measures have also been implemented for *Lophelia* reefs in Norway, Sweden, and proposed for the Darwin mounds in the Northeast Atlantic (see Costello et al. 2005 and references therein).

5.3 Bryozoans

To date no evidence has been found of bryozoan reefs/mounds/clumps in the deep-sea, and their existence is thought unlikely (Dennis Gordon, NIWA, pers. comm.).

5.4 Sponges

Deep-water sponges are poorly known in New Zealand (beyond taxonomic description), and little work is available on them internationally, despite the recent discovery of massive glass-sponge bioherms in the northern hemisphere (Conway et al. 2005, 2007, Cook et al. 2008). In New Zealand there exist anecdotal records of sponge gardens on the Chatham Rise, with the sponges occurring in such densities as to be recorded as “foul ground” by fishers. It was proposed that the Chatham Rise Oceans 2020 programme sample this area, but technical problems prevented this.

5.5 Tubeworms

No information is available for tubeworm biogenic habitats in deeper New Zealand waters.

Treude et al. (2011) reported abundant cat shark (possibly *Galeus melastomus*) egg capsules associated with a dense tubeworm field (*Lamellibrachia* spp) on carbonate crusts in the eastern Mediterranean Sea (500 m water depth) (Figure 40), and dense skate (probably the genus *Bathyraja*) egg capsules with a cold-seep carbonate feature in the south-east Pacific Ocean (700 m water depth). They concluded that deep-water elasmobranchs may use cold seeps (and associated biogenic habitats) for nurseries in many parts of the world oceans.



Figure 40: Shark egg capsules of the deep-water cat-shark in a tubeworm field at the North Alex Mud Volcano, eastern Mediterranean Sea. Shark egg capsules are the brown objects (Source: Treude et al. 2011).

CASE STUDIES OF BIOGENIC HABITAT LINKS TO FISHERIES

Work linking biogenic habitats to actual fisheries production is rare, and likely to be an increasing research focus in the near future. Current fisheries stock assessments and management largely ignore the potential role and influence of habitat. In the following section, we describe three case studies which help bridge the divide. One of the great challenges in linking biogenic habitats to fisheries production is the scaling up of smaller scale studies to the larger scales over which fish (meta-) populations and associated fisheries operate: the first case study describes an approach to this problem using blue crabs in the northern Gulf of Mexico. Feedback from fishing impacts to fisheries production is another challenging area; the second case study quantifies a relationship between the removal of sponges by fishing, and selected fish populations on the North-west Australian Continental Shelf. The third case study shows empirical links between the presence of deep-water corals and catches of sable-fish; as well as empirical meta-analysis on the role of biogenic structure in elevating the abundance of other species, including fisheries ones.

6.1 Blue crabs in the northern Gulf of Mexico

As an example of one possible approach, Jordan et al. (2009) developed a multi-scale modelling framework for blue crab (*Callinectes sapidus*) in the northern Gulf of Mexico. They argued that a key scientific challenge in terms of human impacts on coastal ecosystems was to be able to model and predict the cumulative effects of these impacts on both the ecosystems, and the associated services that they provided to society ('the death of a thousand cuts'). Many of the most valuable coastal fisheries depend on underpinning functional coastal habitats, but few attempts have been made to scale up from the relationships between local scale habitat attributes and (invertebrate) population dynamics that are often measured, to a cumulative impact analysis at the scale of the population and associated fisheries extractions. They suggested that building models linking vital biological rates measured at the patch scale, with regional-scale geospatial coverage and long term fisheries data appeared to be a promising approach, and that such models 'could be used to evaluate a wide range of

scenarios of cumulative habitat loss, alteration, and restoration for their effects on the sustainability of coastal fisheries'. With the addition of economic values, they could also be used in cost-benefit analyses, as a basis for informing management decisions and policies at local, regional, and national scales.

As a proof-of-concept, they looked at the commercial blue crab fishery in the Gulf of Mexico (1980 – 2004 average commercial landings 26 800 t, value over \$US40M – as well as a further 4–20% recreational landings, and by-catch in trawl fisheries). The fishery shows increasing effort and catch over time, but a strong reduction in Catch Per Unit Effort (CPUE) over time. Field and laboratory studies in the Gulf of Mexico and Atlantic coastal environments have shown that vegetated habitats (salt-marsh and seagrass) support higher early juvenile blue crab population densities and survival rates, relative to un-vegetated habitats. This has been attributed to reduced inter- and intraspecific predation (Moksnes et al. 1997, Minello et al. 2003). Aggregate values from eight such studies indicated a 38% survival advantage for marsh and a 41% survival advantage for seagrass over open-water habitats (Minello et al. 2003). To model the potential effects of human-driven changes in the proportions of these habitats, the Alabama Mobile Bay estuary system was overlain with a hexagonal grid, with each polygon representing 55.2 km² (Figure 41a). Land-cover data sets were used to assign to each hexagon respectively, a summed total for each of the following classes: emergent vegetation-marsh edge (ME), soft non-vegetated bottom (SNB), and submerged aquatic vegetation (SAV). Each hexagon was also assigned to a salinity zone based on salinity data: oligohaline, mesohaline, polyhaline, or euhaline (Figure 41b).

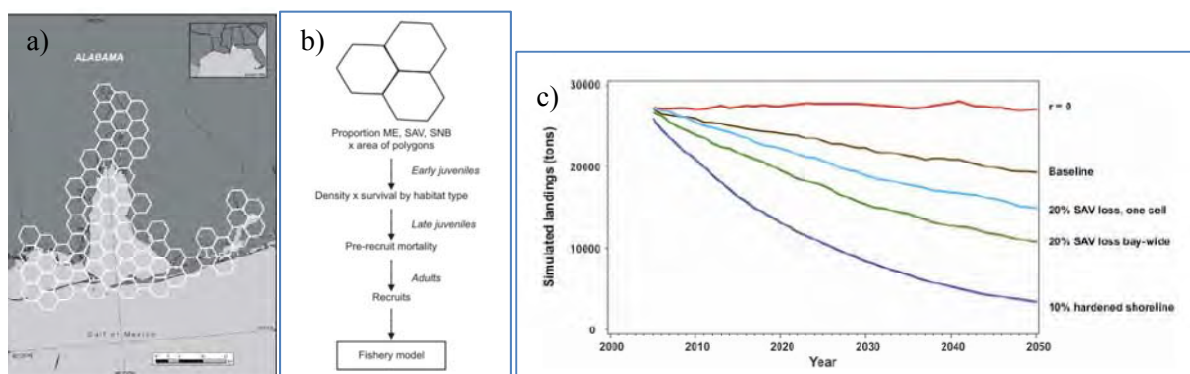


Figure 41: a) Mobile Bay and adjacent Alabama estuaries overlain with a hexagonal grid for estimation of blue crab recruitment from selected habitat types, b) schematic diagram of the habitat model for estimating effects of habitat change on the blue crab fishery. ME – marsh edge, SAV – submerged aquatic vegetation, SNB – soft, non-vegetated bottom, c) simulated blue crab landings based on five scenarios (see text for details). (Source: Jordan et al. 2009).

Published values of average estimated densities (# per m²) of post-larval and juvenile blue crabs (under 10 mm carapace width, CW), for each habitat and salinity combination (Minello 1999), were used to calculate the expected summed production of each hexagon. Each of these summed numbers was then multiplied by the mean survival rates for these survival classes, based on compiled field and laboratory experimental results (Minello et al. 2003). The number of juveniles expected to survive from each hexagon was then multiplied by an estimated proportion of older juveniles (10–124 mm CW) surviving sources of natural mortality before recruiting to the fishery (estimated from fishery-independent CPUE data). As blue crab become less reliant on vegetated habitats as they grow, this two stage formulation, with habitat-dependent survival being applied only to the earlier life stages (under 10 mm CW) was considered reasonable. The salinity stratification was only used for densities; insufficient information was available to calculate survival rates by salinity zone.

The cumulative contribution of all hexagons was used to estimate the number of blue crab individuals recruited from the Mobile Bay system to the adult Gulf of Mexico population. Simulations were then run on the same system; with the habitat coverages being manipulated to model the effects of habitat change within each cell, and within the overall system. The scenarios used were 1) no change, baseline habitat conditions, 2) 20% SAV loss within the system across multiple cells, 3) 20% SAV loss within one cell, and 4) 10% hardened shoreline (i.e., loss of ME and SNB habitat).

A fisheries model was then constructed, using three parameters: S_0 , the initial stock of fishable hard crabs in tons; r , the instantaneous annual rate of population change; and F , the instantaneous annual rate of fishing mortality (see Jordan et al. 2009 for a detailed model explanation). A historical fisheries catch time series (1950–2004) was de-trended for increasing fishing mortality over time, and the residuals used as an estimate of annual recruitment (r), with an associated error structure. The different scenarios of habitat alteration were inputted to the model by computing r from the proportional reduction in recruits for each scenario (with respect to the baseline value). They used this model to project forward to 2050 likely outcomes from the different scenarios, in terms of maintaining the level of catch at the 2004 value (i.e., the probability that the current level of catch will be maintained). These probabilities were directly proportional to the value of r . The baseline scenario suggested a 39% probability of catch being maintained, the 20% SAV bay-wide loss scenario 26%, the 20% SAV loss in one hexagon scenario 35%, and the 10% hardened shoreline (i.e., loss of ME and SNB habitat) 4%. Expressed in a different way, if sustaining catches at the 2004 level was a goal for the blue crab fishery, then the bay-wide SAV loss scenario predicted a 74% chance of failure, and the hardened shoreline scenario a 96% chance of failure (Figure 41c). Jordan et al. (2009) discuss a number of factors that might influence these projections, such as the assumption of a stock size-recruitment relationship, and the possibility of compensatory dynamics at lower population sizes, but argued that these did not seem to be major issues in the context of this study (see the paper for details).

They concluded that the improvement of models of habitat effects will require knowledge about whether certain habitat types are essential to recruitment, or ‘*merely preferred by the organism of interest*’. They noted that while relative or absolute densities in different habitats were important, they were “*less certain indicators of habitat effects than habitat specific observations of critical population parameters, especially survival and growth rates, which are far more difficult to obtain than densities*”. They also argued that “*the full realisation of multi-scale models... will benefit from complete, high-resolution, digital spatial coverage of coastal habitats (i.e. habitat maps)*”, and that “*models which link the structural and functional properties of habitats to populations and their values are promising and essential (Sanchirico & Mumby 2007).*”

6.2 Sponges and fish on the North-west Australian Continental Shelf

Sainsbury et al. (1988) presented a widely cited example of using a large scale experiment to link fisheries catches and benthic structure (sponges). On the North West Shelf region of Australia, research surveys between 1962 and 1983 (Sainsbury 1987, 1988, 1991) found that the abundance of high valued fish (*Lethrinus* and *Lutjanus* genera in particular) declined with the development of trawling, while the abundance of some lower valued fish (*Nemipterus* and *Saurida* in particular) increased. Concurrently, the catch rates of epibenthic organisms, such as sponges, greatly decreased between 1963 and 1979. Photographic surveys in the 1980s showed the higher valued species to occur significantly more often in areas with large (over 25 cm) epi-benthos, while the lower valued species were significantly more frequent in areas without large epi-benthos. Four different mechanisms were hypothesised for these patterns, the first three covering intra- and inter-specific effects, and the fourth

trawl-modification of habitat altering the carrying capacity of the different genera (habitat-limitation model). Sainsbury (1988, 1991) constructed explicit mathematical models to assess the relative likelihood of these different hypotheses, and concluded that field experiments of between 5 to 15 years in duration were best to empirically test the different hypotheses.

Three contrasting management zones were established on the shelf, each covering about 80 miles of coastline (on the adjacent shelf). Two were closed to foreign trawling, in 1985 and 1987 respectively, and the third remained open to trawling. Annual research surveys were planned to monitor fish abundance for the first five years. However, unexpectedly, domestic trawling increased greatly in the second closed area (1987) in 1989 and especially 1990, along with a reduction in foreign trawling in the open area as fishing effort shifted. Due to these unexpected dynamics, the closed (1985) and open area were the simplest to analyse. In the closed area, both the density of fish and the abundance of small benthos increased, and the abundance of large benthos stayed about the same or increased slightly (Figure 42a, c). In the area that remained open to trawling, the abundance of fish decreased, and the abundance of both large and small benthos decreased (Figure 42b, d). A Bayesian analysis based on prior probabilities for the four hypotheses found that the information from the experiment increased the probability of the habitat limitation model to about twice that of the next highest hypothesis. It was concluded that “*this indicates a substantially increased possibility that a high valued *Lethrinus* and *Lutjanus* fishery could be established on the North West Shelf if the habitat could also be protected*” (emphasis ours). As an additional point, Sainsbury (1988) also noted that the observed change in abundance of large (over 25 cm) and small (under 25 cm) benthic organisms in the empirical field experiment was inconsistent with the assumed settlement and growth rates in the initial model. In that model, it was assumed that epibenthic organisms could grow to 25 cm in about 6–10 years; but the experiment indicated that a period of at least 15 years was needed for this growth, and that settlement rates were also probably lower than expected. Video cameras mounted on the net also found that where the fate of benthic organisms over 15 cm encountering the net were observable, 89% of interactions removed the organism from the substrate. There was a very low occurrence of removed organisms being retained by the trawl, meaning that “*most removals would not be apparent from trawl catches of benthic organisms*” (Sainsbury et al. 1988).

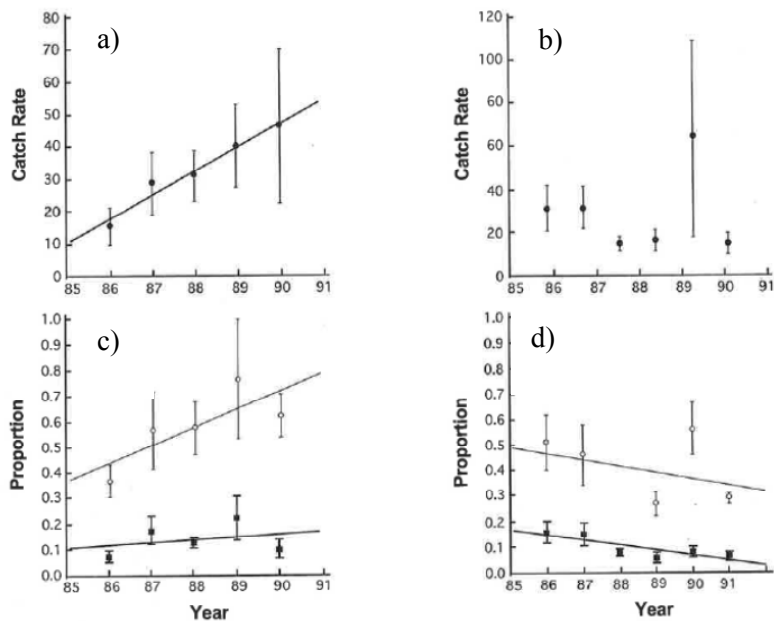


Figure 42: Total catch rates of *Lethrinus plus Lutjanus* (kg/30 min trawl) based on annual research data for a) the zone closed to trawling in October 1985, b) the zone open to trawling; for c) and d), the proportion of seabed with large (closed square) and small (open circle) benthos based on annual research data for c) the closed zone, and d) the open zone. Standard errors and lines of best fit are shown. (Source: Sainsbury et al. 1988).

6.3 Corals and sablefish in Alaska; and a meta-analysis of foundation (biogenic) species

Bracken et al. (2007) examined the relationship between diversity (number of fish species), foundation (biogenic) species, and fishery catches, using data from the 2006 sablefish (*Anoplopoma fimbria*) test fisheries in the inside waters of south-eastern Alaska (see figure 1 of Bracken et al. 2007). Sablefish are a high value deep-water species, with adults being most abundant at water depths of 600–800 m. Annual sablefish stock assessments use long-lining surveys in two areas (each about 125 km long) approximately 150 km apart, using standardised commercial gears. Eighty-two random sets (44 in north area, 38 in south area) were made over suitable habitat, over a seven day period, using multiple vessels. The number of hooks per set was recorded as a co-variate, and for each set the number of sablefish and other groundfish and bycatch species (including Pacific cod, Dover sole, flounders, halibut, sharks, skates, and thornyhead rockfish) were recorded. Pieces of deep-water coral were occasionally snagged, and their occurrence was also logged, as an indicator of biogenic habitat.

General linear models were used to assess relationships between the number of fish species caught, and the abundance of sablefish, and that of all fish species combined (accounting for the number of hooks set, and the geographic area). The abundances of both sablefish and that of all fish caught on sets where coral was present, versus where coral was absent, were also assessed. Modelling of the data found that areas where more fish species were present were characterised by higher catch levels of both sablefish and total fish, suggesting that diversity (in this case fish target and by-catch species, total species pool of 14) may be a reasonable indicator of fisheries yields and productivity (note that this was a benthic orientated study). However, they also noted that this was a correlative study, and that causal mechanisms could not be confirmed without appropriate experiments. They were unable to

completely rule out the possibility that sites with higher catch rates were likely to have more species, simply due to the increased probability of sampling rare species. In terms of the coral by-catch, it was found that the presence of corals was associated with a 67% higher catch of sablefish, and a 58% higher total fish catch (Figure 43a) (noting that coral may not have been detected at all sites where it was present).

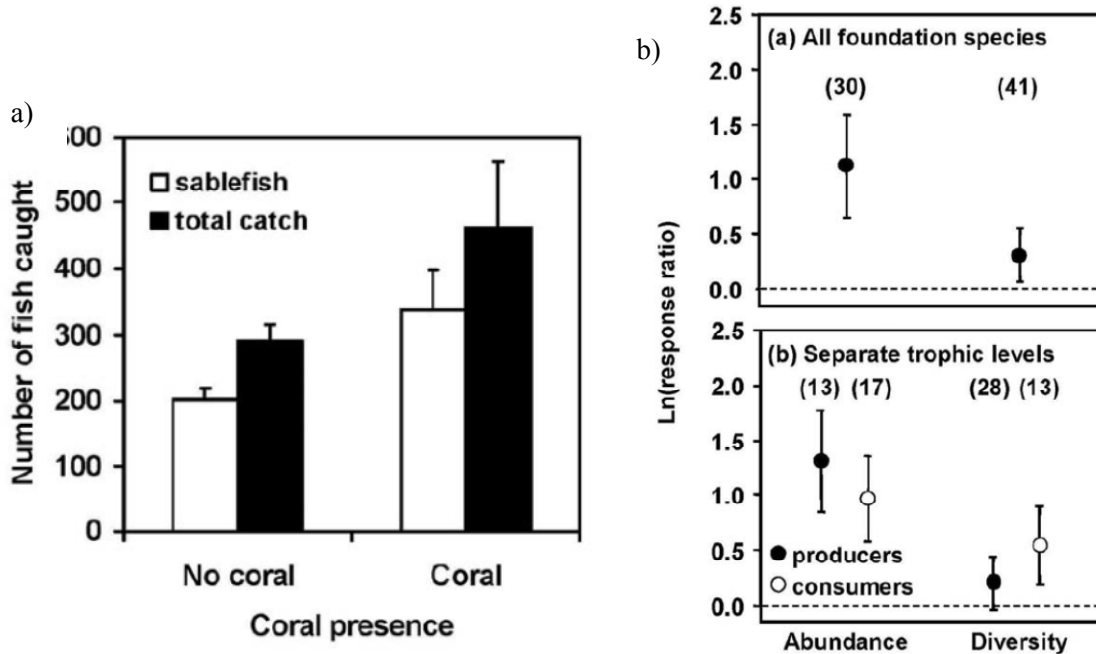


Figure 43: a) the mean number (\pm s.e.) of both target and non-target fish caught in a long-line set, with and without the presence of coral. Catches of both sablefish and total fish (corrected for the number of hooks on a set) were significantly higher where coral was present. b) meta-analyses of abundance and diversity of marine organisms, relative to the presence of foundation species. Mean log-response ratios (foundation species present versus absent) \pm 95% C.I. are shown for all foundation species together (upper graph) and producers and consumers analysed separately (lower graph). Samples sizes are shown in brackets. Effect-size metrics greater than zero indicate positive effects on abundance or biodiversity, metrics less than zero indicate negative effects. (Source: Bracken et al. 2007).

Bracken et al. (2007) also undertook a meta-analysis of published studies on observational or experimental comparisons of either diversity or abundance of taxa where habitat-forming species were present (or at high abundances) or absent (or at low abundances). They identified 30 separate studies which quantified the effect of foundation species on abundances, and 41 separate studies which quantified effects on diversity. Species richness was used as the metric of diversity where possible; with the Shannon-Wiener diversity index being the second choice. Foundation species included bivalves, corals, hydroids, kelps, seagrasses, snails, tubeworms, and tunicates. The log response ratio was used as the effect-size metric, one of the most widely used in ecological meta-analyses (Hedges et al. 1999, Shurin et al. 2002, Borer et al. 2006). It does not require a measure of sample variability, something which many of the studies included did not report. It was also expected to be easy to interpret (it represents the proportional change in the response variable), to show the least bias of the meta-population analyses, and to have an approximately normal sampling distribution (Hedges et al. 1999). Effect sizes were calculated for abundance and diversity, and the individual effect sizes averaged to calculate a grand mean effects of foundation species (\pm 95% C.I.) for abundance and diversity. The effects of producers and consumers as foundation species were also analysed separately. It was noted that not all effects of ecosystem engineers are positive; for instance

many habitat-forming species shade out or otherwise negatively affect other species; the average effects calculated included both positive and negative effects of foundation species.

The meta-analyses results (Figure 42b) showed that when habitat forming species (including corals, kelps, oysters, and seagrasses) were present (or at relatively high densities), both the abundance and diversity of associated species was enhanced, particularly invertebrates and fishes. Back-calculating from the log response ratios indicated that species abundances were 3.1-fold higher, and diversity 1.4-fold higher, in the presence of foundation species. When the roles of consumers and producer foundation species were analysed separately, consumers (e.g. bivalves, corals, and tubeworms) had the same similar positive effects, with species abundances being 2.6-fold higher, and diversity 1.7-fold higher. Producers (e.g., seaweeds and sea-grasses) were associated with a 3.7-fold increase in associated species abundances, but had no consistent effect on diversity. It was concluded that while the effects of producers and consumers on associated taxa were fairly comparable for abundance and diversity overall, producers had a slightly greater positive effect on abundance, and consumers had a slightly greater (and statistically significant) effect on diversity. The outcome of producers not having a consistent positive effect on the diversity of associated taxa was largely attributed to occasional negative effects of canopy-forming seaweeds on both understory algae and fish. Bracken et al. (2007) concluded that in terms of fisheries, as “*foundation species provide essential habitat for fish, the habitat that they provide needs to be considered in management plans, as mandated by the Sustainable Fisheries Act (National Marine Fisheries Service 1997)*”.

As an interesting side-bar, the authors also noted that fishing activities could have negative impacts on the abundances of foundation species. As a specific example, they wrote “*prior to the collapse of the Pacific Ocean perch (Sebastes alutus) stocks in the Gulf of Alaska, commercial fishermen knew that S. alutus were more abundant in areas where deep-water corals were present. However, it was difficult to trawl those areas because the gear became fouled on the corals. A heavy cable was therefore connected to two boats and dragged across the bottom, eliminating the corals before the area was trawled to capture the rockfish (anonymous fisherman, pers. comm.)*”. Similar historical anecdotal accounts exist in the New Zealand context, including the conditioning of grounds initially hard to work due to horse mussels, low foul with associated biogenic species, *Macrocystis* forest on low relief seafloor, and deep water corals on sea-mounts.

SELECTED NEW ZEALAND FISHERIES SPECIES – BIOGENIC HABITAT LINKS

7.1 Snapper (*Pagrus auratus*)

In terms of understanding fisheries-habitat links in the New Zealand context, snapper (*Pagrus auratus*) are arguably the best advanced of any species. Empirical evidence shows that seafloor structure, in particular biogenic habitats, support high densities of juvenile snapper, less than 10 cm in length. Sub-tidal seagrass meadows have returned the highest densities, including evidence of very recent settlement of juveniles directly from the plankton (about 10 mm, semi-translucent bodies, long trailing dorsal fins). High densities have been measured in Parengarenga Harbour (data not yet available), Rangaunu Harbour (about 20 and 150 per 100 m² from two sites), Bay of Islands (data not yet available), Kaipara Harbour (about 5 per 100 m²), Great Mercury Island (to about 45 per 100 m²), and Whangapoua Estuary (Coromandel) (to 5 per 100 m²) (Francis et al. 2005, Schwarz et al. 2006, Morrison et al. 2009, M.M. & M. Lowe, unpubl. data), with consistently bi-modal or even tri-modal peaks from the east coast samples (e.g., see figure 5 of Schwarz et al. 2006) over different years suggesting multiple recruitment events (NB: these density estimates are across a range of seagrass

blade lengths and densities (habitat qualities), sub-tidal seagrass habitat extents, and several different snapper stocks). Experimental artificial units, with varying seagrass blade density as a habitat quality factor, have also been shown to attract high numbers of 0+ snapper (either through direct recruitment from the plankton, and/or aggregation), up to a maximum of 25–50 snapper per 3 m² unit, associated with blade densities equivalent to those found in natural, relatively dense seagrass meadows. This density threshold is suspected to be driven by food-limitation, as fish are visually foraging on passing zooplankton (along with an abundant assemblage of other small fishes, most notably juvenile spotties). Juvenile snapper (and trevally) have also been found in higher abundances with horse mussel beds (Morrison & Carbines 2006, Morrison et al. 2009, Usmar 2010) in estuaries of both coasts of northern New Zealand, and experimental horse mussel patches with attached epifauna have also been shown to elevate juvenile snapper densities (Usmar 2010). Other biogenic habitats in estuaries have also been linked to higher juvenile snapper densities, including sponges and general terrestrial debris such as small tree branches and litter, as well as man-made structures such as mooring blocks and wharfs (Morrison et al. 2009, M. Lowe & M.M., unpubl. data). Current fish-habitat work (March/April 2014) along the East Northland coast has found relatively modest densities of small juvenile snapper in the Te Rawhiti Passage (a coastal area protected by islands) associated with red algae and rhodoliths, as well as higher densities in the Bay of Islands, associated with biogenic habitats including red algal meadows, horse mussels, dog cockles, rhodoliths, and subtidal seagrass meadows (data not yet available). Broadly speaking, the more complex the habitat, the higher the associated snapper densities appear to be (yet to be empirically confirmed).

Out in more coastal rocky reef areas, juvenile snapper are also found, albeit at low densities and with strong inter-annual variations, in some shallow rocky areas. Kingett & Choat (1981) found that 0+ snapper and juvenile red mullet (*Upeneichthys porosus*) occurred in their highest densities on shallow reef systems (Goat Island area) on coralline turf areas (15–40 mm high *Corallina officinalis*, with a mix of other red algae species). The abundance of juvenile snapper was positively correlated with the percentage cover of coralline turf (n=11 transects, r=0.79), with abundances peaking in February–March (consistent with estuarine systems) at up to about 250 fish per 500 m² (50 per 100 m²) at the highest density site (other sites ranging up to maxima ranging from 0.5 to about 60). It was noted that 0+ and 1+ snapper densities were probably under-estimated, especially when at high densities, “*due to these age classes forming dense, localised schools that move rapidly over areas of flat substratum*”. Battershill (1987) reported more than 4.6 0+ snapper per 100 m² at Goat Islands’s ‘Sponge Garden’, and stated that “*small fish persisted on the reef in large numbers throughout the year and observations made on similar reefs along Northland coasts suggests that these areas are important nursery grounds for a number of commercially important fish species*”. Ross et al. (2007) found juvenile snapper (70%) to be concentrated on the boundary between the rocky reef edge and adjacent sand, although it only occupied 17% of the surveyed available habitat. Boulder habitats held 16% of snapper, at 5% of habitat area, and turfing algae 5.5%, at 2.5% of area. Average densities in the most favoured habitat (0–5 m from the reef edge) (sampled 2002) were about 5.6–10.4 per 100 m². All other habitats were utilised less than expected (kelp, sand off reef, mixed algae) or at expected levels (rock flats). Collectively, these studies show that juvenile 0+ snapper do recruit into coastal shallow rocky reef habitats. However, the cumulative densities are probably too low (and highly variable across years) to underpin the adult snapper populations occurring on reefs, and it is suspected that secondary recruitment from other nursery sources is occurring (i.e., soft sediment habitats). Evidence for such processes includes a rapid build-up of large adult snapper at the Poor Knights Island following their full protection, with these snapper being too old to have locally recruited in the time period involved, but capable of being adult immigrants to the reserve (Denny et al. 2004).

On coastal soft sediment systems, Francis (1995) used research trawl data to describe broad scale patterns in the north-western Hauraki Gulf (Kawau Bay to North Whangaparoa Peninsula), with snapper found to prefer a mud substrate over one of muddy sand with a significant percentage of shell. The seabed was described as homogenous and flat, with frequent large holes (up to 150 cm wide by 30 cm deep) from feeding rays, along with numerous invertebrate burrows pockmarking the sediment surface. Two areas were described as having a coverage of large shells (greater than 5 cm wide) covering up to 50% of the seafloor, and to which were attached “a diverse assemblage of branching and cushion-forming sponges, of up to 50 cm in height”. The dominant species were *Crella incrustans*, *Chondropsis kirkii*, *Callyspongia ramosa*, *Iophon minor*, *Halichondria* sp., and *Polymastia* spp. In these two areas, it was suggested that the coarse sediment seafloor, the dominance of filter-feeding sponges, and the general bathymetry were indicative of tide and wind-induced currents. However, snapper abundances associated with these areas were reported to be low, although it was not clear from the paper whether these observations made by divers were directly related to what was encountered as bycatch in the trawl samples. Thrush et al. (2002) used fish traps to assess relative 1+/2+ (172 ± 43 mm length) snapper densities in the Kawau Bay area, and modelled CPUE against seafloor complexity as measured by divers. Habitat features measured included ascidians, coralline algae, chaetopterid (worm) tubes, horse mussels, holes and burrows, hydroids, mounds, scallops (*Pecten novaezealandiae*), sponges, seaweed, and spionid worm tube mats. A statistical model explained 74% of juvenile snapper abundance variation, with a significant and positive influence of variety and number of habitat structure elements on the abundance of juvenile snapper.

In the inner Hauraki Gulf, Compton et al. (2012) related the occurrence of snapper to a) epibenthic biodiversity as measured by the total number of epibenthic species including included sponges, horse mussels (*Atrina zelandica*), ascidians, and anemones, and b) the number of mounds, pits and burrow openings made by benthic organisms, e.g., crustaceans, fishes and rays. Broader scale environmental variables were included, using physical models (orbital velocity, current speed), as well as corrected water depth, month of sampling, and transect width (which varied with water clarity). Boosted regression tree modelling found juvenile snapper (5–15 cm) to be consistently associated with relatively slow tidal current speeds (under 0.3 cm/s) and slow orbital velocities (under 10 dm/s). Juvenile snapper also had a tendency to be observed in the vicinity of (biogenic) sediment structures (mainly where there were 1–4 structures in a video frame). Adult snapper (over 15 cm) were generally associated with a wider range of orbital velocities (0–12 dm/s) and tidal current speeds (0–0.8 cm/s) than juvenile snapper, peaking in occurrence where orbital and tidal current speeds were relatively fast (10 dm/s orbital velocity, 0.6 cm/s current speed). Although benthic diversity explained only a small amount of variation in the total model (5%), the response curves also showed that adult snapper tended to be associated with high benthic diversity. These differing habitat associations of juvenile and adult snapper were reflected in different spatial distributions. The reasons are unclear, but could be food driven, and/or related to predation: adult snapper cannibalise small snapper in this area (Morrison, unpubl. data), and John dory and kahawai are more common in the higher current areas with associated epifauna (Morrison et al. 2003). This implies that habitat use is not simply a matter of increasing structural complexity being associated with higher juvenile snapper densities, but rather an interaction between habitat structure and predator abundances at larger spatial scales, which may vary with environmental context.

Casual observations have also been made of 0+ snapper being associated with individual green fleshy algae *Codium* spp with maerl beds in shallow sheltered waters off the Cavalli Islands, east Northland (C. Duffy, pers. comm). This suggests that other coastal biogenic habitats are probably also playing

some role. A current Coastal Conservation Management field deployment is scheduled to sample this area at the time of writing.

Collectively, the above studies and observations suggest that structured habitats (e.g. seagrass, horse mussels, sponges, terrestrial debris, red algae, rhodoliths, reef edges, wharfs and mooring blocks, and others) are preferentially preferred by juvenile snapper, and provide some advantage, whether it is through increased growth, reduced predation, or some combination of these. This is consistent with similar effects emerging for other coastal demersal fish internationally, with one of the best documented cases being elevated density and survivorship of juvenile Atlantic cod (*Gadus morhua*) and Pacific cod (*Gadus macrocephalus*) with structured habitats (including seagrass), e.g., Lough et al. 1989, Gotceitas & Brown 1993, Tupper & Boutilier 1995, Gregory & Anderson 1997, Lindholm et al. 1999, Laurel et al. 2003, 2009. Such structured habitats are often biogenic, and as such are vulnerable to degradation and loss from both land-based (Morrison et al. 2009), and marine-based human impacts (Kaiser & de Groot 2000). Given this, the relatively large amount of knowledge available on snapper in general, and the ability to remotely map many of these habitats, juvenile snapper-habitat linkages would be a logical choice as a key species on which to focus more detailed research (using the ideas of Beck et al. 2001, Dalhgren et al. 2006, Jordan et al. 2009), with an explicit objective of such research being to provide fundamental inputs into improving spatial management (see also Conclusions section).

7.2 Tarakihi (*Nemodactylus macropterus*)

While already covered to some extent under the Bryozoans section, tarakihi are another coastal demersal species worthy of comment for juveniles associations with biogenic habitats. Vooren (1975) concluded that they were found in close association with “coral” in Tasman and Golden Bays (the coral being bryozoans, *Celleporaria agglutinans* and *Hippomenella vellicata*, Figure 34). Following a 9–12 month planktonic larval phase, juvenile tarakihi months settle to the seafloor in their nursery grounds, where they stay for about three years, before moving out into deeper waters in their fourth and fifth years, and finally departing the area in their sixth year, possibly for the spawning grounds off the west coast of the South Island. In addition to Tasman Bay, Vooren (1975) also looked more broadly at the national scale, using commercial and research trawl samples, for evidence of juvenile tarakihi

nurseries. He identified nursery grounds off the south-western coast of the North Island, in Tasman Bay, along the entire eastern coast of the South Island, and around the Chatham Island (Figure 44a, b). Associated depths ranged from 20–100 m, with locations being mostly 10–30 km from the shore. These nurseries were described as having “*a dense and varied invertebrate benthic epifauna dominated by sponges and small corals*”.

From these data, Vooren (1975) concluded that the major nurseries occurred in the South Island, and that these nurseries probably operated as sources of juveniles at the national scale. Much of the commercial tarakihi catch is taken off the upper North Island region, but juveniles are not seen, with fish under 20 cm being very rare in the R.V. *Kaharoa* research trawls series (e.g. for the six Bay of Plenty surveys, 1983–99, see figure 4h, Morrison et al. 2001). Vooren commented that “*the field notes on the catches off the east coast of the South Island indicate that concentrations of young tarakihi there tend to be associated with areas of a rich invertebrate benthic epifauna containing a variety of sponges, worms, echinoderms, and molluscs. The area around Stn J08/041/69, off Oamaru, for example, is locally infamous for the great qualities of sponge usually brought up by trawl nets and is therefore known among the fishermen as the ‘Hay Paddock’*” (see Tubeworms). He concluded with

the warning that while the New Zealand trawl fleet of the time tended to avoid tarakihi nursery grounds, that larger foreign vessels had begun working outside the 12 nautical miles territorial sea limit off the east coast of the South Island, using heavy trawl gear which could damage the habitats if used intensively on the trawl grounds. Given this, it was “*necessary to study the future developments on the nursery grounds in this region, in order to detect undesirable changes as they occurred. It is also important to determine with which spawning grounds the various nursery grounds are connected*”.

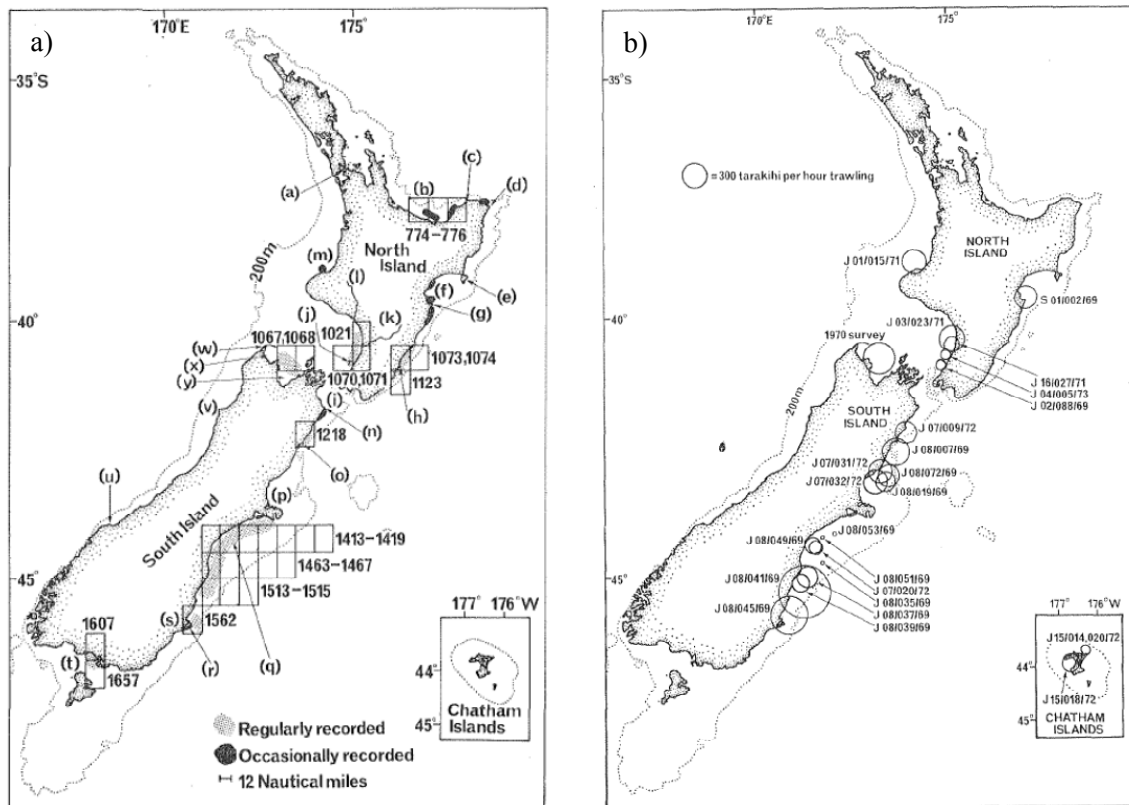


Figure 44: a) Juvenile tarakihi nursery grounds around New Zealand, as identified in Vooren (1975). The numbered grid squares indicate where tarakihi less than 20 cm long were recorded in commercial catches as part of the Catch Sampling Programme 1967–71. No catches from the Chatham Islands were sampled; b) Trawling stations at which young tarakihi were caught by research vessels W.J. Scott (station S01/002/69) and James Cook (all J stations) in 1969–73. The areas covered intensively by these vessels are the trawling grounds around the North Island except off the south-eastern coast, and around the South Island north of a line from Otago Peninsula to Jackson Head. Circle size indicates the number of tarakihi caught per hour. The circle in Tasman Bay shows average catch per hour of trawl survey June 1970). (Source: Vooren 1975).

Despite these recommendations, no further work has been undertaken on the links between juvenile tarakihi and seafloor habitats in the 37 years since. Tarakihi are a colder water species than snapper (although they do co-occur), and there appears to be a broad pattern of tarakihi being found at shallower depths in more southern (and colder) waters. However, tarakihi, as with snapper and many other species, have seasonal inshore-offshore migrations, as well as long-shore, which may or may not be part of spawning activities. The dynamics of and mechanisms driving these large scale movements are very poorly understood, but tagging returns and length data from commercial catch sampling suggest large scale connectivity of the (putatively) different stocks, with the suggestion that one large east coast tarakihi stock exists (other area relationships are unclear). In addition to the nursery

habitats/grounds identified by Vooren (1975), anecdotal observations suggest that shallower nurseries may also exist, associated with seafloor structure. Graham (1956, p. 292) stated that young tarakihi of "no more than 2 to 3 inches in length" (50–75 mm), were very common in Otago Harbour in January–March; Vooren (1972) suggested that these quoted lengths were an under-estimate, as postlarvae collected in December 1968 in Blueskin Bay, close to Otago Harbour, already measured 63–87 mm, and juveniles caught February 1970 had a 95 mm modal length. Vooren (1972) concluded that Graham's (1956) statement indicated "each summer an influx of very small tarakihi into Otago Harbour". In Wellington Harbour, tarakihi smaller than 80 mm were collected in November–December, with subsequent fish samples from January–June growing progressively larger (preserved samples from 1960–71, no collection details given, n = 20). National scale estuarine fish sampling with small-mesh beach nets collected one small tarakihi in the Port Rose estuary north of Dunedin in an area of green algae mats (*Enteromorpha* spp.) in 40 cm water depth (low tide), while two more juveniles were caught in Port Adventure, on the eastern side of Stewart Island, in 1 metre water depth (low tide) in association with dead tree branches. Based on experiences further north with juvenile snapper populations, the presence of these individuals may be indicative of sampling the fringes of the main population abundances, which are in slightly deeper water beyond where beach seines can be deployed (Francis et al. 2005, 2011).

Juveniles are also often seen in general by divers in shallow water coastal reefs in the lower North Island, and South Island. Duffy (1992) recorded small numbers of juvenile tarakihi (about 50–70 mm) at several reef sites along the general Napier region coast-line. A commercial fisher also reported catching 10–13 cm tarakihi in 40 m water depth just south of East Cape in May 2011, matching the seasonal size frequencies of Vooren (1975). North-east of Nelson, Cole (2000) recorded juvenile tarakihi in a mixed habitat of rocks with *Carpophyllum flexuosum*, and ripped sand, 13.6 m water depth. They have also been observed in the Marlborough Sounds at juvenile (6–12 cm) and sub-adult sizes (17–28 cm), with abundances being highly variable between years. These fish are uncommon in the inner Sounds, and mostly present in the central and outer Sounds, where they are abundant around current swept rocks (Rob Davidson, Davidson Environmental Ltd, pers. comm.). Much further south, at Hoho Bay, Snares Islands, schools of juveniles were filmed in 10–20 m water depth (April 2008), in association with a thick layer of leaf litter washed off the island (Figure 45a) (making the fish 'very well disguised', Debbie Freeman, DOC, pers. comm.). In addition to leaf litter, large *Lessonia adamsiae* 'trees' (endemic to the Snares) were present as the main canopy plant, along with lower height patches of *Caulerpa brownie*. Other sheltered bays also exist on the Snares east coast, which could also hold similar benthic habitats. Juvenile tarakihi have also been recorded from the Chatham Islands (Vooren 1975), while a second species of tarakihi ('King tarakihi', Smith et al. 1996) presumably has nursery grounds around the Three Kings Islands or further north (possibly Figure 45b)

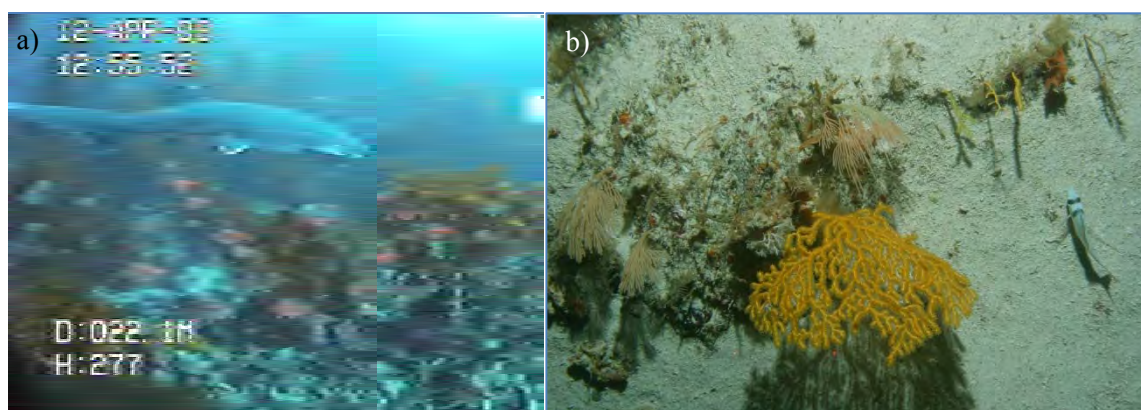


Figure 45: a) part of a dense juvenile tarakihi school filmed by ROV at Hoho Bay, along with a seven-gill shark. Kelp plants are *Lessonia adamsiae*, with a *Caulerpa brownie* patch on the lower left (Source: Debbie Freeman DOC), b) sleeping tarakihi (about 20 cm) adjacent to gorgonian, Three Kings shelf (NB: this may be a ‘king’ tarakihi juvenile, a different species to *N. macropterus*, Smith et al. 1996). The two red laser dots, centre bottom screen, are 20 cm apart. (Source: DTIS, Biogenic Habitats voyage TAN1105).

Collectively, these observations suggest that tarakihi may have a number of shallow water nursery areas still awaiting discovery (including deeper areas of southern harbours and coastal embayments), which appear to have strong biogenic habitat components, and are subject to the same kind of land-based stressors as for snapper further north (Morrison et al. 2009). The more coastal and inner continental shelf nursery grounds (possibly collectively ranging across 20–117 m water depths, depending on location, see table 5, Vooren 1975) also warrant more detailed research, to quantify what the actual fish-biogenic habitat relationships are, and to map the spatial extent of nursery habitat. These habitats are also vulnerable to land-based effects, as well as fishing and other-marine based activities. The rationale for such work matches that for snapper. The total combined tarakihi quota is about 6000 t, along with a significant take by recreational fishers, making it a significant coastal fisheries species. However, stocks are showing signs of stress, with reductions in commercial CPUE, and a size/age truncation in the fished population structures. While the latter effect strongly suggests heavy fishing pressure, it is quite possible that adverse habitat degradation or loss effects may also be flowing through into the fishery as reduced recruitment levels. As no work has been directed towards such effects (but see Kaipara Harbour example for snapper), this suggestion remains speculative.

7.3 Blue cod (*Parapercis colias*)

Blue cod support regionally important commercial and recreational fisheries, concentrated in the South Island. Adult blue cod are strongly associated with rougher seafloors, including rocky reefs, and biogenic habitats such as the bryozoan reefs of the Otago Shelf and Foveaux Strait (Carbines 2004b). Recent DUV sampling has also shown blue cod of all sizes to be strongly associated with tubeworm habitats (see ‘Tubeworms’ section) in Port Underwood (G. Carbines, pers. comm.). Blue cod fisheries are fully exploited, with the Marlborough Sounds region being under stress, with closures and slot limits currently in place for recreational fishers to help promote rebuilding. Blue cod juvenile ecology (less than about 10 cm) is poorly known, but such fish are seldom seen (Figure 46). Those that are, are mainly found at the bottom of reef systems, at the general reef-sediment interface, or in biogenic habitat areas (e.g. Otago bryozoan thickets, M.M & E.J. unpubl. data). In the Marlborough Sounds, they appear at about 5–6 cm on cobble-sand-shell substrata, usually at the foot of cobble banks; and seem widespread, with particular sites seeming to support higher numbers (R. Davidson, Davidson Environmental Ltd, pers. comm.). These transitional habitats, depending on region, may be composed of cobbles, large shell litter (including dog cockles), low relief bryozoan clumps, turfing algae, low density horse mussels, and other low relief components. One possible explanation for the low numbers of fish under 10 cm seen on reefs proper may be that larvae initially recruit ‘off-reef’ or on the reef boundary in deeper water, and then display an ontogenetic shift onto the reef proper as they grow in size and age. Rapson (1956) even suggested that in some areas juveniles might migrate from shelf waters to shallow waters inshore. If so, then the loss of biogenic habitats has implications for juvenile blue cod production.



Figure 46: Juvenile blue cod (about 8–10 cm) in association with live horse mussels in approximately 20–30 m, with a coarse sand substrate, off Goat Island, Cape Rodney to Cape Okakari Marine Reserve (Source: Grant-Mackie 1987).

CONCLUSIONS

Collectively, available evidence points to substantial losses having occurred in the distribution of biogenic habitats in New Zealand, from the inter-tidal out to seamounts (Table 3). Given the limited data available, it is likely that the true magnitude of loss is much greater than what is documented, especially in waters beyond diving depths, and in geographic regions where scientists have undertaken little work. Relatively well documented examples of biogenic habitat loss include seagrass meadows (especially the sub-tidal components which directly support fisheries values) e.g., the 12–14 km² of Whangarei Harbour (but note that there has been about 3.5 km² recovery since 2008), the sub-tidal green-lipped mussel beds of the Hauraki Gulf (about 500 km²), the bryozoan beds of Torrent Bay (about 300 km²) and Foveaux Strait (about 800 km²), and the deep-water coral beds of some seamounts.

Quantitative links between fisheries species and biogenic seafloor habitats remain very poorly known in New Zealand (Table 3). Most of the quantitative fish-habitat work has been completed in estuaries, for habitats such as mangroves (juvenile short-finned eels, grey mullet, and parore), intertidal and especially sub-tidal seagrass (northern New Zealand; juvenile snapper, trevally, parore, piper), and horse mussels (northern New Zealand; juvenile snapper, trevally), and some red algae (juvenile snapper). Out in more coastal locations, fisheries species-biogenic habitat associations include: biogenic pits and burrows, kelp forest edges, horse mussels, and sponge gardens (Hauraki Gulf) (juvenile snapper); red algae and rhodoliths (Bay of Islands, East Northland coast) (juvenile snapper); foliose red algae and bryozoans (Ninety Mile Beach) (juvenile green-lipped mussels); bryozoan mounds at Separation Point and Torrent Bay (the latter now eliminated) (juvenile tarakihi, leatherjackets, snapper, blue cod and red cod), tubeworm mounds at Port Underwood (juvenile and adult blue cod); Otago Shelf bryozoans (juvenile blue cod, red cod, and southern pigfish); east coast South Island continental shelf mixed biogenic habitats (sponges, tubeworms, horse mussels and others) (juvenile tarakihi); and Foveaux Strait bryozoans (blue cod and dredge oysters). In deeper water, fish-biogenic habitat associations are effectively unknown (e.g., there is no evidence that orange roughy are reliant on corals on sea-mounts). In terms of reproduction linkages, observations included the attachment of elasmobranch egg cases to red algae and tubeworms (e.g. skates in the

Marlborough Sounds and Paterson Inlet, Stewart Island; and elephant fish in the inshore Canterbury area), the attachment of piper/garfish egg masses to seagrass; and of Broad squid egg masses to shallow water macroalgae. There is little knowledge of how biogenic habitats may provide elevated food sources for fisheries species, aside from recent work in seagrass meadows, where a mixture of benthic and pelagic food sources are utilised by small fish assemblages, including juvenile snapper and trevally (Lowe 2013). There is some evidence of the importance of habitat quality with artificial seagrass habitat mimics showing that increasing seagrass blade density elevates juvenile fish densities (up to a threshold for snapper and trevally); and artificial horse mussel with epifauna mimics elevates snapper densities.

Some of the above work is semi-quantitative, based on visual observations, or on trawl stations which smooth out fish and habitat variability over smaller spatial scales. This makes it difficult to generate metrics such as densities as inputs to modelling frameworks. Other key metrics, such as survival and growth rates relative to habitat, have not been quantified at all, due in no small part to the difficulties associated with estimating them under realistic field conditions. However, without such measures of how different habitats contribute to adult populations, it is not possible to scale up to the fish population and associated fisheries level. In fact, even such fundamental concepts as ‘what constitutes a nursery habitat?’ have only recently been addressed in the science literature.

Table 3: Summary of known biogenic habitats depth ranges, geographic extents, key associated fisheries species, habitat quality effects, threats, evidence of change, and key references. *, denotes review paper.

Biogenic Habitat	Known depth range	Geographic extent	Key associated fisheries species	Habitat quality effects on associated species shown?	Threats (with a spatial element) – excludes ocean acidification	Evidence of change?	Key references
Salt-marsh	Extreme high tide zone	National	Inanga spawning substrate (?)	Denser stem densities and aerial root thickness have higher egg densities	Reclamation, stock grazing, sedimentation	Yes, clear losses from human settlement – magnitude unknown	McDowall & Charteris (2006), Hickford et al. (2010)
Mangrove forests	To mid inter-tidal zone	Northern New Zealand estuaries, in all harbour systems (but not the Waikato River tidal area).	Juvenile grey mullet, short-finned eels, and parore	Tree/sapling densities (eels); clearer water and coarser sediments (-ve grey mullet, +ve parore)	Reclamation and clearance. However, mangrove extents are expanding rapidly in many northern estuaries	Yes, initial losses from human settlement, but now expanding extent in many estuaries. Large forest more than 1 km wide now established at the head of the Firth of Thames	Morrisey et al. (2007)*,(2010)*
Seagrass meadows	Intertidal up to half tide, sub-tidal down to 7 m in extremely clear waters	Throughout New Zealand, in areas of higher water clarity, protected from high energy waves. Hotspots in Northland (Parengarenga, Rangaunu, Kaipara Harbours), Bay of Plenty (Whangapoua, Tairua, Tauranga Harbours), top of South Island (Farewell Spit, Wanganui Inlet), Otago (Otago Harbour), Southland (Bluff Harbour, Paterson Inlet, Stewart Island) Sub-tidal seagrass meadows also occur in more coastal locations such as the Cavalli Islands (Northland), in the outer Marlborough Sounds, and off Ruapuke Island, Foveaux Strait. There is currently no information on the fish assemblages associated with those habitat areas.	Juvenile snapper, trevally, parore (north); leatherjackets (south); garfish, spotties, triplefins (general)	Sub-tidal seagrass is orders of magnitude more important for high fish abundances than inter-tidal. Clear positive experimental effects of increasing blade density on species abundance and diversity, including juvenile snapper and trevally.	Reclamation, sedimentation, eutrophication, vehicles, propeller damage, black swan grazing	Significant historical losses are known to have occurred from Whangarei, Waitemata, Manukau, Tauranga, Avon-Heathcote and other harbours. Threats include land-based impacts of sedimentation and eutrophication. Sub-tidal elements are the first component to be lost from human induced impacts, yet are the most critical components for fish	Park (1999), Inglis (2003)*, Turner & Schwarz (2006)*, Matheson et al. (2009), Morrison et al. (2009)
Macro-algae, including algal meadows and kelp forests	Intertidal down to lower light penetration levels	National, wide range of species and assemblages, forms both monotypic and mixed assemblages	Many reef fish species, soft sediment assemblages poorly known	Positive effects of kelp density on juvenile wrasses	Declining water quality, algal blooms, and disease interactions. Sedimentation both deposited and suspended.	No empirical evidence, but highly likely in developed harbour systems and sheltered coastal waters	Choat & Schiel (1982), Schiel & Hickford (2001), Shears & Babcock (2004), (2007), Anderson & Miller (2004), Shears (2007), Shears et al. (2008b), Nelson

Biogenic Habitat	Known depth range	Geographic extent	Key associated fisheries species	Habitat quality effects on associated species shown?	Threats (with a spatial element) – excludes ocean acidification	Evidence of change?	Key references
							(2009)
Green-lipped mussels	Intertidal, and down to about 20–30 m in coastal zones	National, especially in harbour systems, and on shallow coastal reefs	Unknown. Large numbers of spotties and triplefins. Elevated invertebrate abundances	Unknown	Removal by harvest, sedimentation, fishing disturbance. Lack of recovery in Firth of Thames may be due to lack of settlement surface or adult cues	Yes, functional loss of green-lipped mussel beds in the inner Hauraki Gulf / Firth of Thames (about 500 km ²). Suspected loss in other systems such as Tasman/Golden Bays	Greenway (1969), Reid (1969), Paul (2012)*, McLeod et al. (2012), Paul (2012)
Oyster reefs (rock and Pacific)	Effectively intertidal	Northern New Zealand, <i>C. gigas</i> is an invasive species	Unknown	No information available. Pacific oysters are associated with the slowing down of current speeds, and accumulation of finer sediments	Pacific oysters are suggested to be out-competing rock oysters. Pacific oysters are expanding in sediment impacted areas	Significant declines in rock oysters, significant increases in Pacific oysters. Anecdotal only	Kirby (2004)*, Beck et al. (2011)*, Kelly (2009)
Horse mussel beds	Extreme low water in estuaries, down to more than 70 m in coastal zone	National, common in estuaries and shallow embayments, also found out on the inner continental shelf. Occurs as both a minor contributor to mixed biogenic habitats, and as dense and extensive beds.	Juvenile snapper and trevally in the north, potentially juvenile blue cod and other species more broadly (?)	Artificial horse mussel experiments in northern estuary show higher juvenile snapper and other small fish species densities in horse mussel with attached epifaunal treatments	Commercial bulk fishing methods (e.g. trawling, dredging, seining), anchoring, sedimentation, sediment dumping	Retractions in range in Mahurangi Harbour, Auckland, due to increasing sedimentation	Ellis et al. (2002), Usmar (2010)
Scallops, brachiopods, and other epifaunal shellfish	Intertidal to continental shelf	National, as filter feeders most common in higher current area, with coarser substrates	Two scallop species are fished. Unknown	Unknown	Land-based effects, especially sedimentation, and fishing	Reductions in scallop densities through fishing (expected), some evidence of loss of some beds and areas	Coen & Grizzle (2007)*
Infaunal bivalves e.g. pipis, cockles, <i>Tawera spissa</i> , dog cockles	Intertidal out to continental shelf, depending on species	National	Unknown	Unknown	Land-based effects, especially sedimentation	Yes for estuarine species such as pipi and cockles, large scale declines.	Grant & Hay (2003)*, Hartill et al. (2004), Dewas & O'Shea (2011)
Sponges	Sub-tidal down to sea-mounts,	National	Some observations for snapper in the Hauraki Gulf,	Unknown	Land-based effects, especially sedimentation.	Little information available, but losses at Spirits Bay	Battershill (1987), Bell (2008), Cryer et al. (2000),

Biogenic Habitat	Known depth range	Geographic extent	Key associated fisheries species	Habitat quality effects on associated species shown?	Threats (with a spatial element) – excludes ocean acidification	Evidence of change?	Key references
	especially on rocky reefs		suggested for juvenile tarakihi in South Island, blue cod in Marlborough Sounds		Fishing impacts from towed gears, also removed by static gears		
Bryozoans	10 m to 130 m, dependent on coastal setting	National, but areas of high abundance / grounds at South Maria/Three Kings Ridge, Wanganui Bight, Separation Point, Otago Shelf, and Foveaux Strait	Dependent on area – juvenile tarakihi, John dory, blue and red cod	Recovering bryozoan areas in Foveaux Strait have higher blue cod densities, diet is more varied on less disturbed areas	Fishing disturbance, sedimentation	Yes, large losses from Tasman Bay (about 300 km ² from Torrent Bay), and Foveaux Strait (about 800 km ² , but contested)	Batson & Probert (2000)*, Cranfield et al. (1999), (2003), (2004), Wood et al. (2012)*
Tubeworm beds/meadows	Sub-tidal to 140 m	National, but especially East Coast South Island (<i>P. socialis</i>), and Marlborough Sounds / Paterson Inlet for <i>G. hystrix</i>	Positive association between <i>P. socialis</i> meadows and juvenile sea perch, range of 'reef-fish' species with <i>G. hystrix</i>	Visual observations suggest healthier <i>G. hystrix</i> mounds have higher biodiversity values, including fish. Similar observations for <i>P. socialis</i>	Physical disturbance by fishing gears, anchoring. Vulnerable as filter-feeders to sedimentation	Suggested <i>G. hystrix</i> reef loss from human disturbance in Paterson Inlet, possible sedimentation effects; anecdotal accounts of spatial reduction in <i>P. socialis</i>	Smith et al. (2005) Davidson et al. (2010)
Burrows	All depths	All regions	Scampi as a burrow former. Many finfish feed on burrow animals	Unknown. There are likely to be effects on bottom associated species such as flatfish.	Unknown: removal of scampi by fishing must reduce burrow densities	Unknown	Meadows & Meadows (1991), Lohrer et al. (2005)
Coastal gorgonians, red and black corals, hydroids, brachiopods, sea-pens, sea-whips	About 15 m to seamounts, species and group dependent	National extent, black corals show deep-water emergence in Fiordland	Unknown	Unknown	Land-based and fishing impacts	Unknown	Grange (1985), Grange & Singleton (1981), Miller et al. (2004)
Deep sea corals	200 to 2000 m, depending on species	National – see Tracey et al. 2011 for all records geographically displayed	Unknown	Unknown	Fishing	Large loss of corals from fished seamounts	Tracey et al. (2011)

Beck et al. (2001) and Dahlgren et al. (2006) provide complementary frameworks for assessing the contributions of juvenile habitats to adult fish populations, based on per unit area, and absolute contributions respectively (using tools such as otolith chemistry). However, both authors acknowledge that these frameworks are idealistic, and that the level of evidence required for showing a habitat to be a nursery is very high and very difficult to achieve, so that both definitions could be seen as providing a view of what a definitive test would encompass, “*so that researchers could arrive at the best approximation of it*”. Examples of themes researchers might best focus on included: factors of density, growth, survival, and movement in putative nursery habitats; the quantification of multiple habitats for a given species; and a better quantification of the movements of individuals between juvenile and adult habitats. They also commented that correlative and case study analyses could also yield many useful insights – such as correlations between loss of inshore habitat and decreases in offshore fisheries production. Any of the above suggestions could be applied to one or more New Zealand species.

New Zealand’s understanding of how biogenic habitats may contribute to fisheries production is at a very early stage, and the data does not yet exist to explicitly link habitats to production. The only exception to this is the snapper stock SNA 8 (the west coast of the North Island), where otolith chemistry (albeit for the 2003 year class only) linked most of the adult snapper taken in the fishery back to the Kaipara Harbour as their natal nursery. Detailed fish-habitat survey work within the Kaipara Harbour has shown that high juvenile snapper densities are strongly associated with biogenic habitat structure on the seafloor, especially sub-tidal seagrass meadows, horse mussels, sponges, and an invasive hydroid (botryzoan). The Kaipara Harbour is known to be under increasing pressure from land-based impacts especially sedimentation, and large changes have occurred in the harbour in living memory, including the loss of sub-tidal seagrass beds (Morrison et al. 2014b). Given this, the fundamental carrying capacity of this system, implicit in the fisheries concept of B_0 (the biomass prior to the establishment of fisheries) may have changed; such changes are ignored in current fisheries assessments.

There is empirical evidence that a number of demersal coastal fish species are strongly associated with biogenic habitats during their juvenile life phases (e.g. snapper, trevally, blue cod, tarakihi, leatherjackets), and, (based on overseas work), that these habitats are likely to be providing advantages for these species in terms of growth and/or survival during their juvenile phases. While it is highly likely that reductions in biogenic habitats (e.g. seagrass, horse mussels, bryozoans) are cascading through as reductions in juvenile recruitment into adult fished populations; with the exception of the Kaipara Harbour work, there is no hard empirical data to demonstrate this for any particular biogenic habitat, or fisheries species. We would argue that this is due to a fundamental lack of targeted work in New Zealand aimed at linking fisheries species productivity to their underpinning habitats, rather than because this dynamic is not important – a viewpoint shared in the international literature (see Armstrong & Falk-Petersen 2008).

Given this, how then best to proceed? Several areas of advancement are suggested

8.1 Consider biogenic habitats as a key element of marine ecosystems

Biogenic habitats in general are important for a broad range of functions extending well beyond the support of fisheries, and are known to be subject to a range of human-driven stressors. Important functions in addition to the underpinning of fisheries can include biodiversity roles, benthic-pelagic coupling, primary production, erosion prevention, nutrient recycling, suppression of algal blooms, and carbon sequestration. Given this, it is logical for different agencies and industries to work together

where practical, to achieve mutual goals around developing comprehensive classifications, mapping, and inventorying of what exists, identifying important threats and stressors, and working to mitigate or remove them.

8.2 A national (fish-) habitat classification

Globally, many countries have identified the need to create marine habitat classifications, which can include quantifying the goods and services provided by different habitats, and relative risk frameworks around the threats and stressors to different habitat types or groups. Such classifications can also help identify information gaps (of which there are invariably many), place studies in a systematic framework, and provide clear guidance on the relative ranking of habitats for management (e.g. spatial extent, rarity, biodiversity and fisheries values). No such classification exists for New Zealand. However, a national estuarine and coastal (fish-) habitat classification (0–200 m) is being currently advanced in the MSI programme “Coastal Conservation Management”, with a particular focus on fish-habitat linkages. This is a very challenging task, given the spatial scales involved, and is being approached as an adaptive process. Aside from the construction of the generic habitat framework, data with which to actually populate it are for the foreseeable future going to be limited, and only slowly added to as new empirical field surveys evolve. One way to speed up this process is to ensure that, where possible, research surveys have sampling protocols that allow the data generated to be incorporated into the generic habitat classification framework. Such an approach has already been used for the OS2020 Bay of Islands programme, and the MPI Biodiversity Fund programme “Biogenic Habitats on the Shelf”. No initiatives exist to create a habitat classification for New Zealand’s deeper waters (beyond 200 m).

8.3 Detection and mapping

On-going work to create an inventory of fundamental biogenic assets, including what and where, in what spatial extents, and how human activities are impacting on these over time, is an underpinning priority for better marine spatial planning (MSP). Remote sensing including aerial photography, side-scan sonar, and single and multibeam sonar offers the greatest possibility for the detection and mapping of biogenic habitats. Based on published studies (e.g. seagrass using aerial and satellite photography; horse mussel beds and bryozoan fields using side-scan sonar), and recent data collections (e.g. Separation Point bryozoan fields and *P. socialis* tubeworm meadows using multibeam sonar) a number of biogenic habitats are already known to be amenable to such methods. A priority should be to formally assess which habitats are detectable by remote sensing methods (limited to technologies realistically available in New Zealand), and to produce an ‘Atlas’ of the form/signal those habitats present in remote sensing data. In turn, where practical these forms/signals should be applied to new mapping data sets as they become available, to identify new biogenic habitat areas. This scenario would allow for marine mapping projects, regardless of their formal objectives, e.g. geology, to provide at low-cost data for other purposes (a whole-of-government approach). Holding these map data in a publicly accessible way, such as through a web portal, would ensure their maximum visibility and availability to those wishing to use them (e.s. see OS2020.org).

Other sources of information on where biogenic habitats may occur should also be assessed where possible, especially Local Ecological Knowledge (LEK), which as well as covering areas not known to scientists, may also capture temporal changes. Capturing this information where it still exists should be a priority, before it is lost as older generations pass on. LEK interviews of 50 retired commercial (largely trawl) fishers were conducted nationally in the ZBD200801 Biogenic Habitats on the Continental Shelf programme (Jones, Morrison, in prep.), as well as of long-time users of the

Kaipara Harbour (Morrison et al. 2014b). Additional national scale interviews could be made of retired non-trawl fishers to gain knowledge on untrawlable seafloor areas; e.g., as fished for rock lobster and grouper. In addition, while the focus of ZBD200801 interviews was the identification of biogenic habitat areas, it became apparent that fishers also held a deep knowledge of fish behaviours and population dynamics, including spawning and movements, not documented in the scientific literature. Interviewers were unable to explore this knowledge in detail, given available interview time and the programme objectives, but there remains a large knowledge store that will be lost with time unless captured through additional LEK interviews.

8.4 Habitat modelling and predictive maps

Given the large spatial domains involved, full and comprehensive mapping of all of New Zealand's territorial seas and EEZ is highly unlikely in the foreseeable future. Predictive habitat modelling and associated spatial predictions are a rapidly advancing field in marine science, and offer the opportunity to extrapolate relatively limited empirical field surveys across much wider domains. Ideally, this should be an adaptive process over time, with empirical field data driving the predictive models, and then in turn new empirical field surveys testing the models in new areas, and so on. Such effort needs to be closely aligned with the habitat classification and detecting / mapping of these habitats.

8.5 Threats and stressors

Ultimately the conservation of important biogenic habitats comes down to the better management of human activities, both land-based and marine. Development of a risk management framework is an important task. A number of systems are in development internationally, as well as in New Zealand for various marine system components, though none are systematic across the full marine domain. For instance, the coastal habitat classification being developed in the Department of Conservation (DOC) Marine Conservation Programme includes the development of a companion threats and risks framework, but the knowledge needed to fully develop understanding at the national scale is not yet available, and will require multiple work streams to achieve (e.g. effects of fishing, land-based effects).

8.6 Fisheries links – from patch to the fishery scale

The specific linking of biogenic habitats to fisheries productivity requires a clear prioritisation of investment and effort, given the large spatial scales involved, and the range of biogenic habitats and fisheries species. Until this work is completed, it is not possible to quantitatively rank the value of different biogenic habitats, or chains of habitats, from a fisheries production viewpoint. Such work needs to integrate both small-scale process studies; e.g., how does growth and survival vary across different biogenic habitats (including quality and landscape setting)?; larger scale connectivity, e.g. how do different habitats link together through ontogenetic or other fish movements, and at what spatial scales, and to what adult populations and associated fisheries?. Frameworks such as that used for the Chesapeake Bay blue crab population (Jordan et al. 2009) could be used as a basis for such work. Otolith chemistry and other possible techniques are now making such work increasingly more tractable and achievable, while initial work on spatial habitat variation in growth rates is also showing promise (e.g., for juvenile snapper, Evans 2014; and juvenile grey mullet, Mohd Zain 2014). However, estimating mortality and survival across different habitats, and within habitats across gradients of differing habitat quality, remains a fundamental challenge.

As a ‘proof-of-concept’, and to allow for generally applicable modelling methods to be created / adapted to link fish-habitat dynamics into stock assessment models and decision making, the selection of one or more specific species for targeted research would be a logical start. Suggested New Zealand species/areas are: 1) juvenile snapper and biogenic habitats associated with the SNA 8 West Coast North Island, where the stock has failed to recover despite quota cuts and associated modelling predictions, detailed juvenile nursery habitat data exists, and mapping of some key habitats (i.e., sub-tidal seagrass meadows) is under way, 2) juvenile snapper in the SNA 1 stock, where a large amount of background knowledge exists, New Zealand’s largest recreational fishery is based (e.g., useful in informing wider society about land-based impacts), and many other end-users and agencies also have strong interest in biogenic habitats; 3) blue cod in a localised region, given their suspected juvenile phase reliance on biogenic habitats, which are susceptible to both land and marine-based impacts – the Marlborough Sounds is one obvious choice, given management concerns around the sustainability of the recreational fishery, and the suspicion that land-based effects may be significant in that system; 4) tarakihi at the national scale, given that this approximately 6000 t fishery is showing signs of stress, that background information suggests that juvenile tarakihi are strongly associated with biogenic habitat nurseries under stress, and that the stock is thought to be operating at the national scale.

Experimental spatial management is a very powerful tool (e.g. Sainsbury et al. 1988) for empirically assessing how biogenic habitats, and associated fisheries production, respond to management actions at spatial scales relevant to fisheries. Short term closures of some biogenic habitat areas to assess their potential as ‘fisheries enhancement reserves’ would be very useful experiments (in terms of habitat regeneration and associated juvenile fish increases). Such an (as yet unrealised) experiment has been in effect at Separation Point since 1980, but with no associated data collection, we do not know if it is functioning as intended; the limited observations available suggest it may be degraded/degrading from land-based sedimentation (Grange et al. 2003). The outcomes of such experiments could also be used to explicitly assess gains in fish recruitment to fisheries stocks, relative to the potential fisheries catch forgone from the closed area (noting that the area involved might be quite small relative to the overall area fished).

8.7 The functioning of the biogenic habitats themselves as living organisms

Once we have a better understanding of which are the most critical biogenic habitats (for fisheries production), then better management of those specific habitats, as living organisms, requires that we understand more about their environmental requirements for healthy populations. For instance, subtidal components of seagrass meadows are largely contained in their depth range by ambient light levels, and better land-management practices with improved down-stream estuarine water quality might allow subtidal seagrass to naturally expand back towards historical extents. Similarly, the retiring of (relatively) small areas of seafloor from trawl/dredge fisheries and other similar disturbances might allow some biogenic habitats to naturally re-establish their abundance, with associated positive effects through to fisheries via enhanced juvenile recruitment. Protecting what biogenic habitats remain, and providing suitable conditions for biogenic habitats to naturally regenerate in areas where they are now probably functionally extinct, is the best way forward, although recovery may/will be on decadal scales. Active restoration is a possibility (although the spatial scales required are a major challenge) with work in New Zealand showing that it can be done for intertidal seagrass in situations where environmental conditions have improved from when it was lost (e.g successful trials in Whangarei Harbour); similarly an experiment in the Firth of Thames has shown that adult green-lipped mussels can survive and grow there if seeded in patches to start new

beds (McLeod et al. 2012). Given the spatial scales involved, such efforts would probably be best directed at establishing small source populations, and then letting natural restoration occur from there.

8.8 Integrated marine spatial planning and ecosystem based management

In conclusion, it is argued that biogenic habitats strongly deserve more specific and explicit recognition in marine management, including their role as ‘Essential Fish Habitat’ (EFH). As marine spatial planning (MSP) and Ecosystem Based (Fisheries) Management (EBFM) mature and evolve in the New Zealand context, we expect that the role of habitats and environment in underpinning sustainable fisheries production will assume a more central role in targeted research and management efforts. Associated with this, management efforts should focus on halting their strong historical and probably contemporary declines, and even potentially reversing these losses through mitigation of stressors, and allowing the natural ‘regeneration’ of some areas, including possibly initiating some (pragmatic) restoration efforts.

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Author affiliations: M.A. Morrison, E.G. Jones, NIWA Auckland, 41 Market Place, The Viaduct, Auckland; M. Consalvey, NIWA Wellington, 301 Evans Bay Parade, Hataitai, Wellington 6021; K. Berkenbusch, Portobello Marine Laboratory, University of Otago, P.O. Box 8, Portobello, Dunedin 9014, and Dragonfly Science, P.O. Box 27535, Wellington 6141.

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