



# Bottom disturbance and seafloor community dynamics: Development of a model of disturbance and recovery dynamics for marine benthic ecosystems

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## EXECUTIVE SUMMARY

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This project expands on a spatially explicit patch dynamic model (Lundquist et al. 2010, Thrush et al. 2005) as a framework to illustrate how increasing rates of disturbance to benthic marine ecosystems influence functional diversity, and ultimately, other elements of biodiversity and ecosystem function such as the abundance of rare species, ecosystem productivity, and the provisioning of biogenic habitat structure. The aim of the model is to provide a heuristic tool that can be used when considering seafloor disturbance regimes in the context of spatial planning and other ecosystem-based management. The model has been designed to assist the Ministry for Primary Industries in assessing operational management strategies and decisions, based on their likelihood of minimising or mitigating the adverse effects of bottom trawling and dredging on benthic communities, and to provide predictions of fishing effects at scales relevant to fishery management. This model also provides a framework for working with resource managers to define suitable model thresholds for disturbance that can assist the management of the environmental effects of fishing. For example the model could be used to suggest management thresholds in the proportion of biogenic structure-forming habitats, or thresholds in the amount of total area that could be fished in a fishing season.

We have modified the original model from one based on simple succession from pioneer to mature communities to a more realistic one based on a mosaic of coexisting species types that change in relative dominance over the seascape as time from disturbance increases. Spatially-explicit dispersal is incorporated into the model by varying the size of the local neighbourhood around disturbed cells from which colonists could be sourced. This links the model to observations of recovery after disturbance that indicate the importance of connectivity between neighbouring patches in influencing recovery rate (Thrush et al. 2008; Thrush et al. 2013). Adult-juvenile interactions add further realism by incorporating interactions between functional groups that either facilitate or inhibit colonisation success (Hewitt et al. 2005, Thrush 1999, Thrush et al. 2001a, Thrush et al. 2006).

Eight functional groups were defined for the model, representing key aspects of the ways organisms in seafloor communities modify their environment and interact with each other. These included: opportunistic early colonists with limited substrate disturbance; opportunistic early colonists with considerable substrate disturbance; substrate stabilisers (e.g., tube mat formers); substrate destabilisers; shell hash-creating species; emergent epifauna; burrowers; and predators and scavengers. While we did not define each functional group as having a particular sensitivity to disturbance, each functional group was allocated a selection of life history traits (i.e., age of maturity, maximum lifespan, seasonality of reproduction, larval dispersal distance). While many of these life history traits are associated with sensitivity to fishing disturbance, we did not define further parameters for each functional group to incorporate sensitivity in the model iterations presented here; rather model scenarios were based solely on biological life history traits.

When disturbance is added, the model predicts changes in the occupancy of functional groups within the model seascape. Some functional groups respond negatively to disturbance, including those known to be sensitive to, and to recover slowly from, disturbance (e.g., emergent epifauna). Other groups (e.g., opportunistic taxa) respond favourably to disturbance in the model, as we would expect. Response to disturbance and recovery rates differ between the eight functional groups, reflecting the different life history characteristics and dispersal characteristics simulated by the model.

The model was run to compare predictions with available inshore (Tasman and Golden Bays) and offshore (Chatham Rise and Challenger Plateau) empirical datasets. These datasets included video data with broad coverage of the seafloor, but relatively poor representation of small-bodied and infaunal groups, in combination with benthic sled, grabs, or cores that better sampled these groups. We used a fuzzy logic approach based on functional traits (e.g., feeding, motility, position in the sediment, size) to allocate 1056 individual taxonomic units (e.g., species) into one of the eight functional groups, and compared relative abundance of functional groups from inshore and offshore surveys to model predictions.

Model predictions were consistent with changes in functional group abundance with increasing rates of disturbance in both the inshore and offshore datasets, with declines in functional group abundance occurring at the approximate disturbance rates predicted by the model. The strong similarity between model and observed community changes with disturbance showcases the value of this heuristic tool, based on fundamental biological parameters, for investigating disturbance and recovery dynamics in seafloor communities. Future research can build on this model framework, varying parameters and assumptions within model scenarios, to inform ecosystem-based management approaches for seafloor communities.

# 1 INTRODUCTION

## 1.1 Overview

As human activities and natural disturbances result in changes in marine systems, it is important to understand how seascapes respond to different spatial and temporal patterns of disturbance. Seascapes consist of a mosaic of different seafloor habitats which are often identified based on structure-forming species. Many of the structure-forming species, as well as other species that serve important functional roles on the seafloor, are sensitive to physical disturbance. Biological traits (e.g., morphology, life history, dispersal characteristics) can determine both the sensitivity of different species to the disturbance impact, and to their ability to recolonise disturbed habitats. Some biological traits associated with sensitivity include being sedentary or having low mobility, protruding from the sediment or having fragile body forms such as shells or branched morphology (Hewitt et al. 2011a, Thrush & Dayton 2002, Thrush et al. 1998).

One general pattern, repeated across broad spatial scales, is that high rates of disturbance to benthic communities reduce habitat structure, resulting in homogenous, simple, low diversity communities, the loss of large and long-lived sedentary species that create habitat structure, and associated reductions in primary production and ecosystem function (Dayton et al. 1995, Thrush & Dayton 2002, Thrush et al. 2008, Thrush et al. 2009, Thrush et al. 2013). These patterns with disturbance have been observed with both natural (e.g., wave disturbance from storm events) and human disturbances (e.g., seafloor dredging, bottom trawling). However, it is unclear what combination of spatial and temporal rates of disturbance results in homogenous low levels of benthic biodiversity. This tipping point is difficult to determine empirically, as broad-scale empirical tests of disturbance at seascape scales are expensive, ethically questionable and logistically difficult. Instead, we must rely on theoretical modeling approaches to predict how increasing rates of disturbance change functional diversity and productivity of marine benthic communities at large scales.

This project expands on a spatially explicit patch dynamic model of marine benthic community structure (Thrush et al. 2005), as a framework to illustrate how increasing rates of disturbance to benthic marine ecosystems influence functional diversity, and ultimately other elements of biodiversity and ecosystem function (such as the abundance of rare species, ecosystem productivity, and the provisioning of biogenic habitat structure). Model predictions were compared to existing datasets of spatial and temporal rates of benthic impacts from fishery trawl disturbance for both inshore and offshore benthic communities. The model framework is suitable for testing disturbance impacts ranging from coastal sedimentation, to increases in storm frequency due to climate change, to fishing impacts on benthic habitats and communities. The model is developed as a tool to help address management questions such as:

- ‘For each conceptual community, what are threshold rates of spatial and temporal disturbance that result in functional extinction of habitat structural attributes of marine benthic communities?’ and
- ‘What functional attributes should dominate benthic communities after 10 years of recovery, or with a rotating harvest strategy of 10% of the seascape fished per year?’

In addition, from an ecological perspective, the model will provide a framework for testing hypotheses about disturbance rates based on the observed functional diversity of communities for which direct or local scale knowledge of disturbance rates is unavailable.

## 1.2 Benthic community ecology

Disturbance is one of the key drivers of biodiversity patterns in marine ecosystems. Temporal and spatial rates of disturbance interact with colonisation and successional processes resulting in the heterogeneous mosaic of patches found in marine benthic ecosystems, both in hard and soft-substrate

habitats (Johnson 1970, Paine & Levin 1981, Pearson & Rosenberg 1978, Pickett & White 1985, Rhoads et al. 1978). The organisms living in these habitats have evolved to cope with and sometimes rely on natural disturbance rates, ranging from small, frequent disturbances such as ray pits (Thrush et al. 1991) or wave disturbance (Sousa 1984), to large but relatively infrequent disturbances such as large storms or hurricanes (Connell 1978). In contrast, anthropogenic disturbances include disturbances from benthic fishing gear including trawls and dredges, seafloor mining or land-based inputs resulting in increased sedimentation, eutrophication or entry of chemical pollutants into the marine environment. These anthropogenic disturbances tend to be widespread and frequent relative to natural disturbances in the marine environment (Thrush & Dayton 2002, Turner et al. 1999). Increases in the intensity of the disturbance regime, relative to natural disturbance rates, are likely to degrade marine systems as they disturb the adult infauna and epifauna through direct mortality. Disturbances also affect the capacity for later recolonisation, as adult populations that serve as a colonist source have been reduced by disturbance. Other indirect changes due to physical impacts of disturbance can modify sediment characteristics and other physical properties that result in changes in ecosystem function and reduced colonisation success.

Benthic seascapes are highly diverse, with high spatial variability, and abundant biogenic structures produced by both epifaunal and infaunal species (Ellingsen et al. 2007, Gray 2002, Snelgrove 1999). To allow general predictions about seafloor community dynamics that are composed of thousands of individual species, marine species can be grouped by functional traits, such as provision of biogenic structure, body size, feeding mode, or mobility. These functional traits interact with ecological, physical and chemical processes in the water column and sediments, and are associated with the provision of particular ecosystem functions (Lohrer et al. 2004). For example, the roles of biogenic habitat structure in subtidal soft sediment communities are extensive, including the provision of settlement habitat and refuge sites from predation, modification of biogeochemical processes and exchanges, modification of flows, and sediment stabilisation (Diaz et al. 2003, Hewitt et al. 2005, Scharf et al. 2006, Thrush et al. 2001b, Turner et al. 1999). While detailed studies of the natural history of most marine species are rarely performed, particularly for soft sediment systems on the continental shelf and slope, functional traits can be used to elucidate the roles of particular species in maintaining ecosystem structure and function. Functional diversity within a community is predicted to be positively correlated with ecosystem function, such that pioneer, highly disturbed communities are predicted to have low functional diversity, while complex, structured communities are predicted to have high functional diversity (and thus larger contributions to ecosystem function).

The interactions between disturbance and colonisation are complex. The extent to which patch colonisation is driven by local, regional, or global dispersers has large implications for community dynamics and resilience to disturbance (Palmer et al. 1996). If larval, juvenile or adult movement occurs over large distances, as is the case for species with long-lived planktonic larvae and long-distance dispersal potential, disturbance to a local area is unlikely to influence the likelihood of recolonisation. However, species with restricted dispersal potential (e.g., species with either short-lived or non-planktonic larvae) are also common, particularly in soft-sediment ecosystems (Grantham et al. 2003, Kinlan & Gaines 2003). In fact, reviews of larval dispersal suggest that many sessile structure-forming species such as sponges and corals have low dispersal potential relative to other taxa (Kinlan & Gaines 2003). For these species with more restricted dispersal, disturbance can result in localised decreases in recruit sources. Although we are unlikely to know the dispersal and colonisation processes of all marine fauna and flora (Cowen & Sponaugle 2009), trends in dispersal potential across taxonomic and functional groups imply that we can develop dispersal scenarios to test a range of relevant dispersal possibilities for soft sediment communities.

Although the particular species and interactions vary between marine communities, increases in the complexity of habitat structure (both infaunal and epifaunal), biogeochemical processes, and species interactions with time from disturbance are common to most marine systems (Cranfield et al. 2004, Pearson & Rosenberg 1978, Rhoads et al. 1978, Zajac 2008). Small scale mechanistic experiments can elucidate the ecosystem functions provided by particular species and feed into models that examine the ecological implications of disturbance on particular ecosystem services (Lohrer et al.



2010). These mechanistic responses to disturbance in terms of nutrient fluxes and other ecosystem functions can be correlated with different elements of biodiversity, productivity, and habitat structure. We can extrapolate results from these small scale disturbance experiments to predict the impacts of varying disturbance rates on ecosystem function across an entire seascape based on changes in diversity metrics along recovery trajectories. Similarities in functional traits allow us to extrapolate the ecosystem functions associated with different functional traits across species for which natural history data are not available. The similarity in response to disturbance across species and systems suggests that a conceptual model of a generalised recovery trajectory can advance our understanding of the role of disturbance on marine community dynamics, and should also allow for generalisation to predictive models of disturbance at scales relevant to fisheries management.

### 1.3 Strategic Relevance

In New Zealand, bottom trawling and dredging are the predominant methods used in many key fisheries (e.g., orange roughy, hoki, snapper, scallop, oyster). While we can infer that fishing disturbance has negative impacts on biodiversity and ecosystem function from both overseas (Hall 1999, Jennings et al. 2005, Thrush & Dayton 2002) and New Zealand studies (Cryer et al. 2002, Thrush et al. 1998), we lack detailed knowledge of the spatial and temporal rates of disturbance that result in negative impacts, and recovery rates from disturbance of different soft sediment communities both in New Zealand and world-wide. This project is designed to develop a conceptual model that will predict disturbance rates that are likely to impact benthic communities, and can be generalised across different habitat types and depths. This project differs from many models of fishing disturbance and recovery dynamics in that the recovery rates of populations are informed by rules that reflect basic life history characteristics. In contrast, many seafloor disturbance models simplify recovery of seafloor communities to population growth functions, which are likely to over-estimate the rate of recovery, as they omit key biological interactions and life history characteristics (e.g., age of maturity) that influence population growth rates, and often result in mismatches between model predictions and empirical reality. The model has been designed to assist the Ministry for Primary Industries in assessing operational management strategies and decisions based on their likelihood of minimising or mitigating the adverse effects of bottom trawling and dredging on benthic communities, and to provide predictions of fishing effects at scales relevant to fishery management.

While the primary objective of this project is to increase our understanding of the role of disturbance in modifying marine communities, we also envisage this project as a stepping stone in progress toward holistic ecosystem-based management of New Zealand's inshore and offshore fisheries. This project develops a decision-support tool that can be used to inform decision-making with respect to benthic fishing, or in fact other agents of seafloor, disturbance. Conceptual models of disturbance in seascapes, developed using this tool, will contribute to a Management Strategy Evaluation (MSE) approach (e.g., Ellis et al. (2008), Sainsbury et al. (2000)) to quantify the relative benefits to functional diversity (and thus ecosystem function) of different management scenarios, such as spatially restricted fishing areas, rotating harvest closures, and reduction of fishing effort (disturbance rates), and methods for monitoring fishery impacts and recovery processes. The decision-making tool can also be used to discuss the scales of existing data management systems such as fishing effort and survey sampling, so that we can inform questions such as 'at what scale is fishing effort data collected and does this affect our ability to detect changes due to disturbance'. The model also provides a framework for working with resource managers to define suitable model thresholds for disturbance that can assist the management of the environmental effects of fishing. For example the model could be used to suggest management thresholds in the proportion of biogenic structure-forming habitats, or thresholds in the amount of total area that could be fished in a fishing season.

## 1.4 Project Objectives

In this project, we present the model development and parameterisation using data from inshore and offshore seafloor communities, with the aim of demonstrating that the model does approximate marine benthic community response to and recovery from disturbance, and can be used as a heuristic learning tool to investigate seafloor management scenarios. The project objectives are:

1. Further develop landscape/seascapes ecological model of disturbance/recovery dynamics in marine benthic communities, incorporating habitat connectivity, based on existing model by Lundquist, Thrush, and Hewitt.
2. Predict impacts of increasing rates of disturbance on rare species abundance, functional diversity, relative importance of biogenic habitat structure, and ecosystem productivity.
3. Use literature and expert knowledge to quantify rare species abundance, biomass, functional diversity, habitat structure, and productivity of various successional community types in the model.
4. Field test predictions of the model in appropriate marine benthic communities where historical rates of disturbance are known, and benthic communities have been sampled.

## 2 METHODS

### 2.1 Disturbance/Recovery Model

The original disturbance model was developed to illustrate how marine benthic systems react to varying spatial and temporal rates of disturbance, and to draw attention to the benefits of spatial management in an Ecosystem-Based Management (EBM) context (Lundquist et al. 2010, Thrush et al. 2005). This conceptual model examined marine benthic communities dominated in terms of habitat structure by relatively long-lived species that would be typified by bryozoan reefs, sponge gardens, bivalve beds, or other important biogenic features that have shown disproportionate decreases with increased anthropogenic disturbance (Cranfield et al. 1999, Rothschild et al. 1994, Thrush & Dayton 2002, Thrush et al. 2005). The seascape was modeled as a mosaic of habitat patches at varying ages from newly disturbed to mature structured habitat, and thus represents a common perspective on marine benthic communities (Zajac 2008). A further iteration of the model examined how mature biogenic habitat responds to spatial restrictions on colonisation of disturbed patches, illustrating the potential for threshold responses as the seascape is increasingly fragmented by disturbance (Lundquist et al. 2010). Spatially-explicit dispersal was incorporated into the model by varying the size of the local neighbourhood around disturbed cells from which colonists could be sourced, as observations of recovery after disturbance have varied with distance from and size of neighbouring patches.

This project expands on this spatially explicit patch dynamic model (Lundquist et al. 2010, Thrush et al. 2005) as a framework to illustrate how increasing rates of disturbance to benthic marine ecosystems influence functional diversity, abundance of rare species, ecosystem productivity, and biogenic habitat structure. The original model considered only the time required for recovery to a mature biogenic community in determining impacts of disturbance. Here, we use a functional group approach, allowing for more complex realisation of benthic community structure, and how different species interact with each other to influence recovery trajectories after disturbance (Lundquist et al. 2010).

### 2.2 Spatial and temporal scale of model

The standard model consists of a  $128 \times 128$  cell grid, with each of the 16 384 cells representing a habitat patch at a certain age. Conceptually, each cell represents a large enough area to sustain a

benthic community, and be reproductively successful such that the cell can serve as a colonist source to other cells. As such, the model is scale invariant; grid cells could be assumed to represent sizes of approximately  $100 \times 100 \text{ m}^2$ , a realistic patch size for a shallow bryozoan reef community, or grid cells could represent substantially larger areas more suitable for modelling deep areas such as that of the Chatham Rise. Choice of a cell size should consider both the size required for a sustainable biological community, but also be relevant to the scale of dispersal of the community members. For example, if dispersal is limited to distances of roughly 1 km, grid cells should be at most 1 km in each dimension. While the standard model includes 16 384 cells, the grid dimensions can easily be increased or decreased in the model code, and the width and length can be modified to represent a specific region. The temporal component of the model is also scale invariant, although here we assume the temporal component to correspond to seasons with four time steps (seasons) per year. This seasonality allows for better representation of temporal variation in availability of recruits of different species.

### 2.3 Model structure and initialisation

A number of assumptions are reflected in the parameterisation of each model scenario. The assumptions used in the scenarios presented here do reflect the impacts of particular disturbances on the recovery dynamics of some seafloor communities, and are used to illustrate the potential for the model to serve as a learning tool in evaluating management scenarios. However, we recognise that many of the assumptions (e.g., disturbance resulting in full mortality of all groups within a cell) can be relaxed to represent other benthic communities or disturbance types. The model is flexible, allowing for ease of varying parameter values (e.g., mortality rates, disturbance impacts) to suit a desired scenario. Diagnostic analyses were performed to evaluate the sensitivity of the model to individual rules or life history characteristics that were included in the model (e.g., maximum life span, dispersal distance, seasonality of reproduction, shell hash rule, adult-juvenile interactions).

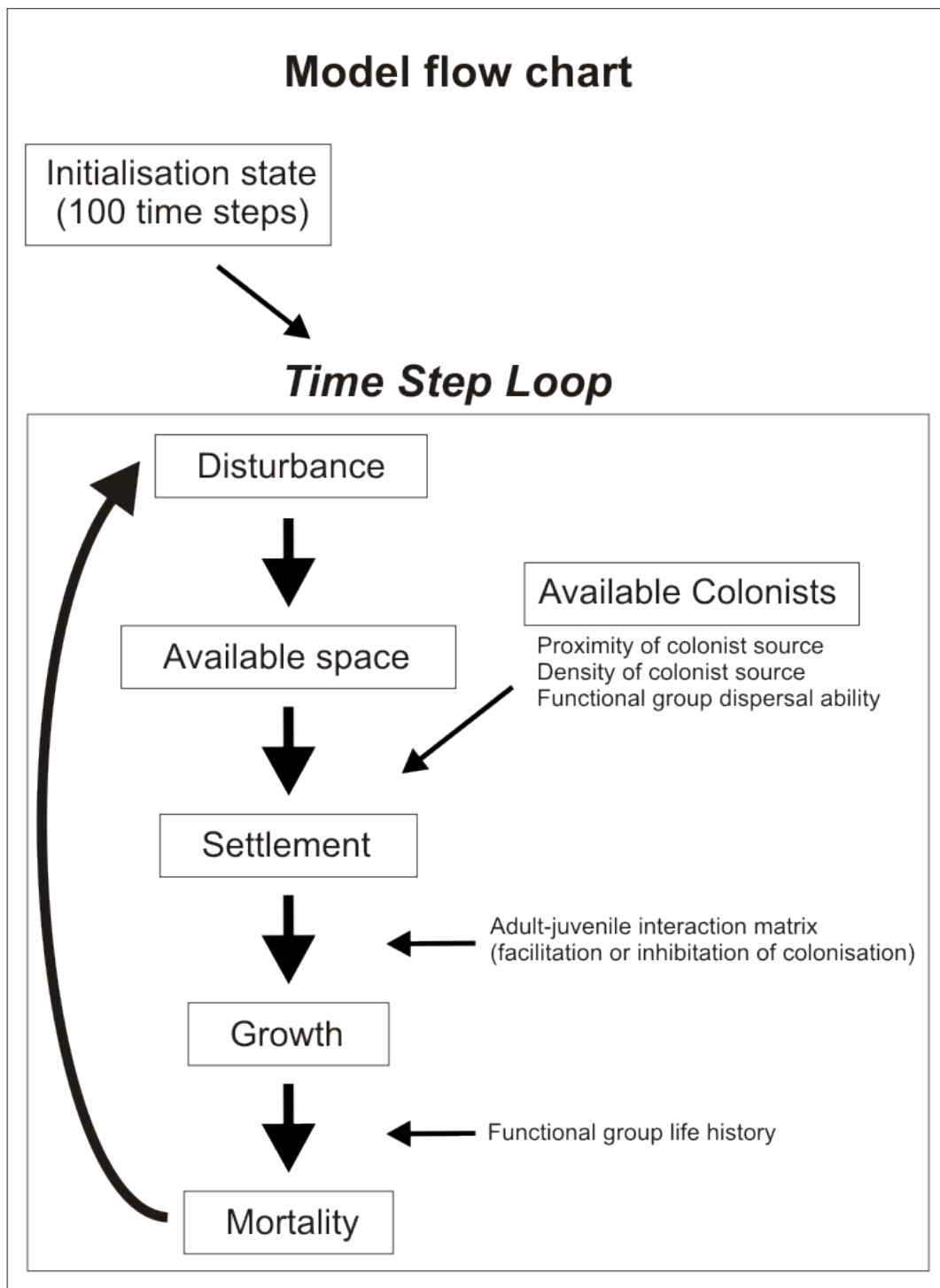
The model consists of disturbance, colonisation, aging, and mortality of cells (Figure 1). The model is initialised by creating a seascape consisting of cells of randomised functional group ages varying from the minimal pioneer age (cell age 1), representing a newly settled juvenile, to a maximum age that varies between functional groups. The model is then run for a set number of time steps without disturbance; we used a start-up period of 100 time steps for the standard model to allow for stabilisation of age distributions for each functional group. This start-up period, in combination with the initial randomness of the age matrix, was sufficient to allow for dampening of any cyclic behaviour of the longest-lived functional groups used in the scenarios presented here. Should a functional group be modified to represent longer-lived taxa (i.e., deep sea corals), additional start-up time would be required to generate equilibrium conditions prior to implementing a disturbance regime. To incorporate disturbance, the model seascape can be disturbed at either regular or random time steps, and disturbances can be placed either within a pre-determined subset of the model seascape, or at randomly selected areas within the full model seascape at each time step. After disturbance occurs or a cell is otherwise vacated, empty cells can be colonised according to rules of dispersal (Section 2.7) and interactions between functional groups (Section 2.8). The age of each undisturbed cell is sequentially increased after each time step. The model records age, colonisation, and occupation of each functional group in all cells within the seascape for each time step.

Disturbances and corresponding source areas for colonisation are simulated assuming periodic boundary conditions (i.e., a torus; neighbours of edge cells are represented by an open boundary that continues on the opposite side of the grid). This allows us to decrease potential unrealistic edge impacts when we reach the model boundary, assuming that benthic communities do exist and contribute colonists from outside of our model region. While we do not do so in the simulations presented here, the model boundary conditions can be changed to allow boundaries to consist of, for example, non-trawled areas, allowing for a larger contribution to colonisation from outside the main model region.

## 2.4 Disturbance

In the simplest model iteration, disturbances are randomised across the seascape in continuous square blocks of sizes representing different percentages of the seascape disturbed and at time steps corresponding to the frequency of disturbance. Here, disturbances are created at random locations using a random number generator, and all cells are equally likely to be disturbed regardless of disturbance history. Disturbance rates can range in spatial scale from 0–100% of the total seascape disturbed in each time step, and in temporal scale from 0–100 individual disturbance events per year. After a disturbance occurs, disturbed cells have disturbance mortality applied to juveniles and adults of all functional groups. This represents an immediate post-disturbance state within the entire cell, and no mature individuals remain to supply colonists from the disturbed cells. In this report, we present results showing scenarios with one disturbance event per time step, and with the spatial extent of the disturbance event being a square area that differs in size (and thus total proportion of the grid disturbed) between scenarios.

Here, we present model simulations where disturbances result in complete removal of all occupying functional groups in the perturbed areas (i.e., disturbance mortality equals 100% mortality rate), mimicking either a natural or man-made disturbance such as storm damage, mining or fishing activity. While complete removal does occur after some disturbance types, this assumption can be relaxed to incorporate only partial mortality, or inclusion of sensitivities to disturbance impact that differ between different functional groups such that some groups are disproportionately affected by disturbance events (e.g., species with fragile morphology or that protrude above the sediment surface).



**Figure 1: Model flow chart.**

## 2.5 Conceptual functional groups

In the original model (Thrush et al. 2005), we conceptually defined the recovery trajectory as representing different successional stages that increased sequentially with time. This original model of community dynamics was based on observed recovery rates for a well-studied New Zealand shallow (less than 100 m depth) bryozoan reef community (Cranfield et al. 2003, Cranfield et al. 1999, Cranfield et al. 2004). Numerous observations of recovery of benthic systems after disturbance in other systems allow us to conceptualise this recovery process for benthic communities in different

regions and at varying depths. For example, a model representing a shallow bryozoan reef would be typified by initial colonisation by opportunistic infaunal taxa such as small polychaetes or amphipods. This pioneer stage is followed by colonisation of hard substrate forming species such as juveniles of large suspension-feeding bivalves. Once these hard substrate-forming fauna have matured, colonisation onto hard substrate and then growth of dominant biogenic reef fauna occurs; without the presence of these hard substrates, biogenic reef fauna do not colonise the surrounding soft sediments. Importantly, each successional stage of the recovery process can be linked to functional traits (and thus functional diversity), biogenic structure, productivity and other aspects of biodiversity and ecosystem function.

Here, we increase model complexity, and realism, by expanding from the single biogenic habitat in the original model (Lundquist et al. 2010, Thrush et al. 2005), to eight interacting functional groups, representing key functional aspects of seafloor communities that contribute to ecosystem function. These eight functional groups allow us to predict disturbance and recovery dynamics for different types of organisms, ranging from small, opportunistic, fast colonising invertebrates, to large organisms forming biogenic habitat structure, to burrowers that bioturbate sediments. The interactions between functional groups that determine colonisation, i.e., the presence of hard substrate increasing likelihood of colonisation of biogenic reef fauna, are the mechanisms that drive colonisation and recovery dynamics in the model structure.

## 2.6 Derivation of trait-based conceptual groups

The eight functional groups were defined at a series of expert workshops attended by a group of NIWA scientists with expertise in inshore and offshore soft-sediment benthic systems. At these workshops, we derived key conceptual types or functional groups that represented our functional understanding of benthic community structure (Table 1). The initial list of functional groups was iterated over multiple workshops during model development, and the inclusion of adult-juvenile interactions during further model development suggested that we subdivide two of the original groups: A) opportunistic early colonists, and B) late colonising substrate destabilisers, based on the extent and depth of typical substrate disturbance, which influences their functional role and interactions with other functional groups.

Life history traits used in the model (age of maturity, age of mortality, reproductive seasonality) were defined with respect to representative species for each functional group in inshore and offshore soft-sediment habitats. We used information based on literature review and expert knowledge (C. Lundquist, pers. comm.) to define life history traits for each functional group (Table 2). Life history information is poorly known for many seafloor taxa, with some aspects (reproductive seasonality, larval information) least quantified. Simplifying benthic communities into broad functional groups does allow us to look for general interactions between disturbance and community structure, but inevitably results in a range of traits being encompassed by each functional group (Table 2). When life history traits were not consistent among species within a functional group, representative characteristics for each functional group were based on expert assessment of the life history traits representative of most species within a functional group (Table 3).

Dispersal is poorly quantified for most marine species; dispersal information for New Zealand coastal and estuarine species was compiled based on literature review and expert knowledge (C. Lundquist, pers. comm.). Further information was supplemented through international literature review to define three main dispersal strategies that were used in the model to define functional groups as having local, regional or global dispersal (Table 3).

Mortality varies across functional groups, and across age of all groups. Small opportunistic groups generally have high mortality rates whereas larger, long-lived invertebrates often have lower mortality rates, particularly for older life stages in large-bodied benthic invertebrates. Larval mortality rates are high for all groups, with individuals often producing millions of larvae, of which few survive to a

settlement stage (Morgan 1995, Rumrill 1990). Larval and early juvenile mortality are included implicitly in the model within the coding of adult-juvenile interactions that either facilitate or inhibit colonisation success. For larval mortality, we assume that our model coding of dispersal (Section 2.7) and settlement success dependent on adult-juvenile interactions (Section 2.8) represents larval mortality dynamics.

In scenarios presented here, we include a ‘natural’ mortality rate within the model which represents extinction of a functional group within a model cell. This parameter representing natural mortality also provides added stochasticity within the model, and dampens location-specific cycles that may occur if a group of neighbouring newly disturbed cells is colonised at the same time step. ‘Natural’ mortality scores for each functional group in each cell (both juveniles and adults) are allocated using a uniform random distribution ranging from 0 to 1; all scores less than the mortality rate defined for a model scenario result in mortality. Further mortality is included when a functional group reaches its maximum life span within a cell. Sensitivity analyses showed that the highest mortality rate we tested (5% per time step) resulted in severely decreased occupancy of most functional groups within the model seascape, though this value does approximate estimated mortality rates of some benthic taxa, e.g., scampi. In the scenarios presented here, we assume an instantaneous mortality rate of 1% per time step (season) for juveniles and adults of all age groups, a low and constant rate for all functional groups, to allow scenarios to focus on other biological aspects of the model. Regardless, this parameter can be varied in future scenarios to incorporate varying mortality rates across age or between functional groups, and further sensitivity analyses can be performed to evaluate the relative influence of natural and disturbance-associated mortality.

**Table 1: General description of fauna classified under eight conceptual functional groups for the disturbance/recovery model based on key functional traits and life history characteristics. Source: conceptual functional groups were determined at expert workshops of NIWA inshore and offshore marine benthic ecologists at workshops held in 2010 and 2011.**

Functional Group	Typical taxa
1 Opportunistic early colonists – limited substrate disturbance	Sedentary species (e.g., paraonid and spionid polychaetes)
2 Opportunistic early colonists – considerable substrate disturbance	Mobile deposit feeders and small scavengers (e.g., phoxocephalid amphipods and other small crustaceans)
3 Substrate stabilisers (Tube mat formers)	Tube mat forming polychaetes (e.g., spionid, sabellid and chaetopterid polychaetes) and tube-building amphipods (e.g., <i>Ampelisca</i> sp.)
4 Substrate destabilisers	Spatangoid echinoids (e.g., <i>Echinocardium</i> sp.), holothurians, ophiuroids (e.g., <i>Amphiura</i> sp.)
5 Shell hash-creating species	Bivalves, gastropods
6 Late colonisers – emergent epifauna	Sponges, bryozoans, sea pens, sea whips, ascidians, gorgonians – primarily sedentary suspension feeders
7 Late colonisers – burrowers	Shrimps, crabs, large burrowing polychaetes
8 Predators and scavengers	starfish, crabs, hermit crabs, large-bodied predatory worms

**Table 2: Life history traits of representative species in each functional group, using data from literature review and expert knowledge.**

Class	Order	Family	Genus	Life Span (seasons)	Age at Maturity (seasons)	Larval Stage Duration	Reproductive Season	Key References
<b>Functional Group 1: Opportunistic (limited disturbance)</b>								
Polychaeta	Capitellida	Capitellidae	<i>Capitella</i>	4–8		1 mo	All year	(Mendez et al. 1997)
Polychaeta	Terebellida	Cirratulidae	<i>Cirratulus</i>	24–40	4–8		All year	(Olive 1970)
Polychaeta	Spionida	Spionidae	<i>Prionospio</i>	4	<4			(Hannerz 1956)
	<i>Representative characteristics for functional group</i>			6	2		<i>Spring, Summer, Autumn</i>	
<b>Functional Group 2: Opportunistic (disturbance)</b>								
Peracarida	Amphipoda	Corophiidae	<i>Corophium</i>	<4	<4		Autumn - Winter	(Peer et al. 1986)
Peracarida	Amphipoda	Photidae	<i>Gammaropsis</i>	4–8		<4 mo	Spring - Autumn	(Powell 1991)
Peracarida	Amphipoda	Pontoporeiidae	<i>Bathyporeia</i>	4	2		All year	(Fish & Preece 1970)
Peracarida	Amphipoda	Urothoidae	<i>Urothoe</i>	4	2		Spring-Autumn	(Fish 1996)
	<i>Representative characteristics for functional group</i>			6	2		<i>Spring, Summer, Autumn</i>	
<b>Functional Group 3: Substrate stabilisers</b>								
Polychaeta	Sabellida	Oweniidae	<i>Owenia</i>	<20			Spring-Summer	(Rouse & Pleijel 2001)
Polychaeta	Spionida	Spionidae	<i>Polydora</i>	4–8				(Giangrande 1997)
Peracarida	Amphipoda	Ampeliscidae	<i>Ampelisca</i>	4–8			Summer-Autumn	(J. Bremner, unpublished data; H.M. Tillin, unpublished data)
	<i>Representative characteristics for functional group</i>			12	3		<i>Spring, Summer</i>	
<b>Functional Group 4: Substrate destabilisers</b>								
Polychaeta	Capitellida	Maldanidae	<i>Euclymene</i>	12–20				(Rouse & Pleijel 2001)
Echinoidea	Spatangoida	Loveniidae	<i>Echinocardium</i>	60			Spring-Summer	(Buchanan 1966)
Malacostraca	Isopoda	Sphaeromatidae	<i>Exosphaeroma</i>	<4	<1			(Henninger et al. 2010)
Polychaeta	Capitellida	Arenicolidae	<i>Arenicola</i>	>24	8–12		Spring-Summer	(Beukema & De Vlas 1979, Newell 1948)
Malacostraca	Decapoda	Porcellanidae	<i>Pisidia</i>	8–12	4		Spring-Autumn	(Smaldon 1972)
	<i>Representative characteristics for functional group</i>			20	5		<i>Summer</i>	
<b>Functional Group 5: Shell hash creators</b>								
Bivalvia	Pterioidea	Pinnidae	<i>Atrina</i>	44–80				(Butler et al. 1993)
Bivalvia	Myoidea	Corbulidae	<i>Corbula</i>	20–24			Summer-Autumn	(Jensen 1990, Yonge 1946)



Bivalvia	Veneroidea	Donacidae	<i>Donax</i>	20	<4		Spring-Autumn	(Gaspar et al. 1999)	
Bivalvia	Pectinoidea	Pectinidae	<i>Pecten</i>	44–80	8–20	<1 mo	Spring-Autumn	(Minchin 2003)	
Gastropoda	Neogastropoda	Buccinidae	<i>Buccinum</i>	40			Spring-Summer	(Himmelman & Hamel 1993)	
<i>Representative characteristics for functional group</i>				60	5		<i>Spring, Summer</i>		
<b>Functional Group 6: Emergent epifauna</b>									
Gymnolaemata	Cheilostomatida	Flustridae	<i>Flustra</i>	24–48	<4	<1 d	Spring-Autumn	(Ryland 1977, Stebbing 1971)	
Gymnolaemata	Cheilostomatida	Bitectiporidae	<i>Pentapora</i>	24–40		<1 d	Spring-Autumn	(Cocito et al. 1998, Lock et al. 2006)	
Anthozoa	Alcyonacea	Alcyoniidae	<i>Alcyonidium</i>	84–200	8–12		Winter	(Hartnoll 1998)	
Anthozoa	Pennatulacea	Virgulariidae	<i>Virgularia</i>			2–10 d	Autumn	(Soong 2005)	
Anthozoa	Pennatulacea	Pennatulidae	<i>Ptilosarcus</i>	60	20		Spring-Summer	(Birkeland 1974)	
<i>Representative characteristics for functional group</i>				200	9		<i>Summer</i>		
<b>Functional Group 7: Large burrowers</b>									
Polychaeta	Opheliida	Travisiinae	<i>Travisia</i>				Winter	(Rouse & Pleijel 2001)	
Malacostraca	Decapoda	Callianideidae	<i>Callianassa</i>	4–8	4	<1 mo	Spring-Summer	(Rowden & Jones 1994)	
Malacostraca	Decapoda	Upogebiidae	<i>Upogebia</i>	12	4		Summer-Autumn	(Tunberg 1986)	
Malacostraca	Decapoda	Nephropidae	<i>Nephrops</i>	36–60	14–18		Winter	(Farmer 1975, Marine Institute 2001, Tuck et al. 2000)	
<i>Representative characteristics for functional group</i>				20	7		<i>Summer</i>		
<b>Functional Group 8: Predator/Scavenger</b>									
Malacostraca	Decapoda	Cancriidae	<i>Cancer</i>	84–200	24–40	2 mo	Winter	(Warner 1977)	
Asteroida	Forcipulatida	Asteriidae	<i>Asterias</i>	24–40	4	<1 mo	Winter-Spring	(Guillou 1983)	
Asteroida	Paxillosida	Astropectinidae	<i>Astropecten</i>	12–20	8–12		Spring-Summer	(Freeman et al. 2001)	
Malacostraca	Decapoda	Polybiidae	<i>Liocarcinus</i>	12–40	<4	<4 mo	All year round	(Choy 1991, Muino 1999)	
Malacostraca	Decapoda	Paguridae	<i>Pagurus</i>	12–20	<4	<1 mo	Winter-Spring	(Lancaster 1990)	
Polychaeta	Phyllodocida	Phyllodocidae	<i>Eteone</i>	4–8			Spring	(Fauchald & Jumars 1979)	
<i>Representative characteristics for functional group</i>				20	7		<i>All year round</i>		

**Table 3: Length of life stages, reproductive seasonality and juvenile dispersal distance parameters defined for all functional groups in the model.**

Functional Group	Juvenile Stage Length (# of seasons, age range in seasons)	Adult Stage Length (# of seasons, age range in seasons)	Reproductive timing (seasons where reproduction occurs; 1=Spring, 2=Summer, 3=Autumn, 4=Winter)	Dispersal length (# of model grid cells)
1	1 (1)	5 (2–6)	1 2 3	10
2	1 (1)	5 (2–6)	1 2 3	10
3	2 (1–2)	10 (3–12)	1 2	5
4	4 (1–4)	16 (5–20)	2	5
5	4 (1–4)	56 (5–60)	1 2	5
6	8 (1–8)	192 (9–200)	2	1
7	6 (1–6)	14 (7–20)	2	5
8	6 (1–6)	14 (7–20)	1 2 3 4	5

## 2.7 Colonisation

The model code allows for many options for the colonisation of recently disturbed cells. The simplest colonisation rule assumes global dispersal of all benthic community members, with no spatial restrictions on colonisation of each cell after disturbance (e.g., Thrush et al. 2005). More complex colonisation rules examine how restricted colonisation processes impact disturbance/recovery dynamics, i.e., what happens if colonisation is based on presence or abundance of neighbours of a particular community stage within a prescribed distance, representing larval, juvenile or adult dispersal distance. To incorporate spatial restrictions on colonisation to the standard model structure, we limit potential colonisation of each functional group to empty cells within a minimum distance to a colonist source. For example, colonisation of an empty cell by a given functional group can occur if there is at least one cell within the cell's neighbourhood equal to or greater than the age of maturity defined for that functional group (i.e., an adult exists within the dispersal neighbourhood to provide a source for colonists). We define the 'neighbourhood' of each cell as all surrounding cells within a particular dispersal distance, and the neighbourhood size varies between functional groups based on literature review of life history parameters (Table 3). For each functional group, colonisation is further limited to seasons where reproduction occurs (Table 3).

Colonisation of cells is determined by first calculating the dispersion of larvae from all cells containing adults of each functional group. While Lundquist et al. (2010) considered all cells within the neighbourhood to have equal likelihood of colonisation success, the model simulations here allow more realism with the ability to weight the likelihood of colonisation with distance from the reproducing adult. In the scenarios presented here, cells are weighted based on distance from the reproducing adult in the centre, using a simple linear decay function. However, other decay functions can easily be used. For example, for a dispersal length of 5 model cells, cells in concentric [square] rings are given values of 5, 4, 3, 2, and 1, respectively, for rings with increasing distances from one to five cells distance from the adult. Values are further weighted at each distance by area (i.e., relative to the total number of cells in the nearest neighbouring ring), resulting in the maximum number of potential colonists in each ring exhibiting a linear decline with distance from the reproducing cell. An additional complexity that is not implemented in the simulations presented in this report is 'directional' colonisation, i.e., the direction of current flow results in unidirectional transport of colonists, which can be easily incorporated using a directional decay function.

A 'colonisation score' for each cell is calculated as the sum of all weighted scores from individual reproducing adults within the cell's neighbourhood. Colonisation scores are then transformed into a proportion representing the likelihood of settlement success, by weighting relative to the maximum potential colonisation score for the cell for a given functional group. These values are then compared to corresponding values drawn from a uniform random distribution, thus simulating stochasticity in colonisation success. Successful colonisation of a cell by a functional group occurs if its colonisation score is greater than or equal to the corresponding random matrix score.

## 2.8 Adult-juvenile and shell-hash interactions

We separate the 'dispersal' step from a distinct 'settlement' step which is based on a model rule in which adults interact with colonists to either facilitate or hinder settlement success. An adult-juvenile interaction matrix between conceptual functional groups was used to provide further biological reality in the colonisation processes in the model. In the expert workshops, we determined an interaction matrix that defines the positive/neutral/negative feedback relationship that an occupying adult of a functional group may impose on potential colonists (Table 4). This interaction matrix, in combination with presence of other functional groups in a cell, is used to determine settlement success for a potential colonist from a given functional group. Values in the interaction matrix are either +1 (facilitation), 0 (neutral), or -1 (inhibition). For example, Functional Group 3 (substrate stabilisers) is defined as a facilitator (+1 score) of colonisation of most other functional groups, whereas Functional

Group 7 (large burrowers) and 8 (predators/scavengers) have a negative effect (-1 score) on colonisation for most other groups via either substrate disturbance or consumption of colonists.

The adult-juvenile interaction score is calculated at each time step for all newly colonised cells as the sum of all positive, neutral and negative interactions based on the functional groups present in a cell. Scores are then compared to a uniform random distribution ranging from the minimum to the maximum possible value obtainable for that functional group based on the adult-juvenile interaction matrix (Table 4). Successful settlement of a functional group in a cell occurs if the cumulative interaction score is greater than or equal to the value for that cell in the random matrix.

We further add a shell-hash interaction, whereby one of the functional groups (group 6 – emergent epifauna) is dependent on the presence of shell-hash forming species (group 5) to occupy a cell. Shell hash accumulates in a cell, even after natural mortality of group 5, but is removed by disturbance. Coding allows relaxation of this assumption, to allow for emergent epifaunal taxa that may not be dependent on hard substrate for colonisation (e.g., sea pens), or to change the rules determining removal of shell hash with disturbance.

**Table 4: Adult-Juvenile interaction matrix used to score functional group interaction in cells of the seascape. Adult-Juvenile: rows = adult, columns = juvenile. Qualitative values signify detrimental effects (-1), neutral effects (0), or beneficial effects (+1). Adults and juveniles of the same functional group have no adult-juvenile interaction in the model, as adults already occur in the cell so it will not require colonisation.**

<i>Adult Functional Group</i>		<i>Juvenile Functional Group</i>							
		1	2	3	4	5	6	7	8
1	Opportunistic early colonists – limited substrate disturbance	na	0	-1	0	-1	0	0	0
2	Opportunistic early colonists – considerable substrate disturbance	-1	na	-1	-1	-1	-1	-1	-1
3	Substrate stabilisers (Tube mat formers)	1	1	na	1	1	1	0	0
4	Substrate destabilisers	-1	0	-1	na	-1	-1	-1	-1
5	Shell hash-creating species	-1	-1	1	1	na	1	0	1
6	Late colonisers – emergent epifauna	-1	-1	0	1	0	na	0	1
7	Late colonisers – burrowers	0	0	-1	-1	-1	-1	na	-1
8	Predators and scavengers	-1	-1	-1	-1	-1	-1	-1	na

## 2.9 Datasets for model parameterisation

We identified all available benthic biodiversity datasets for model parameterisation that exist in New Zealand inshore/coastal regions and offshore deepwater soft sediment commercial fishery areas, subject to dredge or trawl fisheries. For optimal use of a dataset in populating and parameterising the model, a dataset should include: 1) extensive sampling of benthic biodiversity with taxonomic information at the species level, and information on size structure (at least for macro-invertebrates and/or fish), biomass, morphology, and functional roles if recorded, preferably with a sampling design integrating video or photographic images of epifauna with core or grab sampling to detail infaunal communities; 2)

information available on either fishing effort (over both space and time), or known time of closure of an area to examine recovery rates over time; and 3) knowledge of other environment characteristics that may drive patterns in species distribution and otherwise obscure relationships with disturbance. No datasets were available at broad spatial scales that included species-specific information on either biomass or size structure.

Based on best available information, we chose one inshore and two offshore regions to inform model development. For inshore benthic communities, we compiled data from multiple sources in the Tasman and Golden Bay region. Three primary datasets were available for inshore seafloor communities: a DOC/NIWA survey of benthic communities inside and outside of the Tonga Island Marine Protected Area (Hewitt et al. 2004); a NIWA capability fund survey of benthic communities inside and outside of the Separation Point trawl closure area (Handley et al. 2013), and the new data for Objective 4 that was collected by the BEN200701 project in the area (Tuck et al. 2011). For offshore benthic communities, we compiled information available from datasets and reports from the Ocean Survey 20/20 Chatham/Challenger project (ZBD200701) (Bowden 2011, Hewitt et al. 2011a, Hewitt et al. 2011b). Additional information used in the model valuation included maps of the distribution and frequency of bottom trawling effort (generated and updated under Projects ENV2000-05, ENV2003-03, and BEN2006-01) (Baird et al. 2011), which was used to calculate qualitative values of disturbance to the seafloor.

## 2.10 Chatham Rise and Challenger Plateau datasets

The Ocean Survey 20/20 voyages to the Chatham Rise and Challenger Plateau represent the most comprehensive sampling initiative in New Zealand offshore benthic ecosystems (Figure 2), aimed at describing patterns of benthic biotic habitat and biological diversity across extensive areas of the EEZ. To characterise assemblages across a range of organism sizes and spatial scales, samples were collected using several gear types: epibenthic sled and beam trawl which sampled mega-epifauna; multicorer which sampled meiofauna; Brenke epibenthic sled which sampled macro-epifauna and hyperbenthic fauna; and the still image camera and video camera of NIWA's Deep Towed Imaging System (DTIS) which sampled mega- and macro-epifauna, bioturbation and substrate types (Bowden 2011).

As the DTIS video transect dataset had the broadest spatial coverage in the Ocean Survey 20/20 dataset ( $n = 147$  video tows used in the analysis, with 107 Chatham and 40 Challenger datasets), we performed initial model development and comparisons using benthic epifaunal data (sized greater than 50 mm) extracted from DTIS video camera transects. Data included counts of megafauna along the entire length of each transect, with taxonomic resolution from the video available at a range of resolutions, but frequently to species level (Hewitt et al. 2011b). Abundances were standardised to number of individuals  $1500 \text{ m}^{-2}$  of seabed. Functional trait categories were described for all species in the ZBD200701 project (Hewitt et al. 2011a), and additional biogenic features identified in the video (e.g., crab holes, burrows, faecal mounds) were used as further indicators of functional group presence.

One concern with using only the DTIS video dataset was that some infaunal species (e.g., bivalves, infaunal polychaetes and crustaceans) were unlikely to be quantified from video data which consists primarily of mega-epifaunal observations. For larger infauna such as some burrowing species, the derivation of Group 7 was based on video evidence of burrows, tracks and other visual evidence of burrowing fauna; however, small infaunal crustaceans and polychaetes were unlikely to be documented from this dataset as they exhibit limited substrate disturbance. While some conceptual functional groups (e.g., bivalves) were not expected to be abundant in offshore benthic communities, they were similarly unlikely to be documented in the DTIS video dataset.

As expected, initial analyses using only DTIS video data did not adequately enumerate smaller and infaunal conceptual functional groups (see Results). We then analysed data from the epibenthic sled,

using datasets for 76 sleds covering 64 sites on the Chatham Rise and 47 sleds covering 41 sites on the Challenger Plateau (Hewitt et al. 2011b). In this dataset, benthic epifauna (sized greater than 25 mm) were identified primarily to species level. Because the area covered by this gear is not reliably quantitative, abundances were left as counts per deployment. We also investigated suitability of the multicorer dataset at providing additional information on smaller fauna (sized less than 25 mm) that are the primary taxa allocated to functional groups 1 and 3. However, limited samples using the multicorer prevented its usefulness in broad scale analyses across fishing strata. We compare analyses from both DTIS video and epibenthic sled individually, resulting in our final analysis on combined data from the epibenthic sled and DTIS video datasets to derive functional group membership for the Chatham/Challenger data set.

Extensive areas of the Chatham Rise and parts of the Challenger Plateau are commercial fishing areas. Fine-scale position data from commercial trawlers using gear on or near the seafloor were used to measure the intensity and frequency of bottom trawling over 16 years, from 1989–90 to 2004–05, in depths down to 1600 m (Ministry of Fisheries project BEN200601; Baird et al. (2011)). Fishing effort in the Ocean Survey 20/20 survey region was expressed by individual tow polygons representing the estimated swept area of each trawl over a 16 year period, and summarised by 25 km<sup>2</sup> cells for spatial and temporal analysis. It is important to note that no sites were located in the areas of highest fishing intensity (the maximum intensity index being about 70%) (Hewitt et al. 2011a).

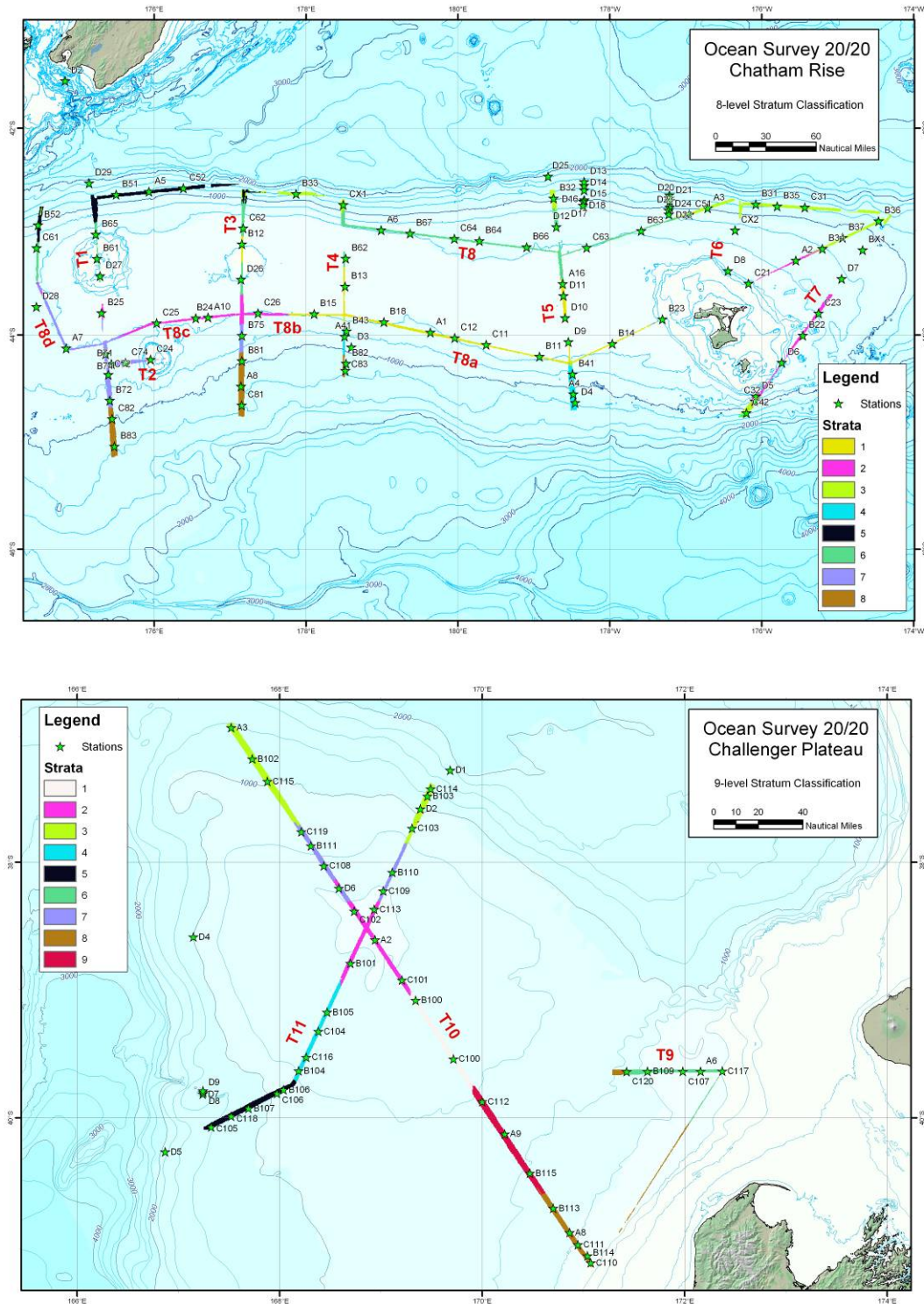


Figure 2: Chatham Rise (top) and Challenger Plateau (bottom) Ocean Survey 20/20 sampling sites, showing acoustic multibeam transects (labelled red with 'T' prefix), *a priori* sampling strata (colour coded in legend), and sampling sites at which benthic invertebrates and sediments were collected (stars). Note, strata were classified separately for each location and thus the numbered strata do not represent the same environments in each. Based on Hewitt et al. (2011b).

## 2.11 Tasman and Golden Bay datasets

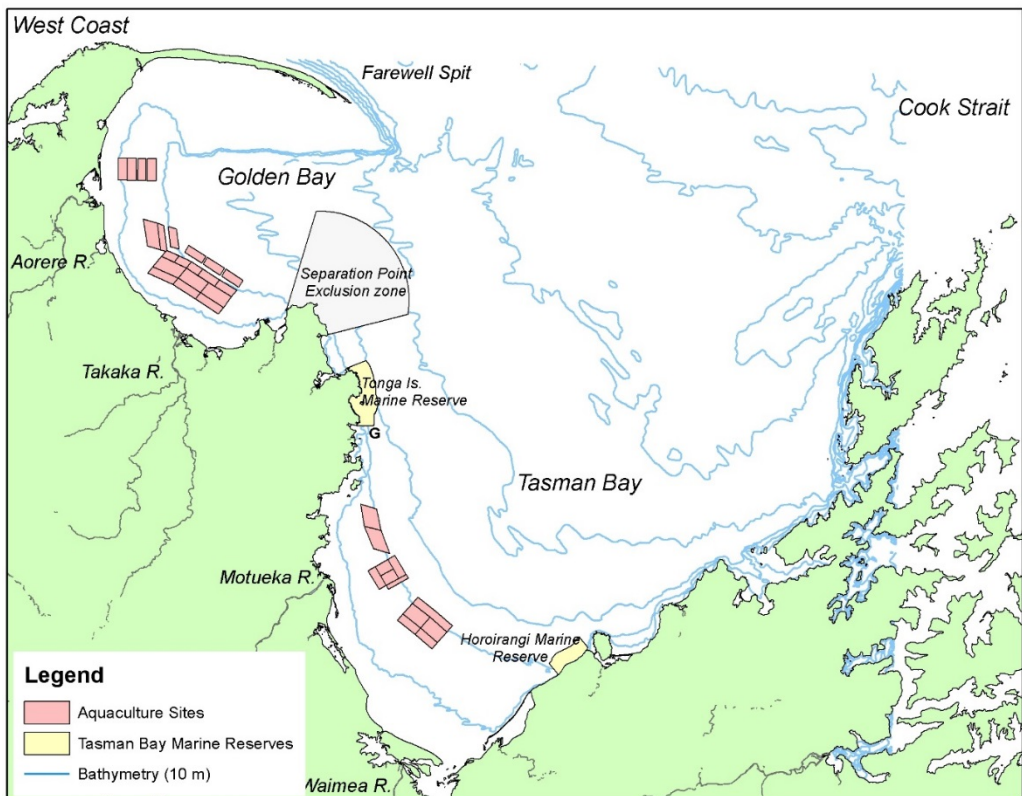
While funding for this proposal was not sufficient to allow for an independent field verification of the model, we collaborated with planned field sampling along a gradient of fishing effort in the Tasman and Golden Bay (TGB) region within the Ministry of Primary Industries Aquatic Environment Project #BEN2007-01 (Tuck et al. 2011). Researchers from both projects (ZBD2009-25 and BEN2007-01) jointly developed the field sampling design, in order to best allocate sampling across environmental and fishing effort gradients. The survey was also designed to test the predictions of the functional diversity model, with understanding of the potential limitations due to the large temporal variability of fishing effort in the sampling area, and the overlapping distributions of three different fishing sectors (oyster, scallop and demersal fin fish). The survey took place in late 2010, collecting video and grab samples at 38 sampling sites in Tasman and Golden Bay (Figure 3). Sample analyses was funded jointly by the BEN2007-01 project and this one, with large taxa (over 2 mm) identified under the BEN2007-01, and smaller macrofauna (less than 2 mm), polychaetes, amphipods and other small crustaceans identified to species within this project. The prior surveys within the region (NIWA Capability Fund Separation Point survey; Department of Conservation project to NIWA to survey Tonga Island (Hewitt et al. 2004)) added to the comparison of benthic biodiversity under different disturbance regimes, and were also used to parameterise the model.

Information used to locate sites for the Tasman/Golden Bay survey included depth, sediment type and fishing pressure (Tuck et al. 2011). Depth, available as 10 m contours from LINZ hydrographic charts, ranged from 10–40 m in the area of interest, and 3 strata were used (10–20 m, 20–30 m, 30–40 m). Sediment was predominantly mud (Mitchell 1987), with occasional patches of clay, muddy sand and sandy mud. However, confidence in the differentiation between different sediment types was low, and sediment was not used explicitly in the sampling design.

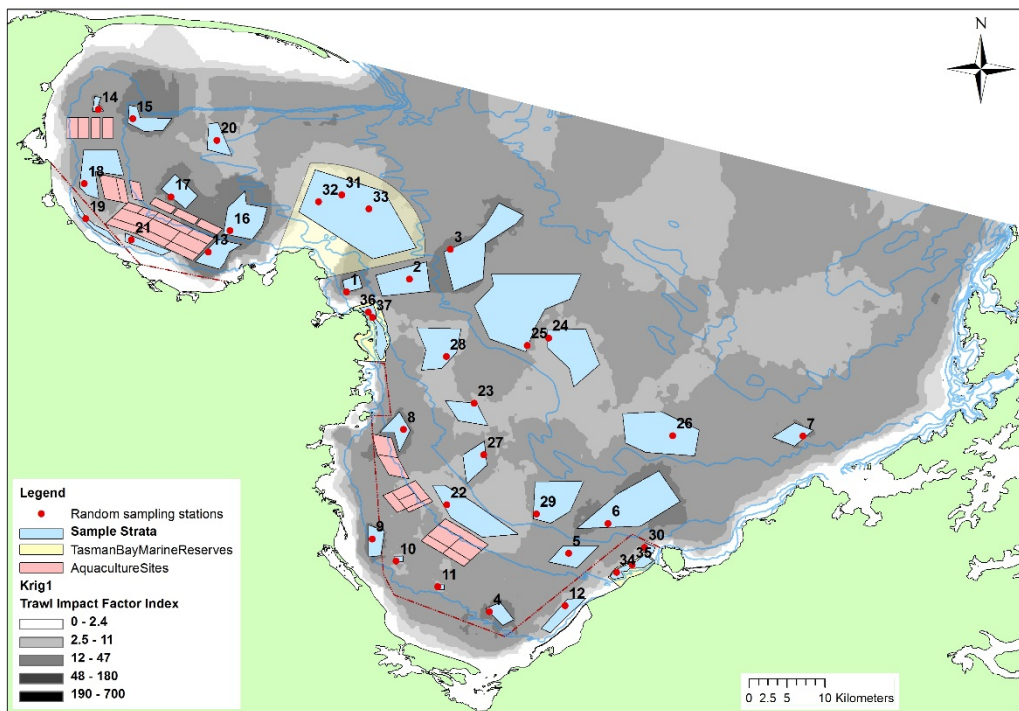
The TGB region exhibits high variation in fishing effort which provides valuable information for testing the model predictions. The region includes three areas with restricted fishing: Separation Point, for which commercial trawling and dredging has been banned since 1980, and two no-take marine reserves, Tonga Island and Horoirangi, implemented in 1993 and 2006, respectively. Fishing pressure was estimated from two sources: past use of scallop sectors (125–160 km<sup>2</sup>), and start points for commercial trawling from October 2007 (when record keeping on the TCE forms started) to 2009 (Tuck et al. 2011)). Fishing pressure was grouped into four strata (including no fishing) (Table 5).

As described in Tuck et al. (2011), to maximise the power of the analysis to separate influence of fishing and environmental variables, polygons were delineated that represented homogenous areas of at least 1 km<sup>2</sup>, e.g., depth 10–20 m, with sand, and high trawl density (Figure 3). Twenty-two polygons were first randomly selected to represent each depth and trawl start point density stratum within each of three spatial areas: Golden Bay and Separation Point, Tasman Bay northwest and Tasman Bay southeast. Additional polygons were then added to provide more representation across each fishing effort stratum, to ensure a good spatial spread across the area, to sample the sediment plume from the Motueka River, and to ensure that sites within a marine reserve were matched by at least one site nearby outside the reserve (Figure 3).





A



B

**Figure 3: Tasman and Golden Bay survey region. A) Study region illustrating fishing restriction zones (yellow and grey), aquaculture zones (pink), and bathymetry contours (blue). B) Sampling design: sites (red circles) were allocated randomly within polygons representing homogeneous seabed areas (blue polygons) within each of three depth strata (blue isobaths), and fishing pressure strata (grey shading). Based on Tuck et al. (2011).**

**Table 5: Fishing effort strata for the inshore Tasman and Golden Bay survey. Based on Tuck et al. (2011). Trawl records are based on reporting for commercial trawling from October 2007 when record keeping on the TCE forms was implemented until 2009. Scallop effort was reported at the scale of the scallop statistical reporting areas (125-160 km<sup>2</sup>), with 2007-2009 data used for most of the region, and 2004-2006 used for Tasman Bay as no scallop trawls were reported between 2007 and 2009 in Tasman Bay. Marine reserves and the Separation Point trawl exclusion zone were assumed to have zero effort.**

Stratum	Trawl start points (number of tows reported from October 2007–2009)	Scallop effort (tows km <sup>-2</sup> )
Absent	0	0
Low	>0 – 50	>0 – 20
Medium	>50 – 200	>20 – 200
High	>200 – 800	>200

## 2.12 Linking model conceptual groups with field data

We used a selection of functional traits including life history, morphological and behavioural characteristics to determine functional group membership of each ‘species’ (n=1066 taxonomic units) found in the inshore and offshore datasets. We collated information from prior research within NIWA’s FRST Coasts & Oceans OBI and Ministry of Fishery project ZBD2004-19 to determine functional traits for each individual species based on morphology, and available natural history information (see e.g., Bremner et al. (2006), Ellingsen et al. (2007), Hewitt et al. (2008)). These functional traits included body size, trophic modes, mobility, habitat structure, morphological form, bioturbation ability, and sediment depth at which the animal is typically found (de Juan et al. 2007, Hewitt et al. 2008, Thrush et al. 2006).

For both inshore and offshore datasets, integrated trait measures (multiple traits) were derived to describe each model functional group (Table 6). Fuzzy coding (e.g. Chevenet et al. (1994)) was used to describe the relative affinity of a species for a given trait, ranging between 0 and 1. For example, feeding trait categories include deposit feeders, suspension feeders and predator/scavengers. A species that is only a predator/scavenger would receive a score of 1 for this trait. In contrast, one that uses an equal mix of deposit and suspension feeding would receive a score of 0.5 for each trait. The criterion for conceptual group membership was that the integrated trait measure for a species must exceed a predefined threshold based on the sum of multiple traits describing that conceptual group. This fuzzy coding system allocated all species except microalgae, macroalgae, salps, and foraminifera (n = 10) exclusively into one of the eight functional groups. As these ten taxa were also not consistently enumerated between surveys (enumerated in some but not all datasets), we excluded them from the full analysis. The full list of species (n = 1056 taxonomic units) was examined in detail by five benthic ecologists (Thrush, Hewitt, Lundquist, Lohrer, Halliday) to confirm that species were allocated to appropriate functional groups based on knowledge of their life history, morphology, mobility, and feeding mode, and that species with similar characteristics were allocated to the same functional groups.

Relative frequencies of functional groups for each sample (site) were calculated by multiplying trait scores by abundance for each species within a functional group and then summing across all species. Average proportions of species and individuals in each functional groups were calculated as the mean of each sample (site) value for each inshore and offshore dataset. Proportions of sites occupied by a particular functional group were averaged for disturbance (fishing effort) for inshore and offshore datasets, and compared to model predictions using chi-square goodness-of-fit tests.

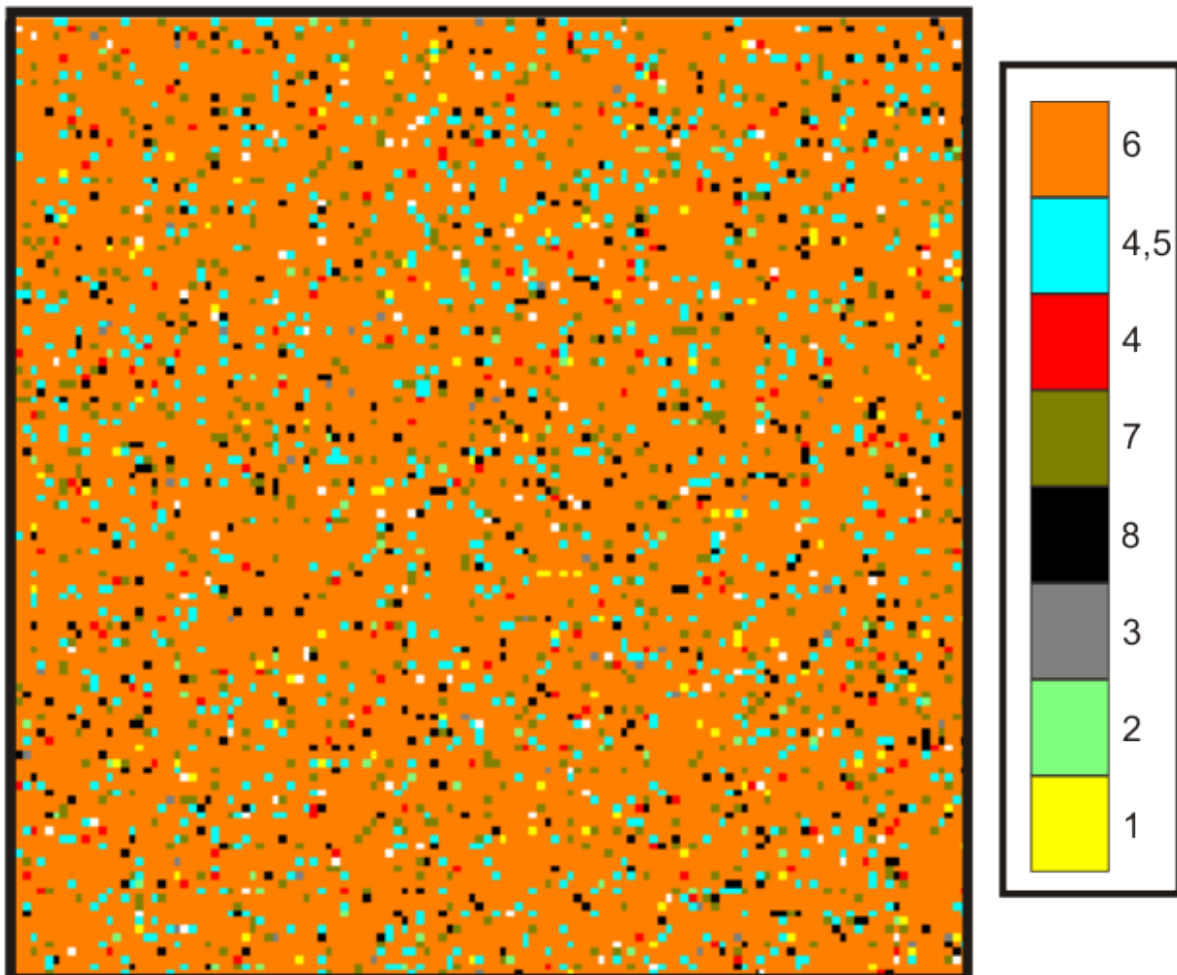
**Table 6: Traits used to derive conceptual functional group membership.**

Functional Group	Group #	Traits used	Number of taxonomic units allocated across inshore and offshore datasets
Opportunistic early colonists – limited substrate disturbance	1	Sedentary Short-lived Deposit feeder	22
Opportunistic early colonists – considerable substrate disturbance	2	Limited or high mobility Short-lived Small bodied Deposit feeder	66
Substrate stabilisers (Tube mat formers)	3	Crustacean or Polychaete Erect structure Intermediate or long-lived	16
Substrate destabilisers	4	High mobility Deposit feeder Surface dweller Intermediate-lived	184
Shell hash-creating species	5	All bivalve and gastropod species	229
Late colonisers – emergent epifauna	6	Surface dwelling Long lived Suspension feeders	284
Late colonisers – burrowers	7	Not surface dwelling Not sedentary	83
Predators/scavengers	8	Predator/scavenger Large bodied Highly mobile	172

### 3 RESULTS

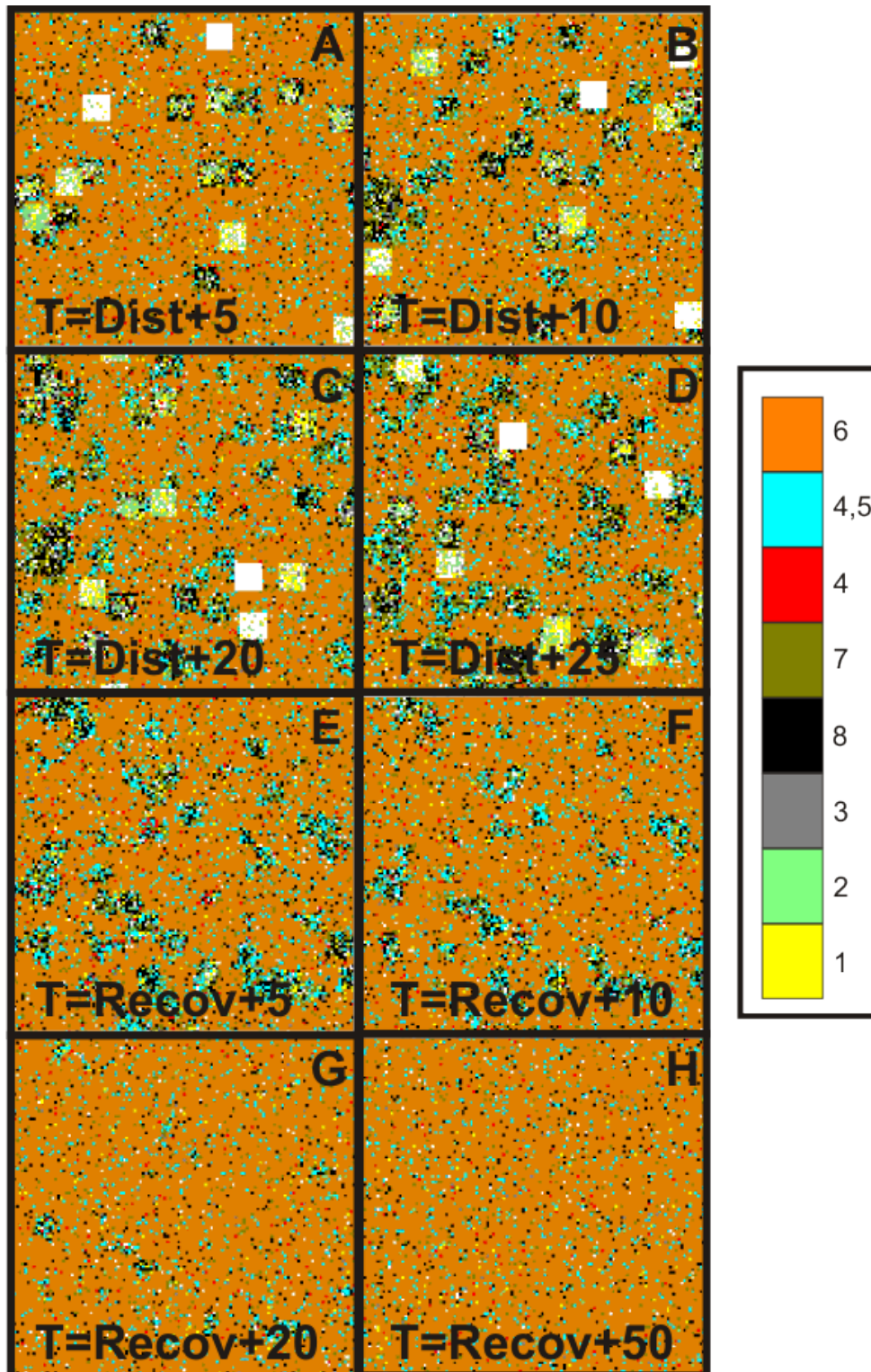
#### 3.1 Model results

Conceptual model scenarios result in a heterogeneous mosaic of patches within the seascape (Figure 4). To simplify the visualisation of the patch mosaic, and rather than presenting individual plots for each model conceptual group, we present a combined seascape plot based on a series of rules for each cell. These rules are designed to present a habitat mosaic as a diver or video might characterise the habitat, based on visual dominance by particular functional groups. In our visualisation hierarchy, we first identify all cells containing group 6 (emergent epifauna). We next identify cells with both group 4 (substrate destabilisers) and group 5 (shell hash-creating), but that do not have group 6. We continue with our classification, with each level of the hierarchy separating out one or more functional groups. Our third cell classification does not have group 5 or 6, but has group 4. Our fourth classification lacks group 4, 5, and 6, and contains group 7 (burrowers). Our fifth classification lacks group 4, 5, 6, and 7, and contains group 8 (predators and scavengers). Our final classifications contain group 3 (substrate stabilisers), then group 2 (opportunistic colonists with considerable substrate disturbance), then group 1 (opportunistic colonists with limited substrate disturbance).



**Figure 4:** Model conceptualisation of stable seascape community mosaic, subject only to natural mortality. Visualisation mosaic of different group classifications as defined in the text.

Our conceptual model scenarios show a range of patterns with increasing rates of disturbance. Scenarios were run for a range of disturbance rates, with 100 time steps (25 years) of model initialisation, followed by 150 time steps (37.5 years) of disturbance, and concluding with cessation of disturbance and tracking of recovery dynamics for 200 time steps (50 years). For lower disturbance rates (e.g.,  $10 \times 10$  cell disturbance per time step or about 2.44% of the seascape disturbed per year), seascape mosaics showed the direct influence of disturbance in clearing the seascape, but also the capacity of the seascape to recover after disturbance within short (5–10 year) time frames after the cessation of disturbance (Figure 5). In lower disturbance scenarios, key structural groups (e.g. group 6, emergent epifauna) are reduced in dominance in disturbed cells within the seascape, but sufficient portions of the seascape are undisturbed, and provide colonists to disturbed cells to facilitate the recovery process. For higher disturbance rates (e.g., about 5.49% of the seascape disturbed per year), seascape dynamics differ substantially, with the conceptual model suggesting alternative stable states resulting from high disturbance rates, with loss of longer-lived and structure-forming functional groups (Figure 6). These high disturbance scenarios also demonstrate reduced heterogeneity of functional groups in the seascape, with functional extinction of many of the conceptual functional groups.



**Figure 5:** Snapshots of the model seascape at disturbance rate of about 2.5% per year (10 cell  $\times$  10 cell disturbance per time step). For each functional group, the seascape is plotted at eight time steps: (A) 5 years after disturbance begins; (B) 10 years after disturbance begins; (C) 20 years after disturbance begins; (D) 25 years after disturbance begins; (E) 5 years after cessation of disturbance; (F) 10 years after cessation of disturbance; (G) 20 years after cessation of disturbance; (H) 50 years after cessation of disturbance. Visualisation mosaic of different group classifications as defined in the text.

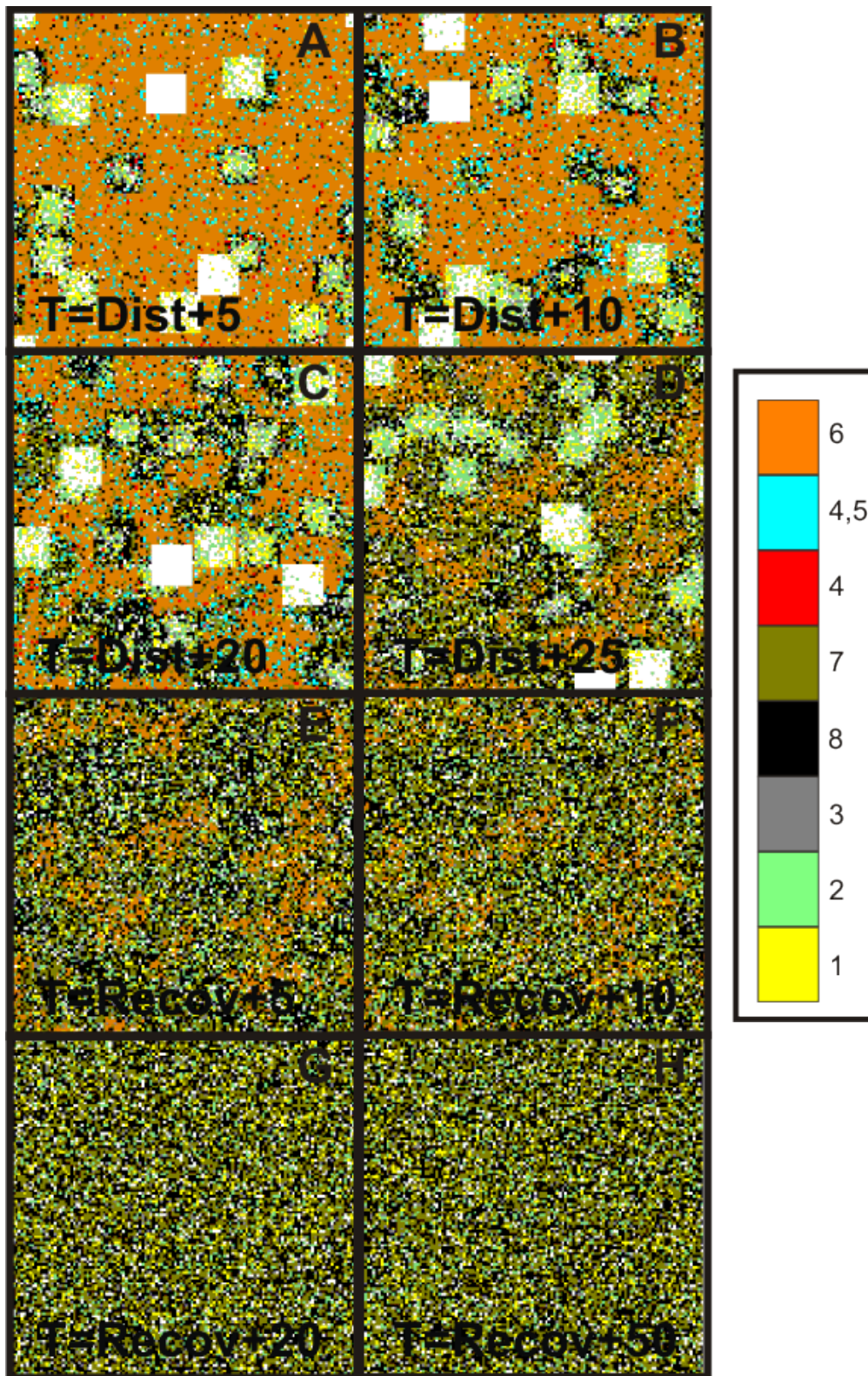


Figure 6: Snapshots of the model seascape at disturbance rate of about 5.5% per year (15 cell  $\times$  15 cell disturbance per time step). For each functional group, the seascape is plotted at eight time steps: (A) 5 years after disturbance begins; (B) 10 years after disturbance begins; (C) 20 years after disturbance begins; (D) 25 years after disturbance begins; (E) 5 years after cessation of disturbance; (F) 10 years after cessation of disturbance; (G) 20 years after cessation of disturbance; (H) 50 years after cessation of disturbance. Visualisation mosaic of different group classifications as defined in the text.

The mosaic snapshots (Figure 5, 6) give a general idea of patterns of recovery. We also illustrate temporal patterns before, during and after disturbance, for the eight functional groups at three disturbance rates (about 2.44%, 5.49%, and 9.77%, referred to from this point onwards for simplicity in figures as 2.5%, 5.5% and 10%). We demonstrate the impacts of disturbance of life history of each of the eight functional groups, illustrating temporal changes in the proportion of cells in the seascape occupied by a functional group (Figure 7); the proportion of cells in the seascape occupied by mature adults of a functional group (Figure 8); the mean age of a functional group across the seascape (Figure 9); and the proportion of empty cells that are successfully colonised by a functional group (Figure 10).

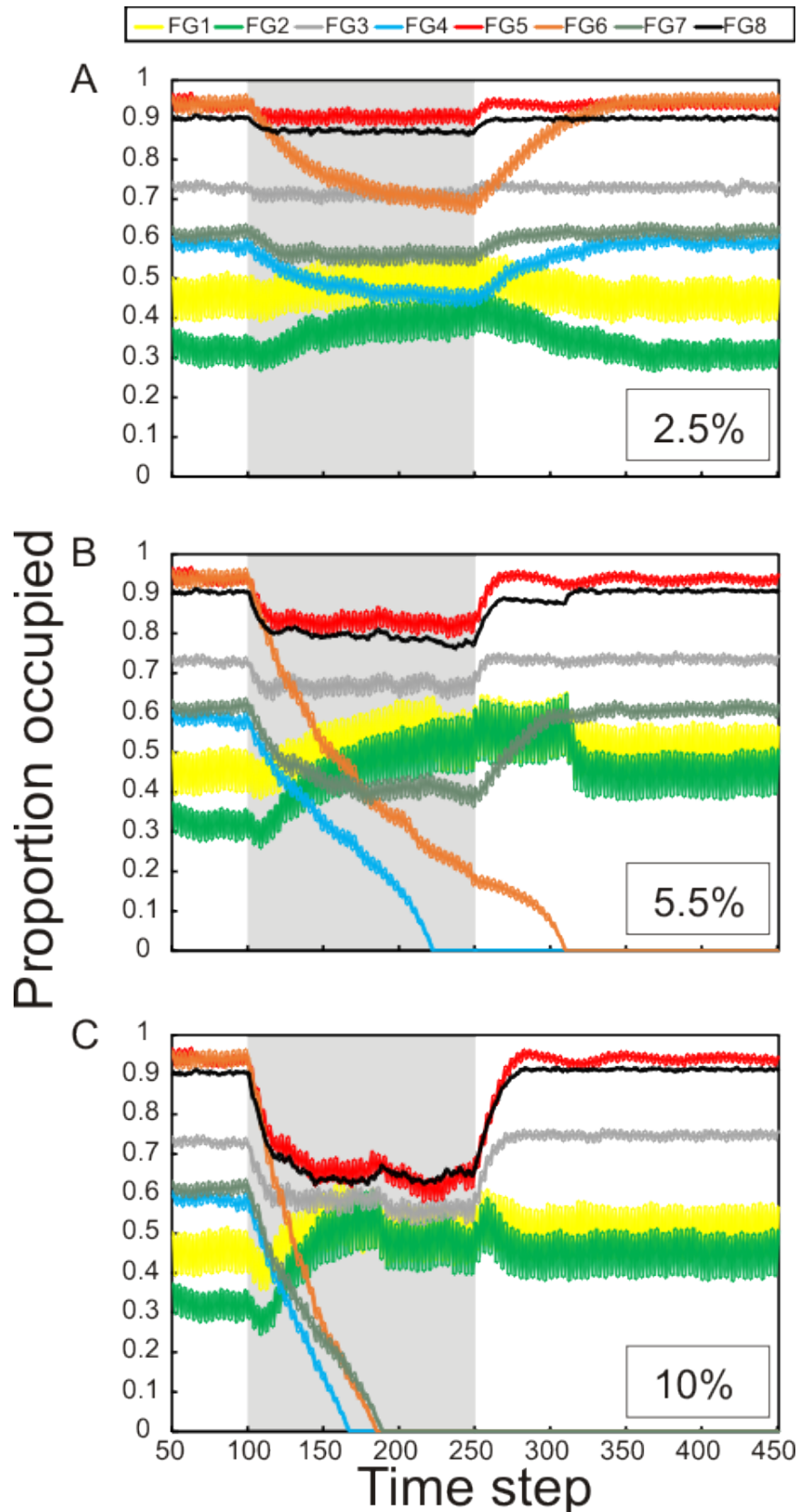
The plots of proportion of the seascape occupied demonstrate differences that we would expect to see between different functional groups (Figure 7). At all rates of disturbance, the opportunistic groups (groups 1 and 2) respond positively to disturbance with an increase in occupied area. Most other groups respond negatively, with the relative decrease in proportion of the seascape occupied becoming larger as disturbance rates increase. In the lowest disturbance rate shown (2.5%), all functional groups return to prior equilibrium levels after the cessation of disturbance (Figure 7A). In contrast, at the higher disturbance rates (Figure 7B, 7C), functional extinction occurs for some functional groups (groups 4 and 6 at 5.5% disturbance rate; groups 4, 6, and 7 at 10% disturbance rate). At the higher disturbance rate (10%), three groups are removed from the seascape during the disturbance phase, and have no mature individuals remaining to contribute to recovery after the cessation of disturbance (Figure 7C). However, at the medium disturbance rate (5.5%), group 6 is still present, but at low levels of occupancy (about 10% occupancy) and is subsequently unable to recover (Figure 7B). The removal of some functional groups from the seascape also impacts on occupancy of other groups, with higher occupancy by the opportunistic groups (1, 2) after the cessation of disturbance compared to equilibrium, undisturbed levels. Seasonal fluctuations are present for all groups that experience seasonal reproduction.

The plots of the proportion of mature individuals across the seascape for each functional group show similar patterns to the proportion occupancy (Figure 8). The increase in opportunistic groups with disturbance is also apparent in the proportion of mature cells, and similar declines with increasing disturbance are observed for groups 4, 6 and 7, that show the most sensitivity to disturbance (Figure 8). Most groups, with the exception of the opportunistic groups, show a decline in the proportion of mature cells with increasing disturbance. As in the occupancy plots, all groups at low disturbance rates return to equilibrium proportions of mature individuals in the seascape.

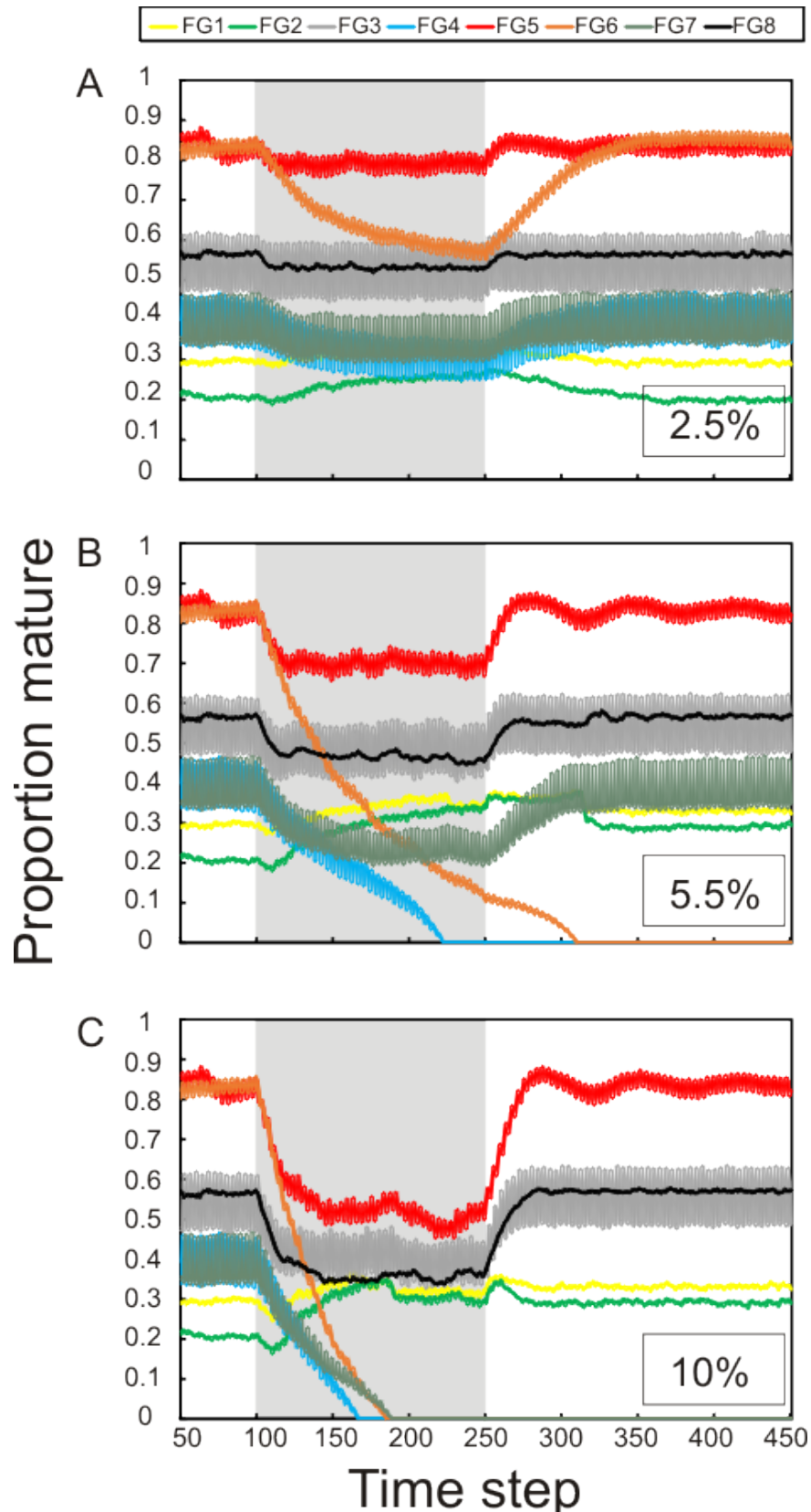
The plots of mean age of occupied cells of each functional group across the seascape also show similar patterns, with all groups except opportunistic groups (1, 2) showing decreases in the mean age with increasing rates of disturbance (Figure 9). The plots of mean age also potentially give a more mechanistic explanation for the lack of recovery of group 6 in the 5.5% disturbance scenario, as the mean age is barely above the age of maturity of this group (8 time steps) after the cessation of disturbance.

The plots of colonisation success also provide additional mechanistic explanations for slow or lack of recovery after cessation of disturbance, and for differences in sensitivity to disturbance of the eight functional groups (Figure 10). Groups 5 and 6 show the largest decline in colonisation success, and this is apparent even in the lowest disturbance rate scenario (Figure 10A). The opportunistic groups (1, 2), whose defined life history characteristics in the model include global dispersal potential, generally show increases in successful colonisation, presumably due to lower occupancy of other groups which decreases the potential for adult-juvenile interactions that decrease colonisation success for these opportunistic groups (Figure 10). Strongest effects of disturbance on colonisation success are seen for group 6, which has the most limited dispersal potential defined in the model life history characteristics (Figure 10). Groups with mid-range dispersal potential (3, 4, 5, 7, and 8) show differences in colonisation success after disturbance, showing that a number of interacting life history characteristics affect colonisation (Figure 10). These include dispersal potential, the proportion of the seascape that is mature adults contributing as sources of colonists, and adult-juvenile interactions that either facilitate or inhibit colonisation.

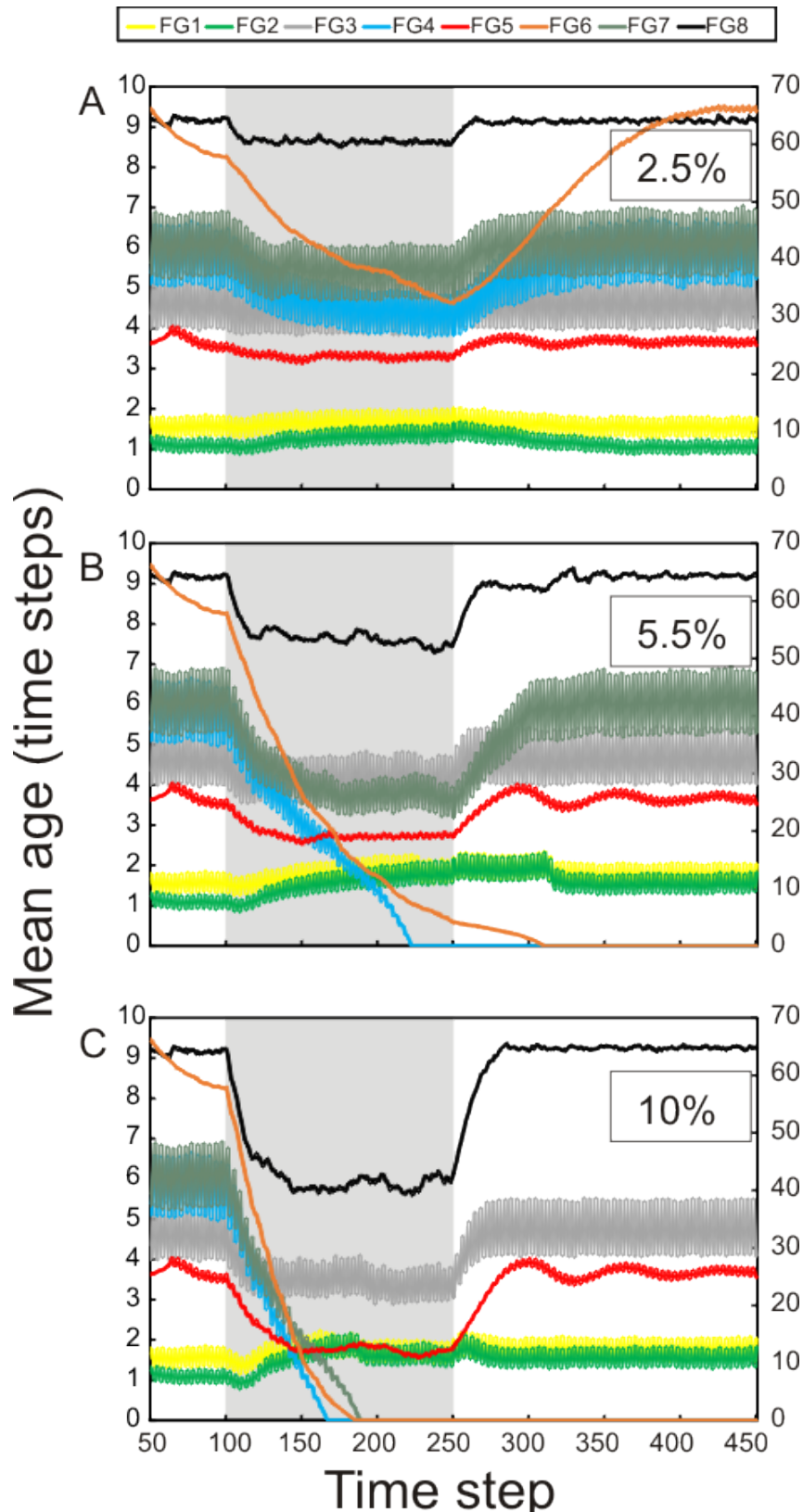




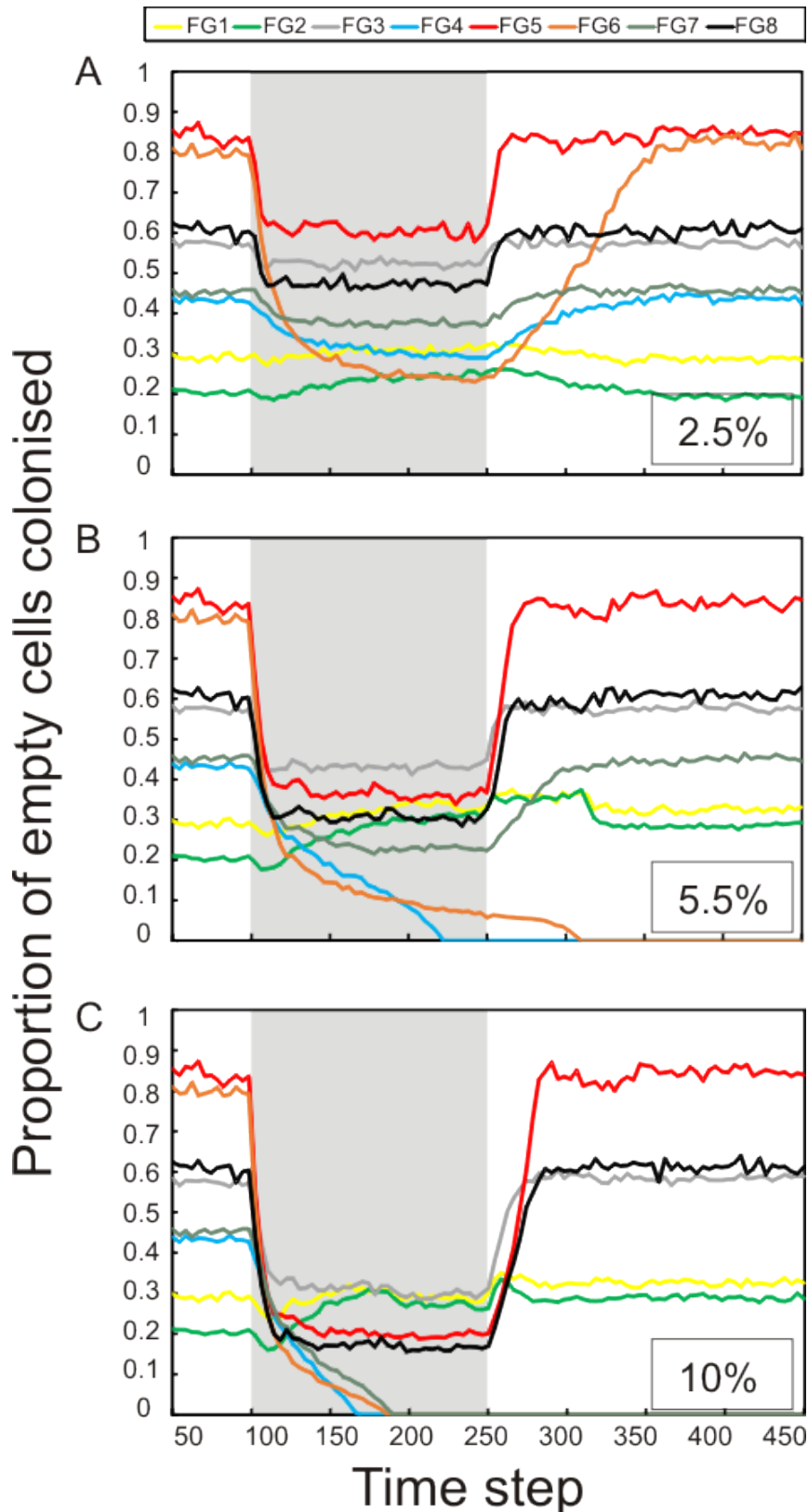
**Figure 7:** Percentage of model grid occupied over time for each of eight functional groups for three rates of disturbance. A. disturbance of  $10 \times 10$  cells per time step (2.5% of the seascape per year); B. disturbance of  $15 \times 15$  cells per time step (5.5% of the seascape per year); C. disturbance of  $20 \times 20$  cells per time step (10% of the seascape per year). Shaded area indicates disturbance interval.



**Figure 8:** Percentage of model grid occupied by adults over time for each of eight functional groups for three rates of disturbance. A. disturbance of  $10 \times 10$  cells per time step (2.5% of the seascape per year); B. disturbance of  $15 \times 15$  cells per time step (5.5% of the seascape per year); C. disturbance of  $20 \times 20$  cells per time step (10% of the seascape per year). Shaded area indicates disturbance interval.

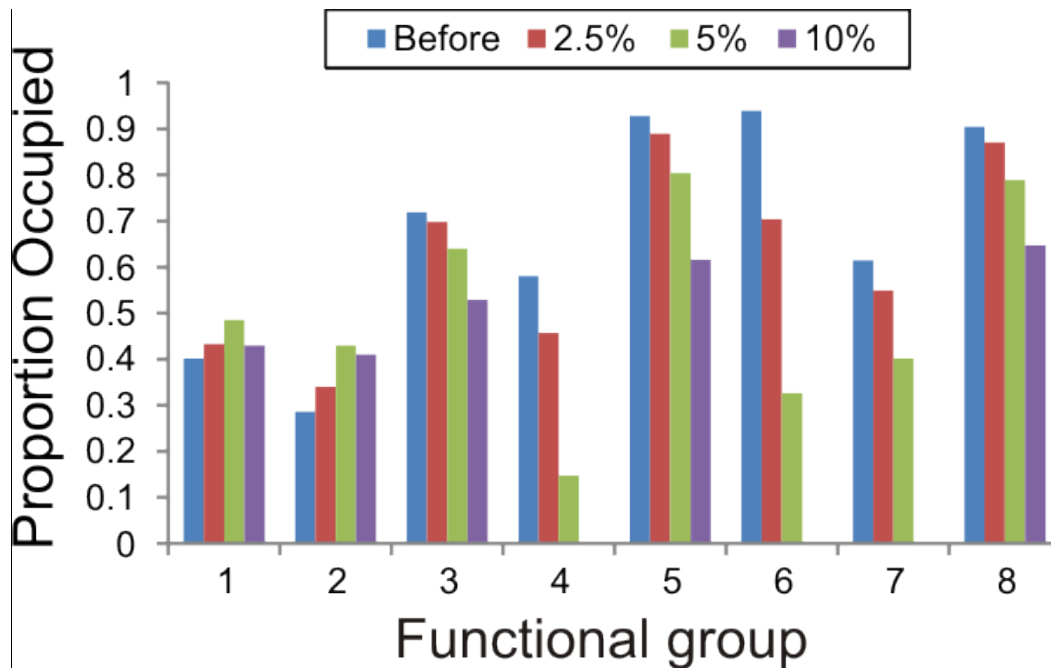


**Figure 9:** Mean age across the model grid over time for each of eight functional groups for three rates of disturbance. A. disturbance of  $10 \times 10$  cells per time step (2.5% of the seascape per year); B. disturbance of  $15 \times 15$  cells per time step (5.5% of the seascape per year); C. disturbance of  $20 \times 20$  cells per time step (10% of the seascape per year). Shaded area indicates disturbance interval. Mean ages of groups 5 and 6 are plotted on the secondary y axis.



**Figure 10:** Proportion of empty cells in model grid successfully colonised by each of eight functional groups at each summer time step for three rates of disturbance. A. disturbance of  $10 \times 10$  cells per time step (2.5% of the seascape per year); B. disturbance of  $15 \times 15$  cells per time step (5.5% of the seascape per year); C. disturbance of  $20 \times 20$  cells per time step (10% of the seascape per year). Shaded area indicates disturbance interval.

Summary histograms of functional group occupancy show changes in each functional group across the seascape with increasing disturbance rates (Figure 11). While the two most opportunistic groups (1, 2) generally show increasing occupancy with increases in disturbance, most other groups show declines in occupancy. Three groups (4, 6, and 7) are most sensitive to disturbance in the model, and the highest disturbance rates shown (10%) result in removal of these groups from the model seascape. Disturbance sensitivity in the model is due to a combination of life history traits that limit their recovery, including dispersal potential, age of maturity and age of senescence, and adult-juvenile interactions that facilitate or inhibit colonisation success.



**Figure 11:** Predicted differences in occupancy by each functional group between undisturbed seascape, and disturbance rates of 2.5%, 5%, and 10% of the seascape per year, after 25 years of disturbance. Note that groups 4, 6, and 7 under 10% disturbance have gone extinct in the model.

### 3.2 Model parameterisation using offshore datasets

For our initial model development and comparison to offshore seafloor datasets, we used the Ocean Survey 20/20 DTIS video datasets, as these were the most extensive datasets available for the offshore Chatham Rise and Challenger Plateau surveys. We first determined whether our fuzzy logic approach to functional group allocation was successful, by investigating whether taxonomic groups were allocated into expected functional groups (Figure 12). For example, bivalves and gastropods are consistently classified as group 5 (shell-hash creating species), while epifaunal groups such as bryozoans, hydrozoans, sponges, and crinoids are classified as group 6 (emergent epifauna) in our fuzzy logic approach. As expected, the video did enumerate large numbers of individuals and taxa in group 4 (substrate destabilisers) and group 6. However, enumeration of small-bodied taxa (primarily groups 1, 2 and 3) and infauna (e.g., bivalves) were poorly represented in the video datasets (Figure 13).

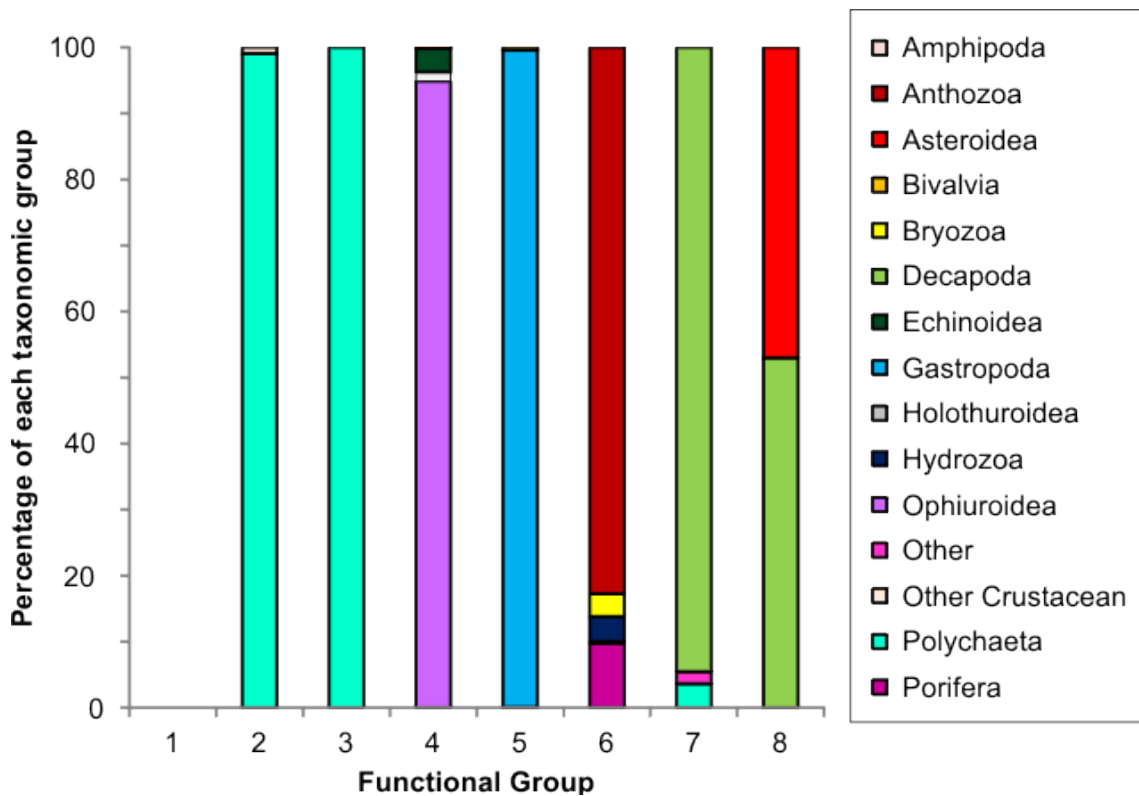


Figure 12: Functional group membership for Ocean Survey 20/20 Chatham and Challenger analyses based on percentage of total abundance of each functional group represented by particular taxonomic units, averaged across all DTIS video datasets.

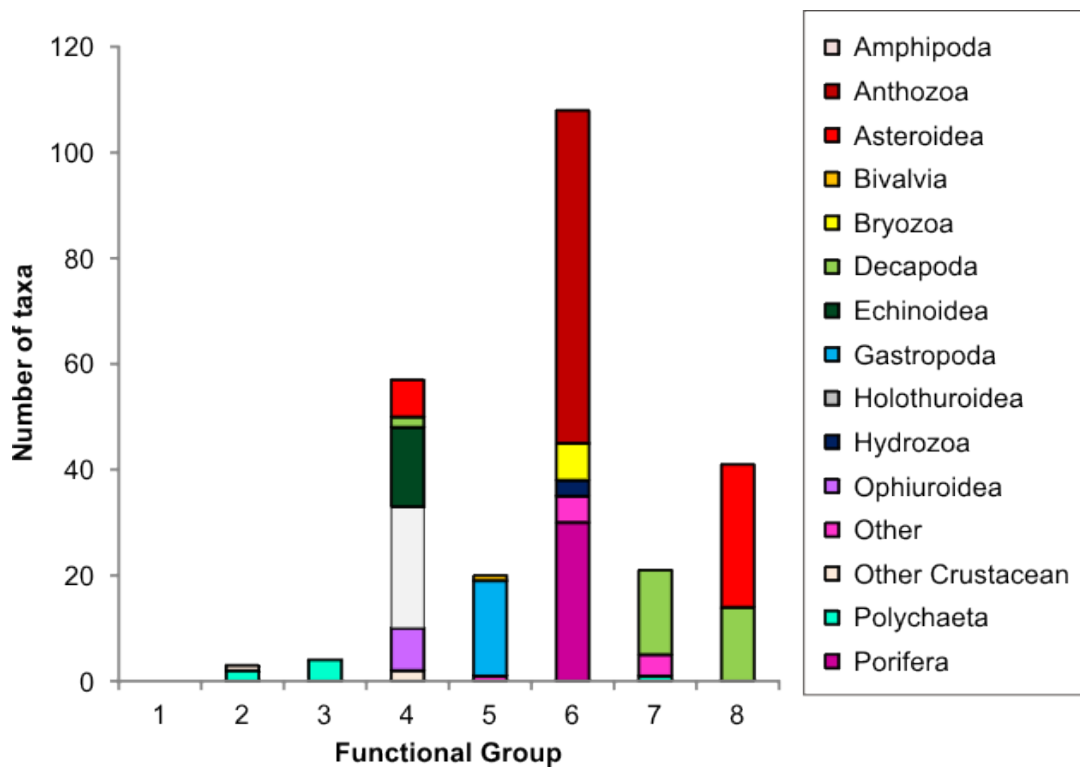
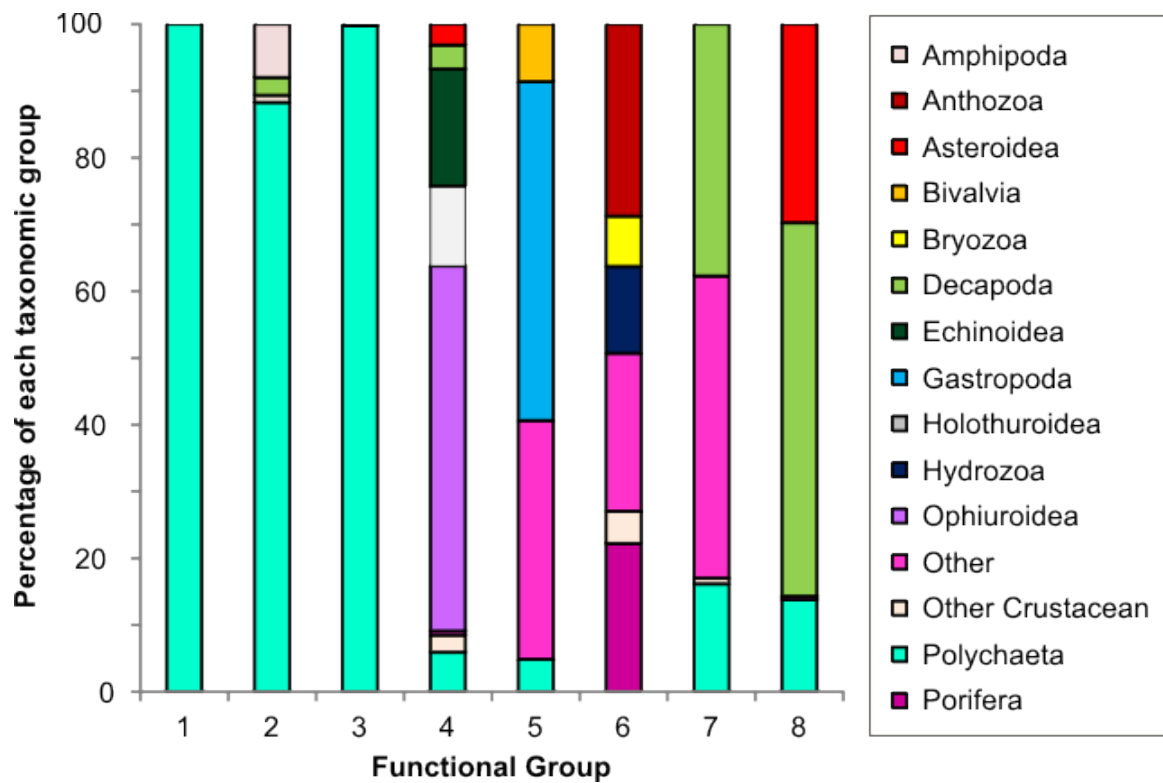
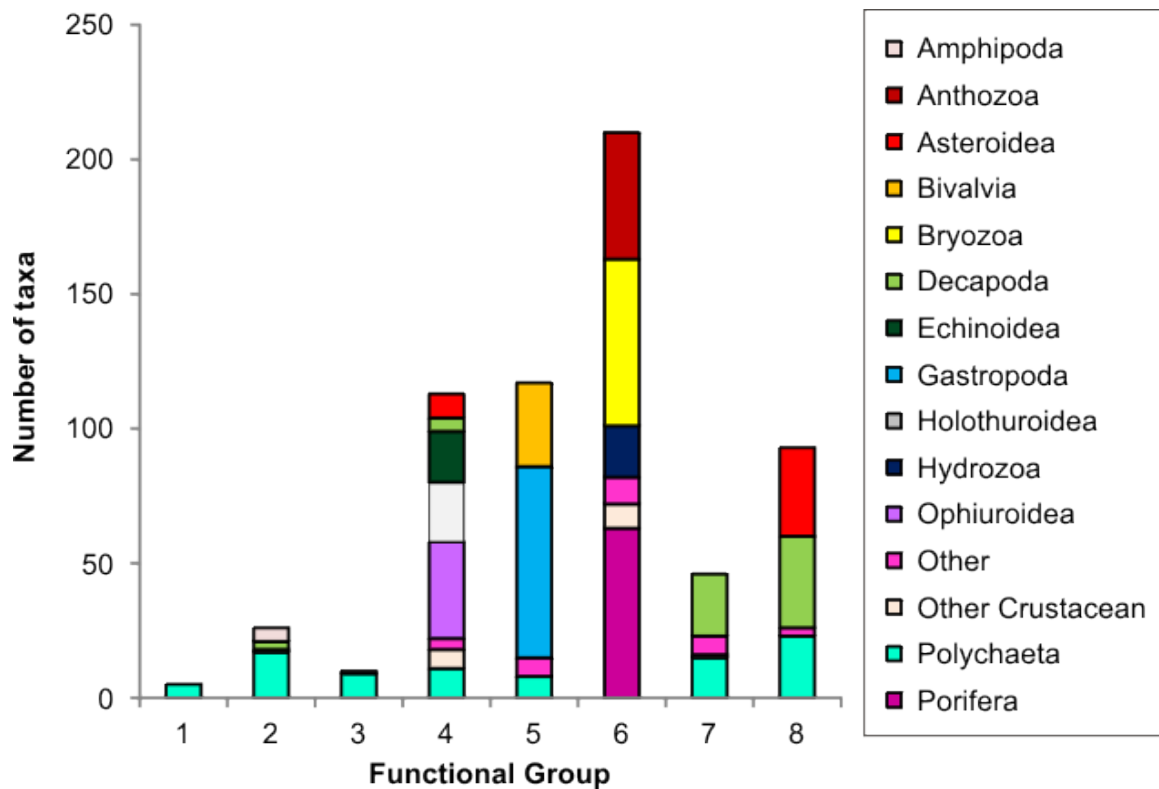


Figure 13: Functional group membership for Ocean Survey 20/20 Chatham and Challenger analyses based on total number of taxa in each functional group, averaged across all DTIS video datasets.

We repeated analyses using benthic sled data to determine whether sled data provided better representation across the eight functional groups. Sled datasets sampled a larger total number of taxa, with more diversity of taxa within functional groups (Figure 14, 15). Benthic sled data sampled a larger range of small-bodied taxa and infaunal taxa, though the total number of species allocated to functional groups 1, 2, and 3 is low relative to other groups such as group 6 (emergent epifauna) for which over 100 taxa were sampled in the DTIS video, and over 200 taxa were sampled in the benthic sled datasets.



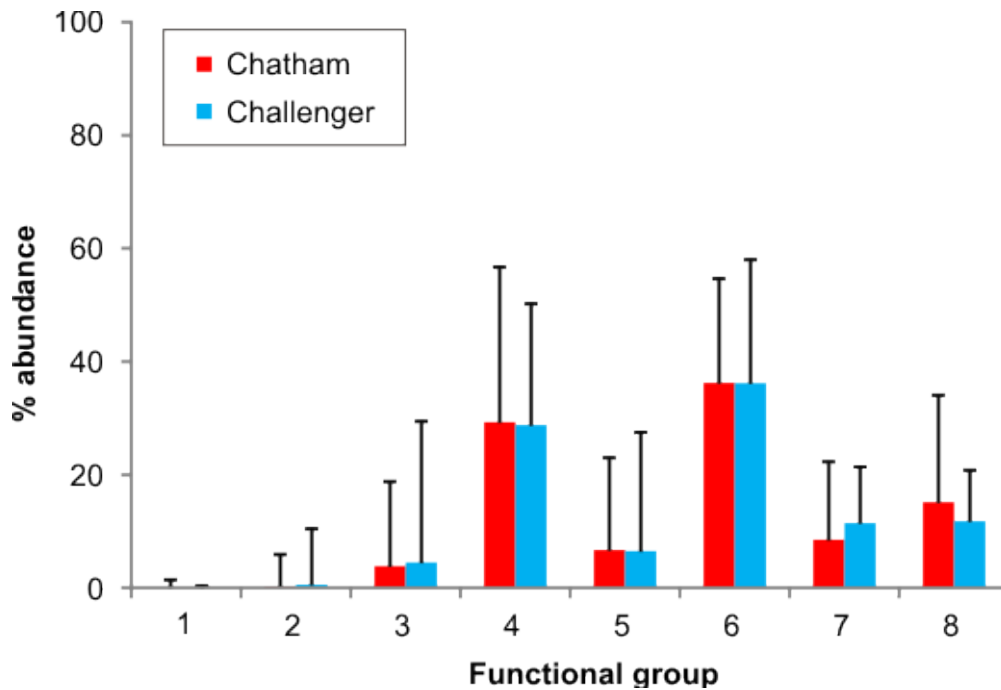
**Figure 14:** Functional group membership for Ocean Survey 20/20 Chatham and Challenger analyses based on percentage of total abundance of each functional group represented by particular taxonomic units, averaged across all benthic sled datasets.



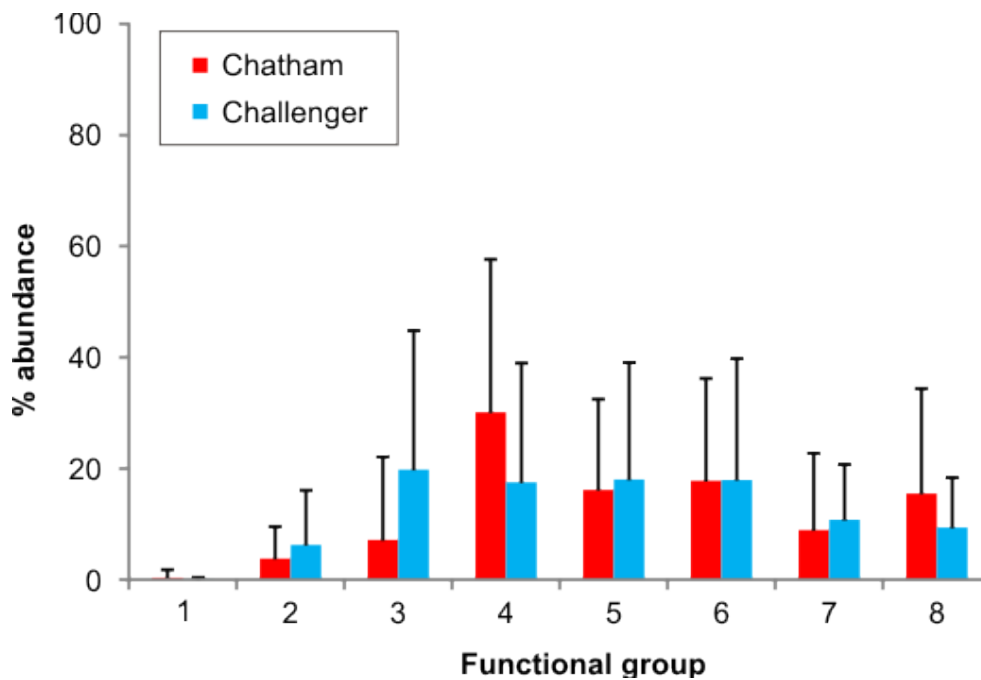
**Figure 15: Functional group membership for Ocean Survey 20/20 Chatham and Challenger analyses based on total number of taxa in each functional group, averaged across all benthic sled datasets.**

Relative abundance of each functional group follows a similar trend to the number of taxa sampled with the DTIS video and with the benthic sled, with low abundance of small-bodied and infaunal groups, and dominance in the DTIS video datasets of groups 4 and 6 (Figure 16). In contrast, the benthic sled samples smaller and infaunal groups (e.g., groups 2, 3, and 5) in larger proportions than the DTIS video (Figure 17). Group 1 showed low abundance using both methods, likely due to poor enumeration of this group by both video, and by benthic sled which sampled taxa greater than 25 mm, resulting in few taxa being classified to this opportunistic functional group with limited substrate disturbance. Generally, the Chatham Rise and Challenger Plateau datasets showed similarity in terms of relative abundance across functional groups (Figure 16, 17).





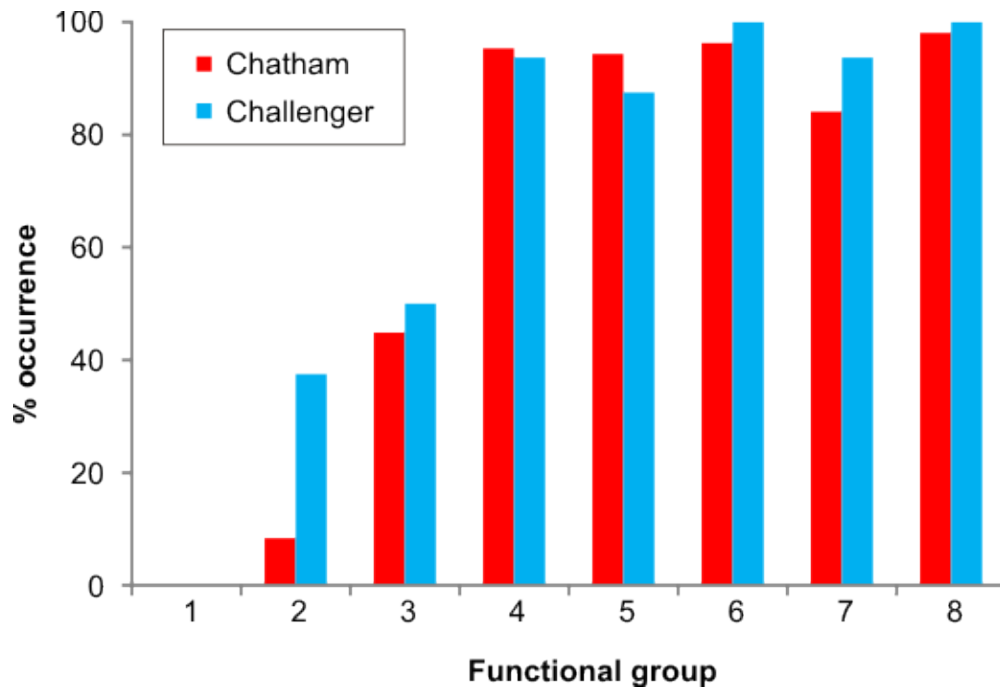
**Figure 16:** Relative abundance across all functional groups for Ocean Survey 20/20 Chatham and Challenger analyses, averaged across all DTIS video datasets. Error bars represent one standard deviation.



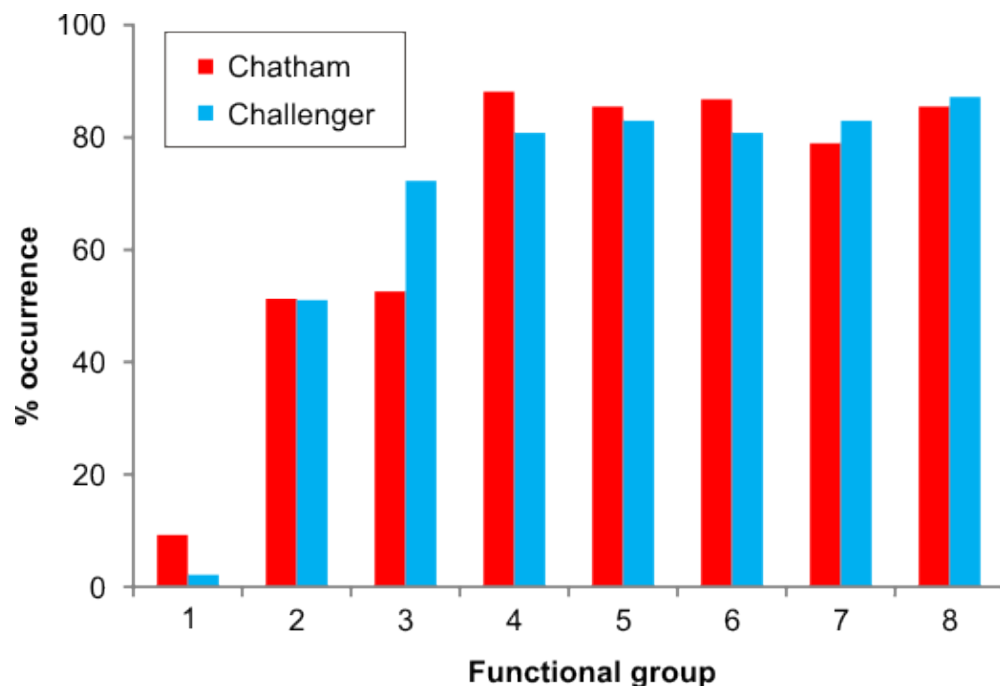
**Figure 17:** Relative abundance across all functional groups for Ocean Survey 20/20 Chatham and Challenger analyses, averaged across all benthic sled datasets. Error bars represent one standard deviation.

The video datasets generally show high proportions of sampling sites occupied by most functional groups, with lower rates of occupancy by the smaller, opportunistic groups (Figure 18). Benthic sled datasets showed higher representation of groups 1, 2, and 3. This was as expected as they more adequately enumerated small-bodied, infaunal taxa than did the DTIS video sampling method,

although group 1 was poorly represented in both datasets (Figure 19). Percentage occurrence across all sampling sites was similar between Chatham Rise and Challenger Plateau datasets, with notable differences only in smaller functional groups, with group 2 in DTIS video and group 3 in benthic sled having larger percentage occurrence in the Challenger Plateau (Figure 18, Figure 19).



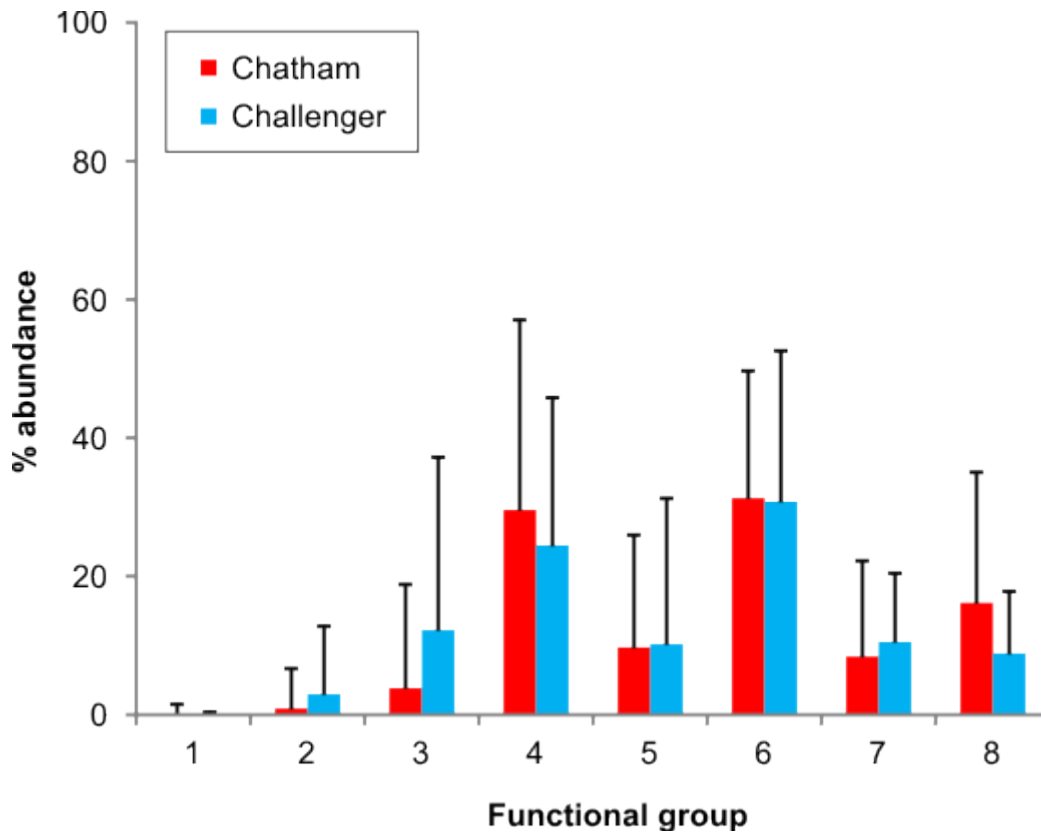
**Figure 18:** Proportion of DTIS video datasets for Ocean Survey 20/20 Chatham and Challenger analyses containing members of each functional group.



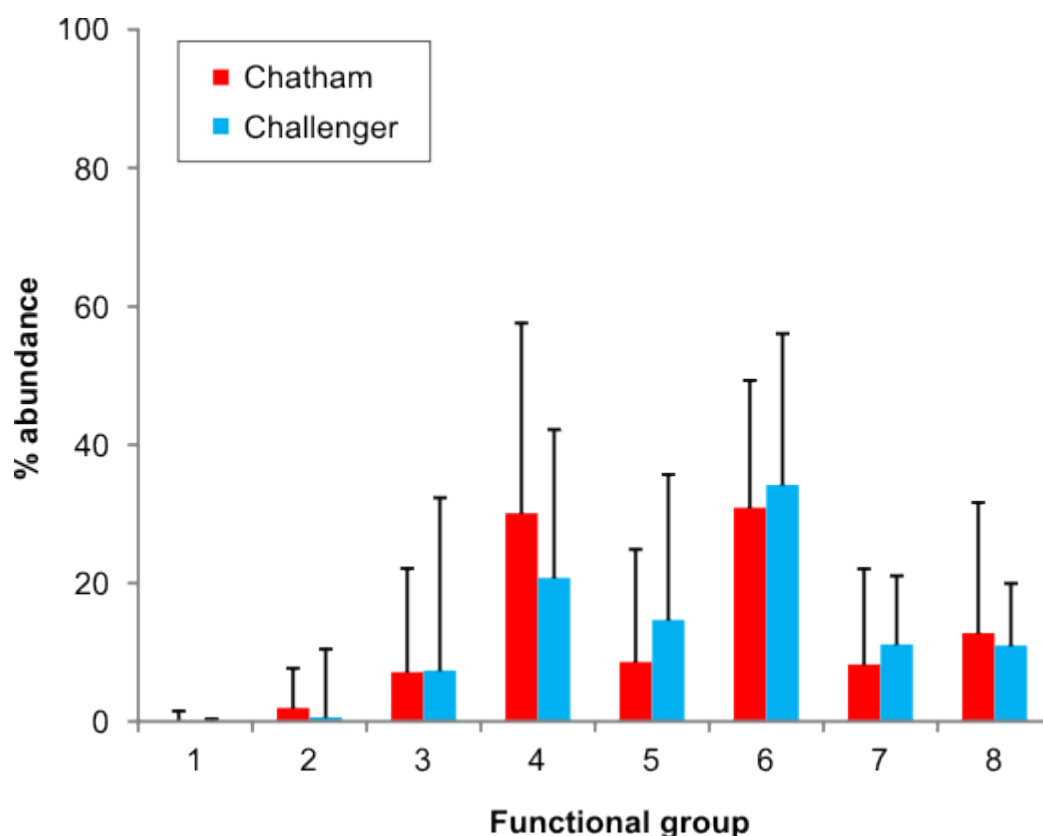
**Figure 19:** Proportion of benthic sled datasets for Ocean Survey 20/20 Chatham and Challenger analyses containing members of each functional group.

### Combined analyses using both sled and DTIS video data

Recognising the benefits as well as the limitations of both DTIS video and benthic sled datasets at enumerating all functional groups, we combined benthic sled and DTIS video data in our final analysis. Abundance data were calculated as the maximum of the sled or DTIS data samples for each conceptual functional group at each site, and converted to a mean proportion of taxa in each conceptual functional group across full data set. To determine whether we could rationalise including sites that were only sampled with one methodology (thus increasing replication across different disturbance and environmental strata), we compared analyses between a subset of sites where both sled and DTIS video sampling methods were used (Figure 20), with the full set of sites where either sled or DTIS video sampling (or both) occurred, again using the maximum value of abundance for each conceptual functional group at each site (Figure 21). Both analyses showed similar frequencies of each conceptual functional group (Figure 20, Figure 21, Table 7), with percentage occurrence also being similar between Chatham and Challenger datasets (Figure 22, Figure 23). Thus, for all further analyses, we use a combined analysis using data from sites with either (or both) benthic sled and DTIS video datasets to determine functional group membership, allowing for increased resolution and increase in taxonomic diversity for groups, with large proportions of smaller and infaunal taxa in sled data, and an increased coverage of larger, more widespread taxa in the video data.



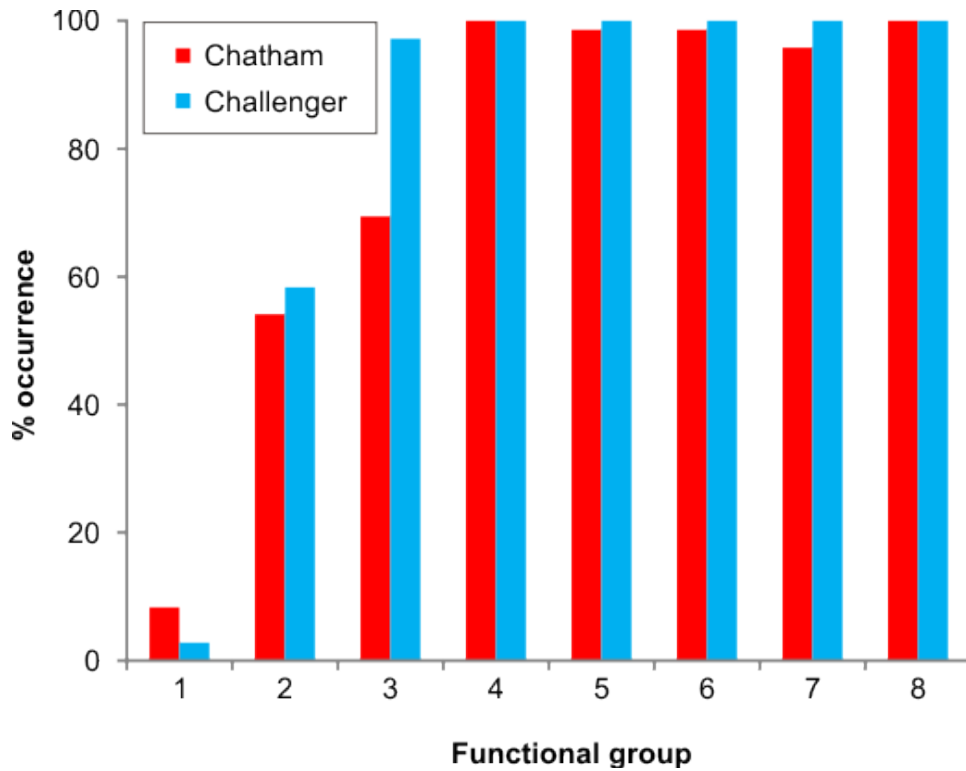
**Figure 20:** Functional group frequency based on the mean proportion of taxa in each conceptual functional group in a sample for 95 sites where both sled and DTIS video sampling methods were used for Ocean Survey 20/20 Chatham and Challenger analyses. Error bars represent one standard deviation.



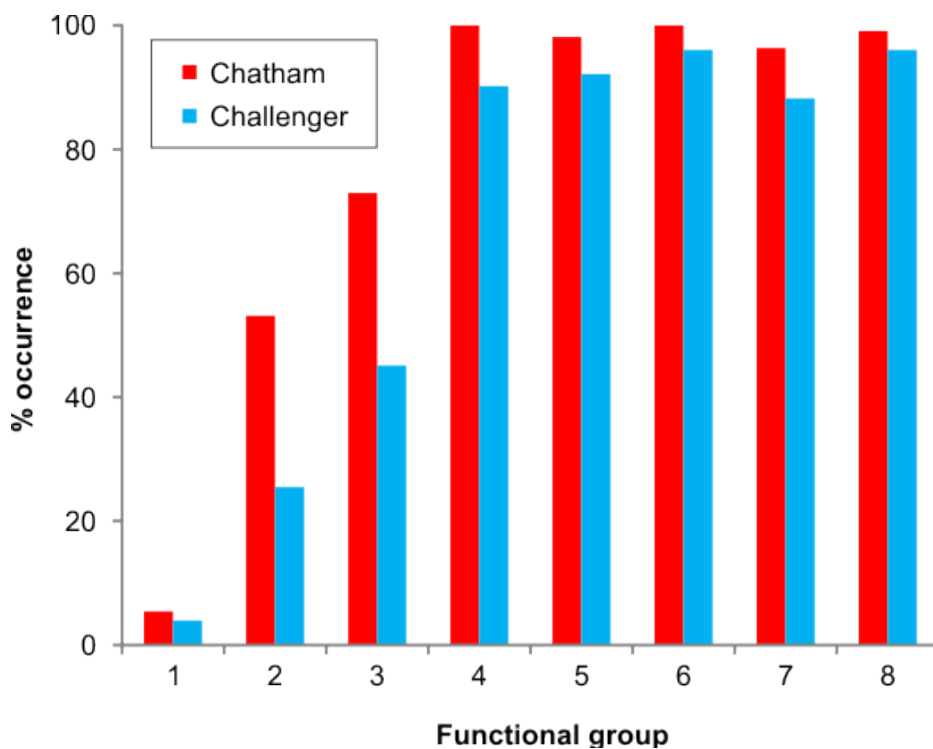
**Figure 21:** Functional group frequency based on the mean proportion of taxa in each conceptual functional group across the full dataset where either sled or DTIS video or both sampling methods were used, for Ocean Survey 20/20 Chatham and Challenger analyses. Error bars represent one standard deviation.

**Table 7:** The difference in proportion of functional trait groups between the subset analysis [concurrently sampled with both sled and DTIS video] and the full site analysis [combination of sites sampled with one or both DTIS video and sled sampling method]. Data presented as (Percent frequency with full dataset – Percent frequency with subset of data).

Functional Group	CHAT	CHAL
1	0.03	0.00
2	1.08	-2.32
3	3.27	-4.83
4	0.53	-3.64
5	-1.06	4.48
6	-0.35	3.47
7	-0.15	0.65
8	-3.34	2.20



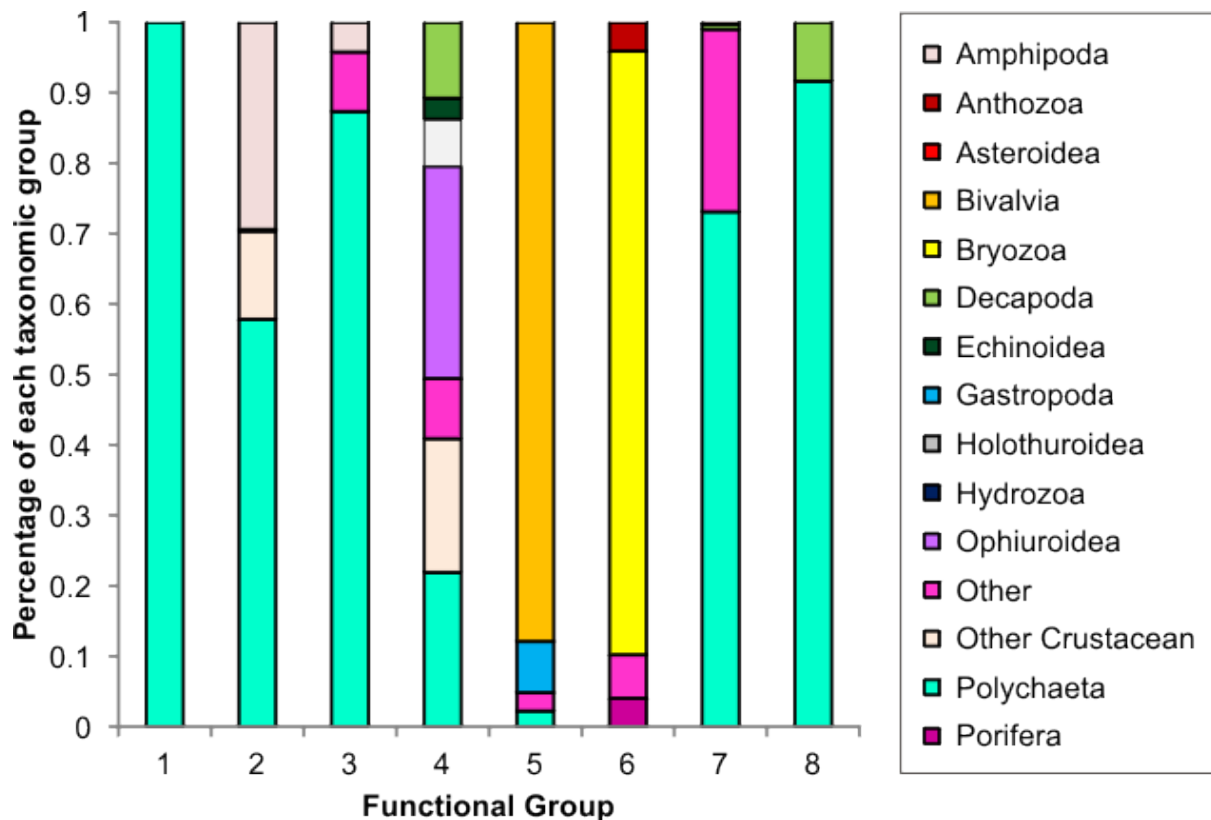
**Figure 22:** Proportion of datasets containing members of each functional group, across the subset of data where both sled and DTIS video sampling methods were used, for Ocean Survey 20/20 Chatham and Challenger analyses.



**Figure 23:** Proportion of datasets containing members of each functional group, across the full dataset where either sled or DTIS video or both sampling methods were used, for Ocean Survey 20/20 Chatham and Challenger analyses.

### 3.3 Model parameterisation using inshore datasets

To parameterise the model for inshore datasets, we used available data from the NIWA/Department of Conservation survey of Tonga Island marine reserve and neighbouring areas. This inshore dataset did show some notable differences with the offshore datasets. As this dataset was based on macrofaunal core samples (10 cm diameter) sieved at 0.5 mm, it adequately sampled all small-bodied and infaunal groups. For example, bivalves, as expected, were a dominant community member, and the other small-bodied and infaunal groups were better represented in the inshore compared to the offshore surveys (Figure 24, Figure 25). Relative abundance of each functional group also reflected these differences in taxa compared to the offshore surveys, with small-bodied and infaunal groups forming a large portion of total abundance (Figure 26). However, the sampling based only on core samples also showed paucity of group 6 (emergent epifauna) in the dataset (Figure 26), as these larger epifauna are generally sampled poorly with only cores. The proportion of samples including each functional group was high for all groups except groups 3 (substrate stabilisers) and group 6 (Figure 27). For further analyses using experimental data from BEN200701, we thus used a combination of both grab samples (including infauna) and video data.



**Figure 24:** Functional group membership for NIWA/DOC Tonga Island inshore analyses based on percentage of total abundance of each functional group represented by particular taxonomic units, averaged across all macrofaunal core samples.

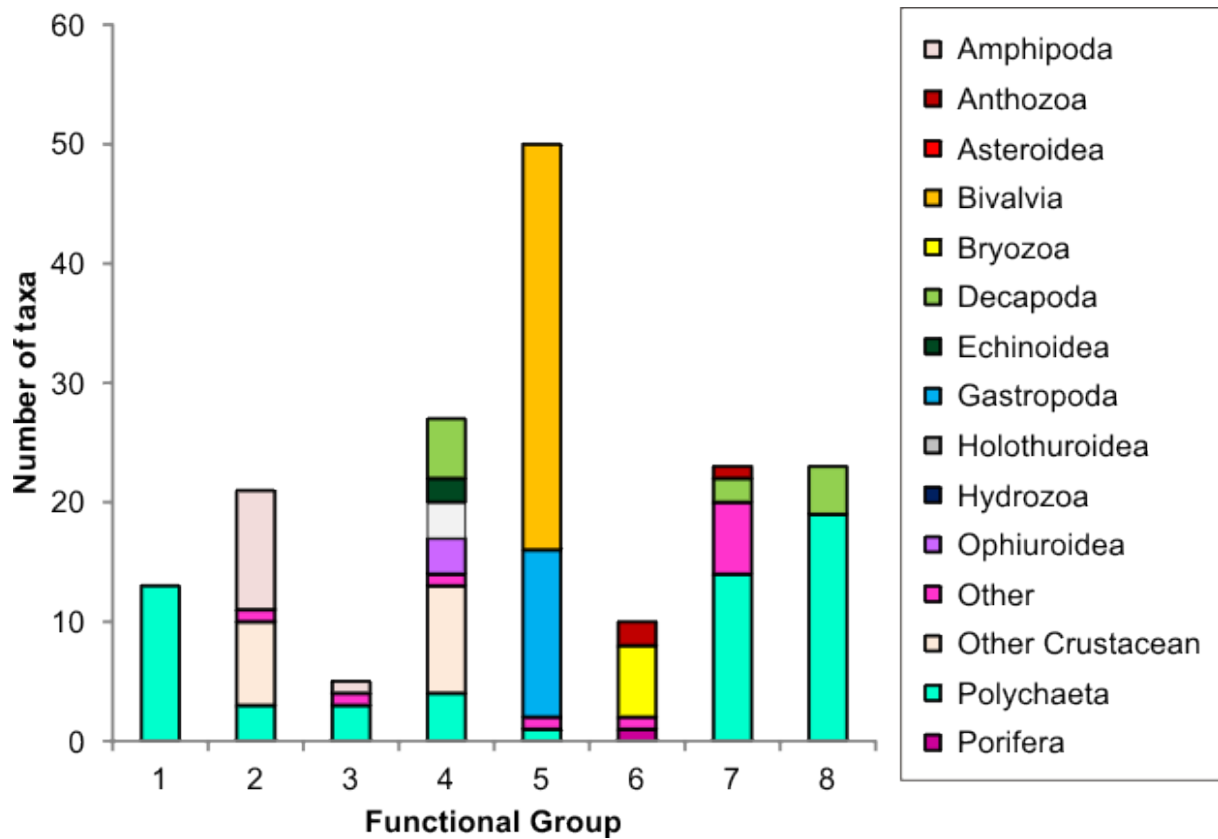


Figure 25: Functional group membership for NIWA/DOC Tonga Island inshore analyses based on total number of taxa in each functional group, averaged across all macrofaunal core samples.

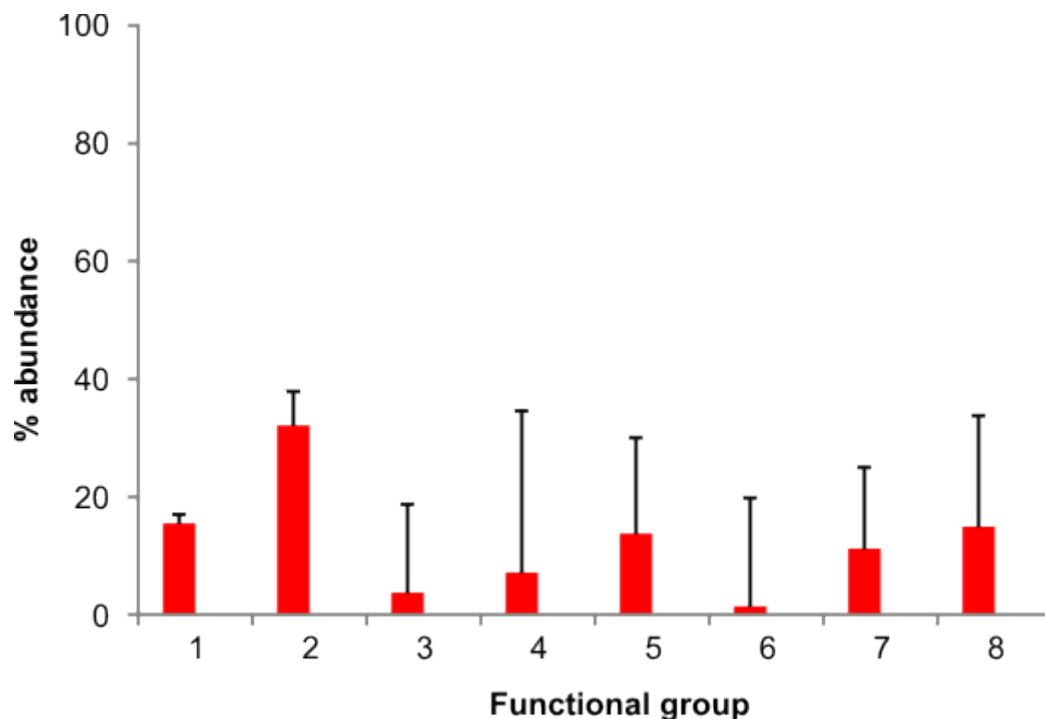
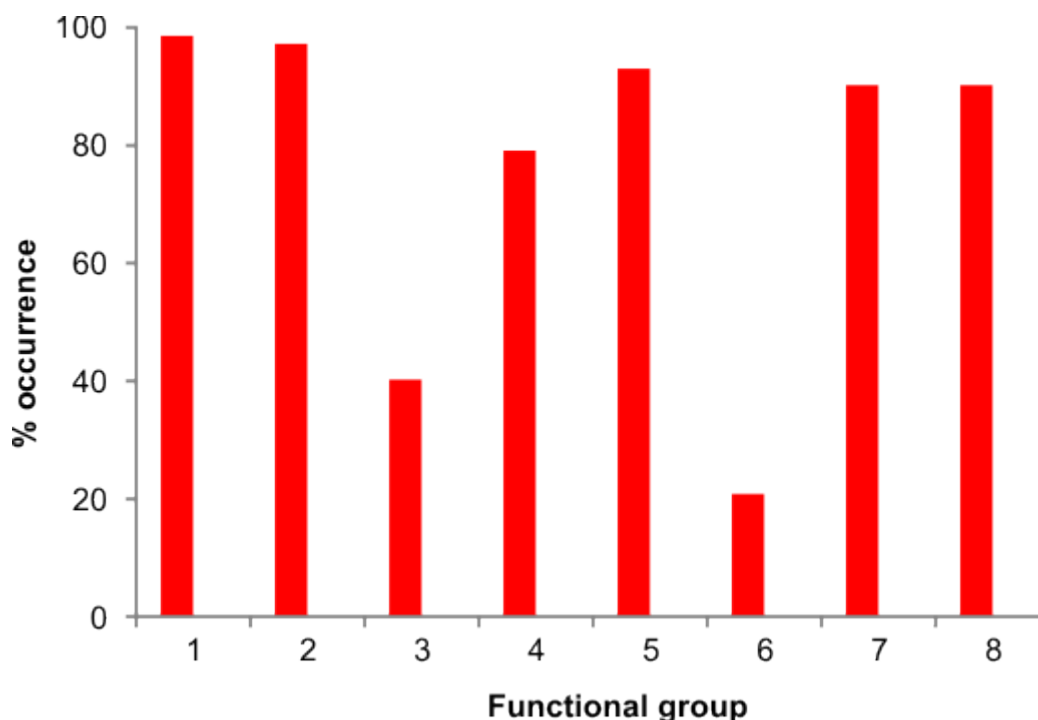


Figure 26: Relative abundance across all functional groups for NIWA/DOC Tonga Island inshore analyses, averaged across all macrofaunal core samples. Error bars represent one standard deviation.



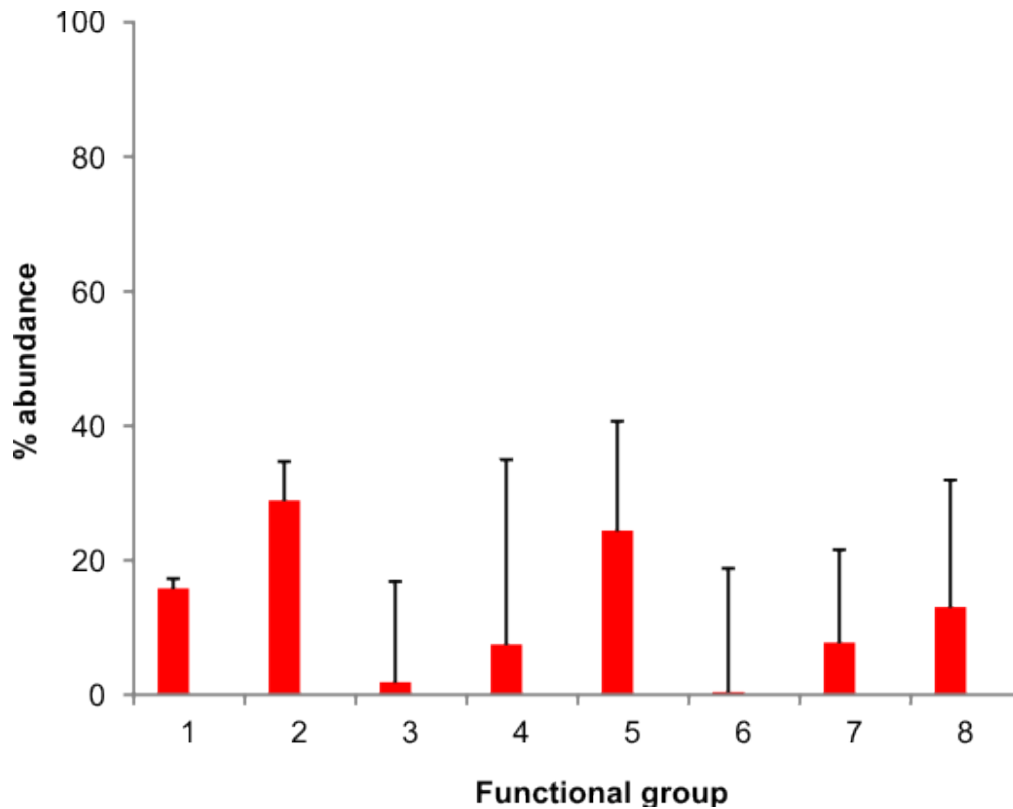
**Figure 27: Proportion of macrofaunal core samples for NIWA/DOC Tonga Island inshore analyses containing members of each functional group.**

### 3.4 Field verification in Tasman and Golden Bay

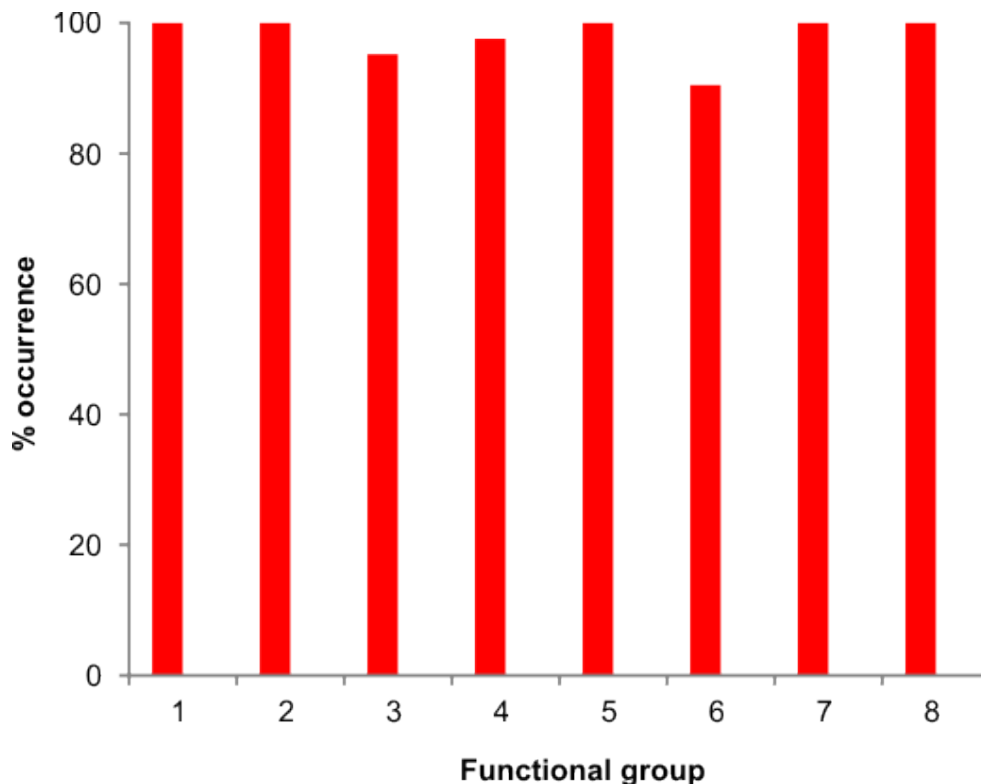
Following the same fuzzy logic protocol developed for allocating species to conceptual functional groups (Table 6), we used combined grab samples (193 samples, representing 38 sites; 166 taxa) and video data (38 samples, representing 38 sites; 25 taxa) from the BEN200701 experimental survey of fishing disturbance to derive functional group abundance for the inshore Tasman and Golden Bay region. Seven replicate grabs were sorted to 500  $\mu\text{m}$  for each site; seven replicates of the twelve available replicate samples were analysed based on statistical analyses of the minimum number of cores per site estimated to determine the total number of taxa collected across all cores at a site. We combined abundance scores for each site as a sum of a) mean abundance of each taxa across all grab replicates and b) abundance of all taxa from video. We also used samples from a NIWA core funding project at Separation Point to provide additional sampling sites for the experimental survey (4 sites surveyed, 12 grab samples per site; video data available for all sites).

Functional group membership in terms of relative frequency of abundance of each functional group in the Tasman and Golden Bay survey was similar to inshore surveys done in the region using the Tonga Island dataset (Figure 26, Figure 28). The opportunistic groups (1 and 2) again showed high proportion of relative abundance compared to offshore datasets, and the emergent epifauna as well as the sediment stabiliser group (groups 6 and 3) were poorly represented in the Tasman and Golden Bay dataset (Figure 28). The combination of both video and grab sample datasets showed better representation of larger taxa and epifauna, with occurrence of all eight functional groups at most sites (Figure 29). Generally, paucity in abundance of group 6 was apparent at all sites; this could be anecdotally associated with the high historical fishing effort in the Tasman and Golden Bay region, as well as high natural disturbance with sedimentation from the neighbouring catchment (Tuck et al. 2011)





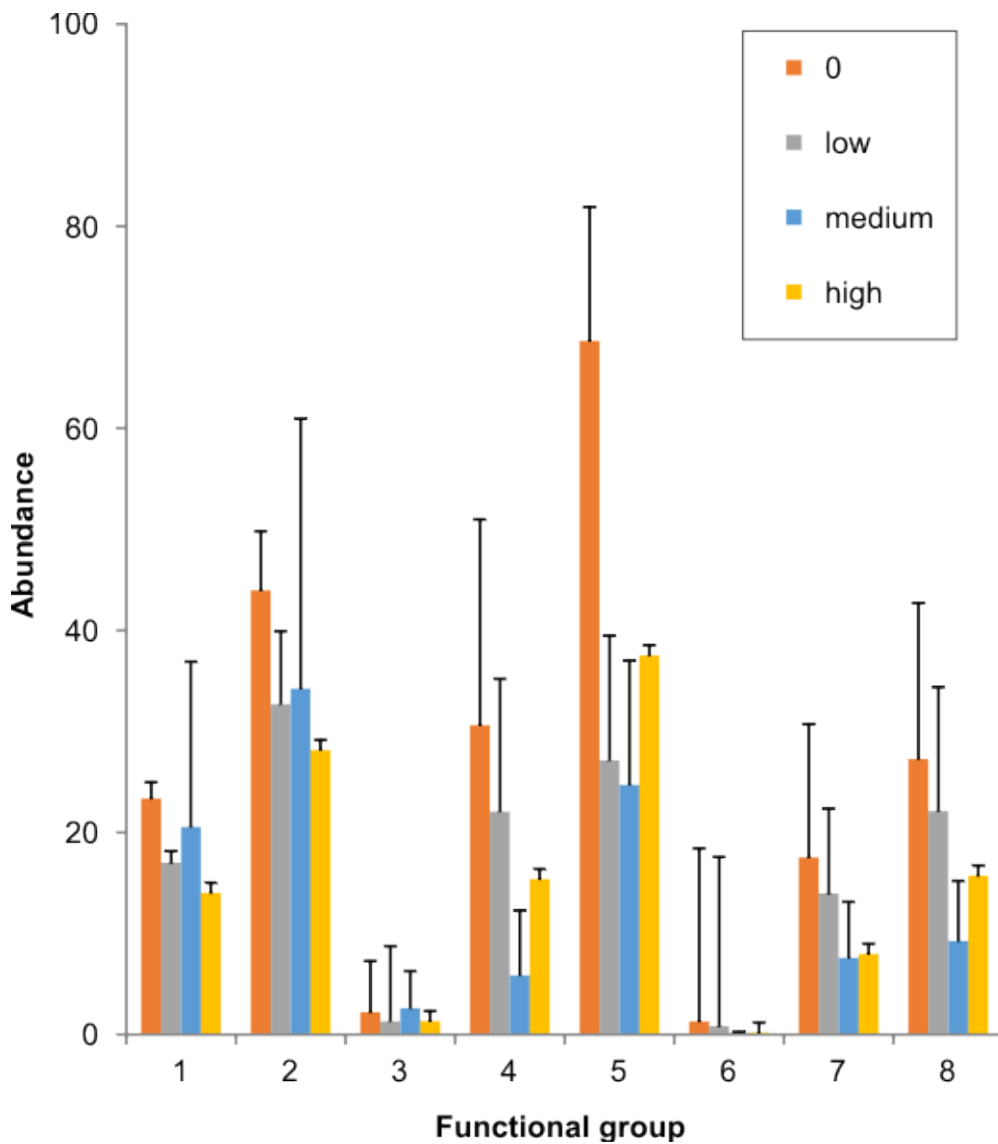
**Figure 28:** Relative abundance across all functional groups for BEN200701 Tasman and Golden Bay and Separation Point inshore analyses, averaged across all 42 sampling sites using both grab samples and video data. Error bars represent one standard deviation.



**Figure 29:** Proportion of sites for BEN200701 Tasman and Golden Bay and Separation Point inshore analyses containing members of each functional group, using combined datasets of both grab samples and video data.

### 3.5 Comparison of model and field results

Comparison of functional group abundances across Tasman and Golden Bay levels of fishing effort (zero, low, medium, and high) demonstrate similarities with the model, with functional group abundance decreasing with increasing rates of disturbance for a number of functional groups (Figure 30). Here we denote qualitative levels of fishing effort based on fin fish trawling start points and sector-based estimates of scallop effort (Table 5). Unfortunately, it is impossible to match the field survey to the total percentage of the benthic seascape that is disturbed, due to the overlap of three major methods of fishing (oyster, scallop, fin fish trawling) within the Tasman and Golden Bay regions, as well as the lack of sufficient resolution of fishery information (e.g., trawl start points only; sector-based scallop effort). We also note the paucity in abundance of functional group 6 (emergent epifauna) in the dataset; taxa within this functional group are predicted by the model to be the most sensitive to benthic disturbance. Our results suggest that these structure-forming species have not yet returned to the previously anecdotally high abundances in the Tasman and Golden Bay regions.



**Figure 30:** Histograms of relative abundance of each functional group for the Tasman and Golden Bay inshore dataset at zero, low, medium and high disturbance rates. Fishing effort strata as described in text. Error bars represent one standard deviation.

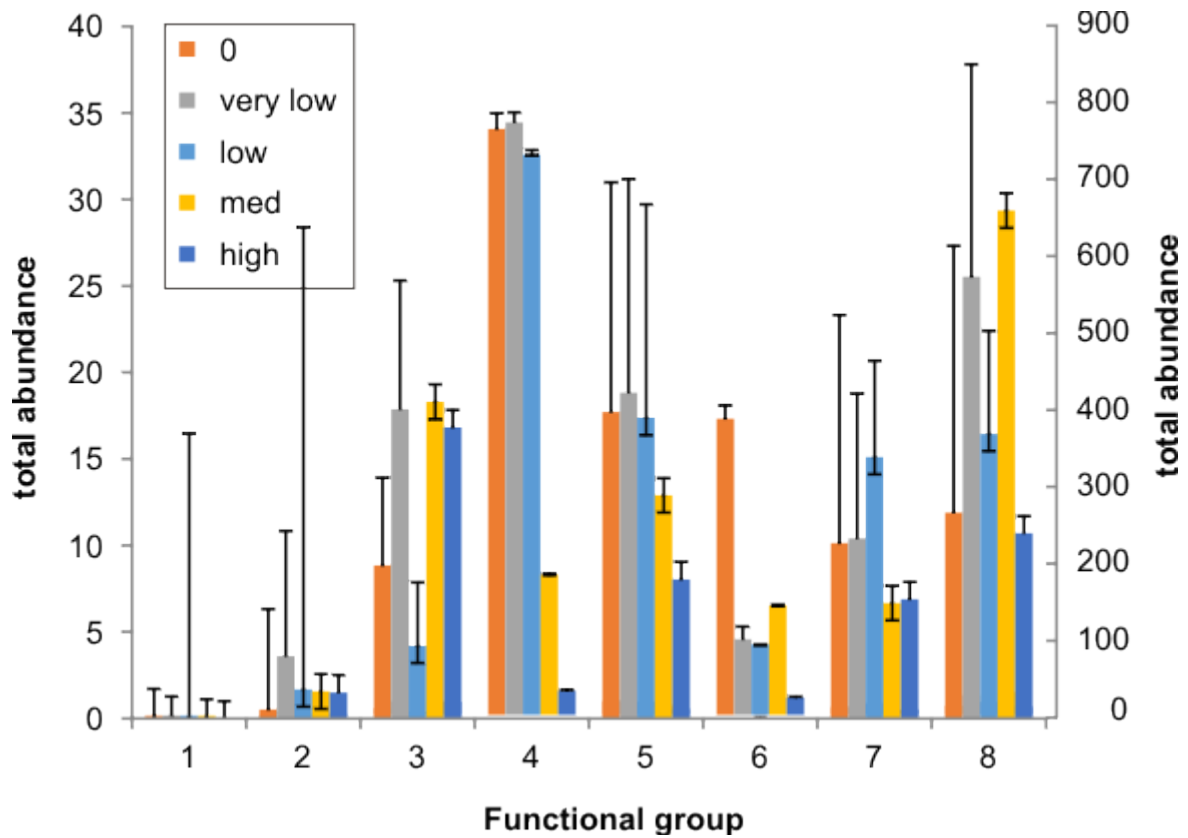
In analyses of functional group abundance with increasing rates of fishing disturbance for the offshore datasets, we combined the Chatham and Challenger datasets, noting similarity in functional group relative abundance and occurrence between both sites (Figures 20–23). Fishing effort is generally lower on the Challenger Plateau than on the Chatham Rise (Baird et al. 2011); however, sampling sites cover a similar range of fishing effort for both regions, with the majority of sampling sites within lower fishing effort, and few replicate sites in high fishing effort locales in both regions (Table 8).

For the Ocean Survey 20/20 offshore datasets, we had access to more accurate estimates of the percentage of each area subject to benthic trawl disturbance (Baird et al. 2011). We grouped fishing effort into five strata, combining Chatham and Challenger datasets (Table 8). For simplicity, we calculated annual fishing effort assuming equal temporal distribution of fishing effort within a sector across the 16 years of fishing effort data. Comparison of functional group abundances across levels of fishing effort combining Chatham and Challenger datasets demonstrate similarities to the predicted changes by the model of functional group abundance with increasing rates of disturbance (Figure 31, Figure 32).

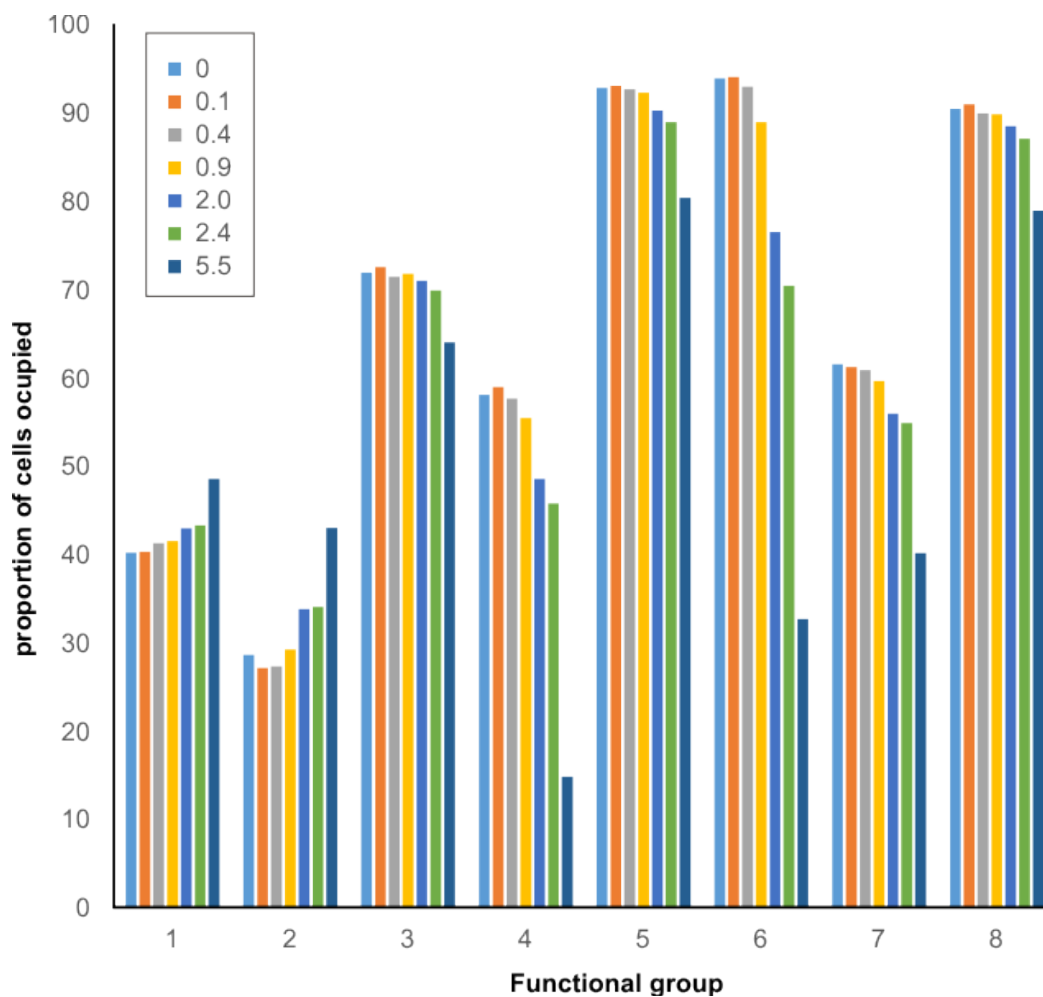
To facilitate statistical comparison between observed and expected values, we used the percentage of sites occupied by each functional group. For each fishing stratum in the Ocean Survey 20/20 dataset, the proportion of occupied sites by each functional group was normalised to the sum of the combined occupancy of all functional groups. Model data for each functional group was also normalised to the sum of the combined predicted occupancy of all functional groups. As the sampling regime did not adequately represent taxa in groups 1 and 2, we omitted these from further analysis. Relative proportions of observed versus expected values for each functional group were compared for groups 3 through 8 using a chi-square goodness of fit test. The  $\chi^2$  value is 28.9, and is smaller than the  $\chi^2_{0.05, 20}$  of 31.4; thus, we do not reject the null hypothesis, and conclude that the statistical distributions for the expected and observed values could be from the same distribution, i.e., that the model is adequately simulating observed functional group presence within the Ocean Survey 20/20 seascape over a range of fishing disturbance rates.

**Table 8: Fishing effort strata for Ocean Survey 20/20 Chatham Rise and Challenger Plateau datasets used to compare functional group abundance at site replicates to model predictions.**

Stratum	Fishing effort range (% of total seascape disturbed over 16 years)	Fishing effort range (% of total seascape disturbed per annum)	Number of site replicates (Challenger sites)	Model fishing effort equivalent used (% of total seascape disturbed per annum)
Absent	0	0	43 (32)	
Very low	0.01–1.00	0.01–0.06	68 (14)	0.10
Low	1.49–7.26	0.09–0.45	26 (2)	0.39
Medium	8.00–13.65	0.50–0.85	20 (1)	0.88
High	16.27–34.37	1.02–2.15	5 (2)	1.98



**Figure 31:** Histograms of relative abundance of each functional groups for the Ocean Survey 20/20 offshore dataset at low, medium and high disturbance rates. Fishing effort strata as described in the text. Abundance values for groups 4 and 6 are plotted on the secondary y axis. Error bars represent one standard deviation.



**Figure 32:** Histograms of proportion of the seascape occupied by functional groups as predicted by the model for a selection of fishing disturbance rates (% of the seascape disturbed per annum).

## 4 DISCUSSION

The project results suggest that we can generalise across inshore and offshore benthic communities to create adequate representations of benthic community dynamics and response to disturbance based on our understanding of the ecology, natural history and functional roles of the different species found in these regions. The accordance of the field observations and the model are encouraging, and suggest that the heuristic tool created by this project can serve in future as a framework for exploring potential management scenarios to mitigate seafloor disturbance.

The model results and field verification also suggest broad generalisations about the effects of fishing on functional diversity, and other elements of biodiversity and ecosystem function (such as the abundance of rare species, ecosystem productivity, and the provisioning of biogenic habitat structure). Functional groups representing emergent epifauna and substrate destabilisers (e.g., surface burrowers like *Echinocardium* spp.) are predicted to show the strongest negative impacts from benthic disturbance based on the model and field observations presented in this report. Emergent epifauna form much of the above-sediment habitat structure. Rare species are disproportionately included in both of these functional groups; substrate destabilisers and emergent epifauna represent 24 and 36%, respectively of rare species observed in the Ocean Survey 20/20 DTIS video dataset, and 18 and 39%, respectively, of rare species observed in the Ocean Survey 20/20 benthic sled dataset. While no datasets were available that quantified biomass of individual functional groups, if we assume that abundance broadly correlates with biomass and ecosystem productivity, the largest decreases in

abundance with increasing fishing effort also occurred in functional groups representing emergent epifauna and substrate destabilisers in the Ocean Survey 20/20 datasets.

In the data collected from the Chatham Rise and the Challenger Plateau, and the Tasman and Golden Bays region, the proportion of species in each functional group shows similarity between inshore and offshore regions. This suggests that the conceptual functional groups defined in our model represent broadly applicable functional roles of key taxa in benthic marine ecosystems, and that minimal model changes are required in conceptual functional groups to translate the model framework to new regions. Similarly, our fuzzy coding approach allows us to allocate species across the eight functional groups using easily definable functional traits. In addition to developing the model framework, the project has also contributed to a database of functional traits for over 1000 benthic taxa found in New Zealand's EEZ that can be used to compare model predictions to observed benthic communities at other locations.

Our objective was to present a generalised model of seafloor disturbance and recovery. The model is coded to allow for many options in the way we examine disturbance, and the scenarios we present here are based on a set of assumptions about life history characteristics (e.g., maximum life span, natural mortality rates of each functional group), disturbance regime (e.g., we assume disturbance results in 100% mortality within a model cell), and functional group interactions (e.g., we assume that one group – emergent epifauna – is dependent on the presence of shell hash for colonisation). The assumptions chosen to display the model framework in this report are applicable to many seafloor disturbance scenarios, and the similarity in inshore and offshore functional group abundance and occurrence suggests broad applicability of the functional groups chosen in the model to represent key functional attributes of benthic communities. In some cases, it could be useful to modify functional group attributes to represent key target species (e.g., scampi) and their associated biodiversity, and model assumptions could be modified to better represent life history characteristics of target species. Parameters are easy to change in the model, and additional sensitivity analyses can be run to determine changes in coding of new functional groups, or in coding of new disturbance regimes. For example, to represent the observation that trawls do not always result in complete mortality within a patch, we can simulate disturbances of different intensity for each functional group. For example, particular community members (e.g., large mobile carnivores) could be left intact, while other community members (e.g., biogenic structural species) are more likely to be impacted by trawling disturbance. This aspect of the model is particularly relevant to our ability to examine differences in functional diversity with increasing rates or intensities of disturbance, as observations often show that organisms with different functional traits differ in their ability to survive direct impacts of trawling disturbance (Cryer et al. 2002, de Juan et al. 2009, de Juan et al. 2007, Thrush et al. 1998).

## **5 MANAGEMENT APPLICATION**

We foresee a number of ways of exploring management scenarios with this newly developed heuristic tool. For example, while in this report, we present results only for model simulations that include randomised, square disturbances, the model is coded to allow us to change dimensions of disturbances to approximate rectangular blocks more representative of fishery trawls. Fine scale patterns of fishing effort can also be incorporated (i.e., effort analyses currently in process in BEN201201), to investigate local scale impacts of fishing, as compared to the broad estimates of fishing disturbance used in our model scenarios with disturbance assumed to apply equally across each model cell. We can also incorporate spatial correlation of disturbances, representing aggregated distribution of trawl effort (Friedlander et al. 1999) or sedimentation events from terrestrial runoff (Thrush et al. 2004). We can also include multiple types of disturbance; e.g., modelling the effect of both natural disturbances such as storms and trawling disturbance; or modelling overlapping fishing gears that differ in their impacts on the seafloor; or modelling implications of overlapping fishing and mineral exploration. Continued communication with fishery scientists, managers, and those involved in the regulatory process will benefit model development and stimulate future applications of the disturbance/recovery model in informing decision-making, and its ability to test different management scenarios.

One challenge in verifying the model is the minimal replication across the full range of fishing disturbance in most of the New Zealand benthic datasets. For example, the Ocean Survey 20/20 Chatham Rise and Challenger Plateau surveys were designed to survey the offshore regions to maximise information on variability between predicted environmental variables that were anticipated to drive patterns in benthic community structure. A less important aim of the survey was to examine the effects of fishing, so the dataset did include observations of benthic communities across a range of fishing disturbance. Unfortunately few sites were allocated within sectors with high rates of fishing disturbance, though these few samples within higher fishing effort cells do suggest that model predictions are adequate in predicting the rate of disturbance when impacts to benthic communities will be detectable.

In addition, our model can be used to suggest modifications in the collection of fisheries information (i.e., temporal and spatial scale) that can improve management understanding of local versus broad-scale disturbance rates, and better define and compare the disturbance regimes associated with fishing and other impacts to the seafloor.

We also were challenged in our ability to represent all functional groups, including smaller opportunistic taxa, when sampling gear did not always optimise representation of all groups included in the model. Our techniques of combining video and infaunal (sled, grab or multi-corer) sampling datasets suggest the requirement in surveys of collecting both broader scale information on more widely distributed, larger taxa such as epifauna, while concurrently collecting adequate data to quantify abundance of smaller, infaunal taxa. A recent survey in June 2013 [Tangaroa voyage TAN1306, NIWA project MPI13304, “Chatham Rise Benthos – Ocean Survey 20/20 2013”] will provide adequate replication at a range of fishing efforts for further verification that the model adequately represents disturbance and recovery dynamics at higher rates of disturbance. In this survey, a combined sampling design of DTIS video and multi-corer samples will provide quantitative estimates of abundance across all functional groups used within the model framework, including smaller, opportunistic taxa.

The strong similarity between model and observed community changes with disturbance showcases the value of this heuristic tool, based on fundamental biological parameters, for investigating disturbance and recovery dynamics in seafloor communities. Future research can build on this model framework, varying parameters and assumptions within model scenarios, to inform ecosystem-based management approaches for seafloor communities.

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