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Drivers of long-term change in the Foveaux Strait oyster (*Ostrea chilensis*) fishery (OYU 5)

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EXECUTIVE SUMMARY

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Concerns of over-exploitation and the effects of fishing on essential oyster habitat have led to this assessment of drivers of long-term change in the Foveaux Strait oyster (*Ostrea chilensis*) fishery (OYU 5). Data from the fishery and fishery independent research are used to assess the relative roles of the effects of disease and the effects of dredging essential oyster habitat on oyster abundance. Information on trends in oyster abundance, mortality caused by *Bonamia exitiosa*, recruitment of oysters to the population, bycatch data, and climate and environmental data from the last 30 years of research were used to determine key drivers of OYU 5 productivity. Questions asked at a stakeholder workshop and in scope for this programme are addressed. Data show that:

- The extent of the oyster fishery area described in 1906 has not been reduced by fishing.
- The spatial distribution and locations of 'oyster beds' have remained constant through time, and oyster densities within them wax and wane.
- The principal driver of oyster availability to the commercial fishery, i.e., large numbers of oyster beds with high densities of commercial-sized oysters, is mortality from *B. exitiosa*.
- Fishery and logbook data recorded at the spatial scale of 1 nautical mile squares show no relationship between dredging intensity during the winter oyster season and levels of fatal infections of *B. exitiosa* the following summer.
- Mortality caused by *B. exitiosa* may be difficult to predict because there are no regular cycles of mortality events and the lack of an adequate lag (one or more years) between non-fatal and fatal infections.
- Co-infections are likely to be important in *O. chilensis* in Foveaux Strait, 80% of a sample population of oysters had at least one or more pathogens (*B. exitiosa*, Apicomplexan X (APX), *Alcicornis longicornutus*, *Microsporodium rapuae*, and or *Rickettsia*- and *Endozoicomonas*-like organisms (RLO\ELOs), most co-infections with *B. exitiosa*.
- The report shows some support for the hypothesis: the incidence of shellfish disease is determined by a three-way interaction between host, pathogens, and environmental variables and disease may affect recruitment as well as mortality.
- Regular high recruitment to the oyster population shows productivity of the oyster fishery is high and is not likely to have changed substantially over time.
- Essential habitat to maintain oyster production is characterised by low complexity habitat that comprises mainly stable sediments of pea gravel and coarse calcareous sand, and the dead shells of bivalves. This is consistent with the earliest descriptions of commercially fished areas in the early 1950s.
- Attempts to adjust long time series of disparate oyster abundance data since 1948 to be comparable for stock assessment modelling may have overestimated both the productivity of OYU 5 prior to the 1985 *B. exitiosa* epizootic and estimates of B_0 (the mean oyster population size before fishing began).

Future research could include metadata, databases, or database tables which should be constructed to preserve and make more readily available the wide-ranging data not currently included in the Fisheries New Zealand Oyster database. Key knowledge gaps are identified and options for long-term monitoring programmes are discussed. Updating the OYU 5 strategic research plan with current research priorities for the fishery and its management is highly recommended.

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[1] National Institute of Water and Atmospheric Research (NIWA), New Zealand.

1. INTRODUCTION

The Foveaux Strait oyster (*Ostrea chilensis*) fishery (stock OYU 5, Figure 1) is delimited by the western fishery boundary as a line from Oraka Point to Centre Island to Black Rock Point (Codfish Island) to North Head (Stewart Island), and the eastern boundary is from Slope Point, south to East Cape (Stewart Island). The OYU 5 fishery is unique and, worldwide, is the largest of the remaining wild fisheries for oysters. It has been fished for over 150 years and is still productive. It is nationally and locally important, with a long tradition established around the Bluff oyster season and has high socio-economic importance to Southland. Oysters are highly valued by customary fishers of the Awarua Runanga (Ngāi Tahu) as a taonga species and by recreational fishers who dredge and dive for oysters. A brief summary of the origins and early history of the Foveaux Strait oyster fishery is given in Appendix 1.

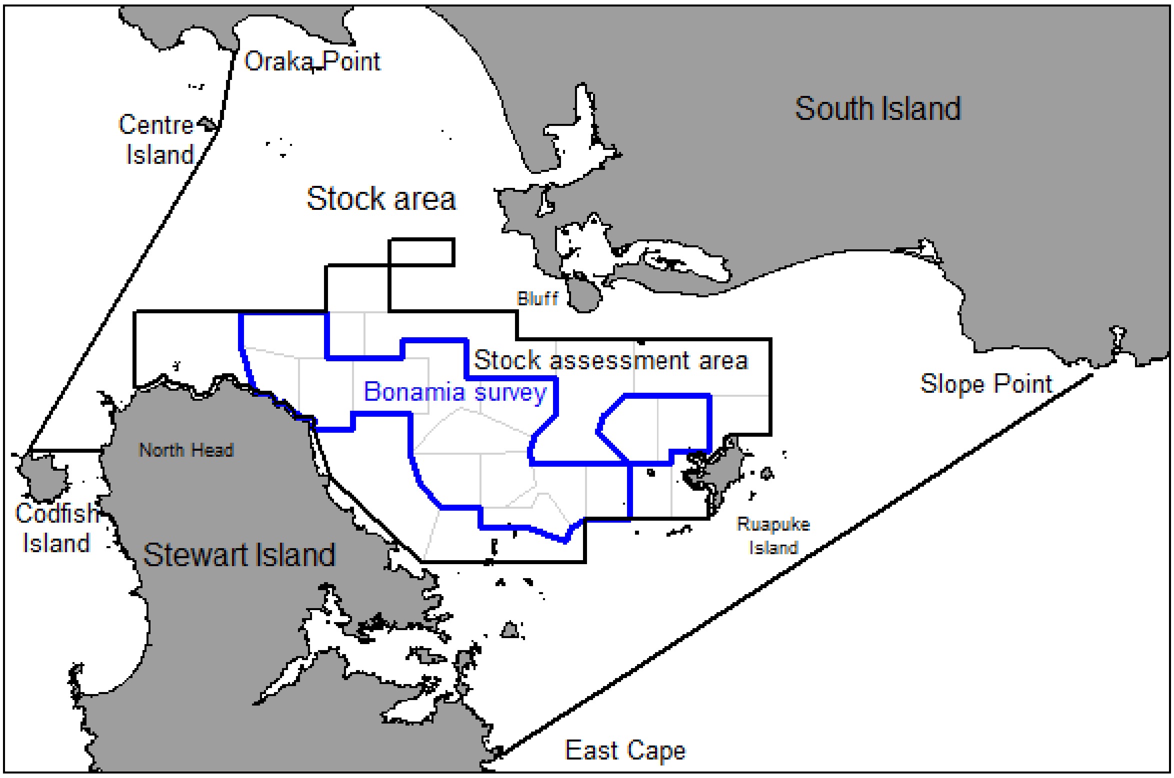

Figure 1: The Foveaux Strait oyster (OYU 5) fishery boundaries, survey area with the stock assessment survey boundary shown as a heavy, black outer line, and the core commercial fishery area (Bonamia survey area) shown as blue lines. The stock assessment survey strata are shown as grey lines.

Between the mid-1960s and mid-1980s the Foveaux Strait oyster fishery was characterised by high catch rates, high effort, and high annual landings (Cranfield et al. 1999a, Fisheries New Zealand 2019). A *Bonamia exitiosa* (Berthe &Hine 2003) epizootic caused the recruit-sized population to decline by more than 90% between 1986 and 1992 (Doonan et al. 1994, Cranfield et al. 2005). Recurrent mortality from *B. exitiosa* in 2000–2005 (Dunn et al. 2003, Michael 2010a) and 2013–2016 (Michael et al. 2023a) has not allowed the oyster population to rebuild to the levels before the 1986 *B exitiosa* epizootic. Concern of the sustainability of the OYU 5 stock has polarised and politicised both public and scientific opinion on the drivers of long-term change in the Foveaux Strait oyster fishery. The fundamental positions fall between the effects of disease mortality caused by the putative reintroduction of the oyster pathogen *B. exitiosa*, and the effects of fishing on essential oyster habitat as the key drivers of change since 1985. The Fisheries New Zealand Shellfish Working Group concurs that changes in the OYU 5 stock are primarily driven by disease mortality (Fisheries New Zealand 2019). Early literature on the effects of fishing (Cranfield et al. 1999a, Cranfield et al. 2003, Knight 2008) formulated hypotheses based on fisher interviews of bycatch from commercial oyster fishing and from the interpretation of side scan sonar images that Foveaux Strait was extensively covered in epifaunal reefs. This literature proposed hypotheses that these epifaunal reefs primarily comprised the bryozoan *Cinctipora elegans*, and that commercial densities of oysters occurred only on these reefs, that 130 years of fishing had removed these reefs, and that oyster density had not rebuilt on oyster beds abandoned by fishers [after fishing]. At the time of this research in the late 1990s, individual quotas were granted in April 1997, and quota holders were permitted to fish their entire quota on one vessel. Soon after, the numbers of vessels in the fleet declined from 23 to 11 with many crews made redundant. Hill et al. (2010) undertook a structured survey of fishers' local ecological knowledge that found divergence in fishers' opinions. Based on the interpretation of the hypotheses in the literature as scientific fact, disaffected fishers and stakeholders lobbied the Ministry for Primary Industries for closure of the fishery, contrary to the advice of the Shellfish Working Group, and led to a Parliamentary Select Committee Hearing around management of the OYU 5 fishery and numerous requests for information under the Official Information Act. This research project aims to investigate the drivers of long-term change in the Foveaux Strait oyster fishery, specifically changes to essential oyster habitat. This study does not investigate other changes to benthic habitat caused by dredging and other bottom contact gears such as bottom trawling.

The drivers of long-term (generational) changes in the Foveaux Strait oyster fishery are location, species, and fishery specific. Localised, high densities of oysters ('oyster beds') that constitute the OYU 5 fishery occur throughout the strait with almost all the population located within the 2007 stock assessment survey area (1070 km^2); however, most of the oyster beds, representing ~70% of the population, are in a smaller area (492 km^2), the Bonamia survey area shown in Figure 1. Oyster beds appear to be spatially stable and occur in a relatively deep, high-energy environment that is atypical of other oyster fisheries. Reproduction in *Ostrea chilensis* is complex and highly variable at spatial and temporal scales. *Ostrea chilensis* is a larviparous, protandrous hermaphrodite (Cranfield 1979) that broods its young to near full term. The larval biology of *O. chilensis* has given rise to the hypothesis that localised populations are self-recruiting (Cranfield 1968a, Cranfield 1979, Cranfield & Michael 1989); however, Michael (2019a) suggests greater dispersal and mixing of larvae in Foveaux Strait. The stock recruitment relationships for the Foveaux Strait dredge oyster can be weak, i.e., spawning stock size is not a reliable predictor of recruitment, and low recruitment can persist during periods of high spawning stock size and spawner densities. Counter-intuitively, high recruitment can occur at times of low stock size and densities (Michael & Shima 2018). *Bonamia exitiosa*, a pathogen of flat oysters (subfamily *Ostreinae*) (Hine et al. 2001),causes recurrent oyster mortalities in the Foveaux Strait population and is the main driver of oyster abundance during epizootics (periods of heightened disease mortality). *Bonamia exitiosa* can kill 80% of recruit-sized (legal-sized) oysters within three years (Cranfield et al. 2005), while the oyster fishery will catch less than 2% of recruit-sized oysters in any year. Until now, the effects of *B. exitiosa* and co-infections of other pathogens, environmental conditions, and oyster habitat characteristics on oyster life history have not been considered.

The western entrance to Foveaux Strait is the most exposed coastal area in New Zealand (Gorman et al. 2003), with large oceanic swells that produce a high-energy environment (Pickrill & Mitchell 1979). Mean significant wave height exceeds 3 m more than 29% of the time, and 10 m or larger 1% of the time (Gorman et al. 2003). Tidal currents are swift and accelerate west to east (Stanton 2001). This gradient in current speed is likely attributable to the decrease in depth west to east, and to constrictions caused by the shoals, rocks, and islands that extend across much of the shallow eastern entrance between Stewart Island and Slope Point.

The seafloor of the fishery area comprises gravel substrates overlaid with sand in some areas (Cullen 1962, Cullen 1967). Current flows greatly increase during storms. Storm events can mobilise sediments that scour channels and/or form sand waves, banks, and dunes (e.g., Carter & Lewis 1995, Hemer 2006). Benthic habitats vary with depth, substrate type, and wave exposure (Michael 2007). High primary production (Bradford et al. 1991) supports diverse and abundant benthic epifaunal and infaunal communities (Michael 2010a), including high densities of *O. chilensis* that comprise the Foveaux Strait oyster fishery. The benthic taxa that have evolved in this high-energy environment are likely well adapted to disturbance, and therefore recolonisation could be reasonably quick (Cranfield et al. 2001). Most of the abundant and diverse infaunal bivalves are ubiquitous across the fishery area. Importantly, the species compositions of epifaunal communities vary across the fishery area and are well described by Rowden et al. (2007). Additionally, the likely effects of climatic or environmental drivers, such as storms on seabed communities including oysters, have not been considered in the literature on the effects of fishing from Foveaux Strait.

The overall objective of this research programme is to identify key drivers of long-term (generational) change in oyster abundance, productivity, and oyster habitat, and to design a monitoring programme of these factors. Specific objectives are:

1. To identify and describe essential oyster habitat,
2. Describe long term changes to oysters and oyster habitat,
3. Design long-term monitoring programmes for key drivers of change in oyster abundance, productivity, and oyster habitat,
4. To present this report, after Shellfish Working Group review, to a second stakeholder workshop (shown as workshop (2)). Objective 4 is not included in this report.

This research summarises the available information on the status of the fishery and its key drivers. Specifically, the report uses new information and knowledge, as well as survey and fishery data since 2000, to review changes in essential oyster habitat in the context of OYU 5 effects of fishing literature (Cranfield et al. 1999a, Cranfield et al. 2001, Cranfield et al. 2003, Cranfield et al. 2004, Cranfield et al. 2005, Knight 2008, Hill et al. 2010).

Fundamental to characterising potential drivers of productivity and long-term change in oyster abundance and fishery productivity is an assessment of available data and the literature to determine essential oyster habitat (Objective 1), and how it may have changed with and without fishing. The concept of essential fish habitat is defined in the Magnuson-Stevens Fishery Conservation and Management Act (North America) as "...those waters and substrata necessary to fish for spawning, breeding, feeding, or growth to maturity"[2] and assumes each stage is closely associated with discrete and identifiable marine habitats. Loss or modification of essential fish habitats will therefore have an effect on recruitment, and thereby the sustainability of the species.

Essential oyster habitat in Foveaux Strait can be defined as habitat that facilitates survival and growth of spat, juveniles, and large oysters. Oysters have four key life history stages: brooding of fertilised larvae, a planktonic phase when competent larvae are dispersed by tidal currents, a settlement phase where oyster larvae settle on clean substrata as spat, and a post-settlement phase where oysters remain on settlement substrata, or for large oysters on the seabed. Anecdotal evidence suggests that settlement substrata with oyster spat attached and large oysters may be moved by strong tidal currents generated by storms.

Benthic habitats vary between regions and at relatively small spatial-scales across the fishery area. Essential oyster habitat that enhances survival is likely to be areas with low predation and over-colonisation by other benthic taxa. These habitats may include those occasionally covered by coarse, calcareous sediments that minimise predation and over-colonisation. Recruitment to the population, and the fishery, is primarily driven by reproductive success. Many factors including climate, high numbers of juveniles to ensure sufficient male spawners, oyster pathogens, and primary production are all likely to affect reproductive success (Michael 2019b, Michael et al. 2023a).

Fundamental to defining essential oyster habitat is whether oysters require complex biogenic reefs to provide settlement substrata for larvae and post settlement survival, or whether oysters and their shells are essential oyster habitat and also the foundation species for other colonising taxa. Two hypotheses of essential oyster habitats are investigated in this report:

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[2] https://www.fisheries.noaa.gov/insight/understanding-essential-fish-habitat

1. Commercial densities of oysters occur only on epifaunal reefs (primarily comprising the bryozoan *Cinctipora elegans*); mortality of oysters is probably lower, and recruitment and growth may be higher, within the reef habitat; oyster density has not rebuilt on oyster beds abandoned by fishers [after fishing] (Cranfield et al. 1999a).
2. Oyster larval settlement, spat survival, and growth, and thereby oyster densities are higher on gravel and sand dominated substrates occasionally covered by mobile coarse calcareous sand. These areas have less competition for settlement substrata, less predation especially of oyster spat and juveniles, and are less likely to be over-colonised and smothered by other taxa.

Essential oyster habitat is identified in Objective 1. Both potential habitat and the distributions of oysters over time are mapped to enable long-term changes in oyster distribution in relation to habitat, and to identify potential drivers of any identified change (Objective 2). Data on the historical distributions of oysters extend back to 1906 (Sorenson 1968); however, these descriptions are general, and the precision of navigation was low. Surveys since the 1960s have provided more detailed spatial distributions of oysters and qualitative data on their habitats (Fleming 1952, Cullen 1962, Cullen 1967, Stead 1971a, Stead 1971b, Street & Crowther 1973, Street et al. 1973, Street 1997). Fishing is very localised but has been reported at large statistical reporting areas since the 1960s and at fine spatial scale in fishers' logbooks since 1999. Long-term changes in oyster distribution in relation to habitat need to consider the effects of disease on reproductive capability (the flow on effects of disease selectivity resulting in higher female mortality and the subsequent low recruitment and thereby low numbers of males), the effects of natural disturbance, and fishing effects.

A stock assessment model that integrates data from many sources to inform management of the OYU 5 stock is preferred by Fisheries New Zealand. Critical to developing alternative stock assessment models is an understanding of key drivers of change in oyster abundance and productivity, spatio-temporal variations in key drivers, and the interactions amongst drivers. Long time-series data on these key drivers are needed to inform assessments. Proposed designs for long-term monitoring programmes (Objective 3) are based on our findings from Objectives 1 and 2, and primarily be focussed on the most important driver, the oyster disease process.

The inclusion of all interested stakeholders in discussions helped a collaborative approach to developing the key research questions and data available and provided for effective engagement. Fisheries New Zealand facilitated a workshop with stakeholders in Bluff to determine the scope of work for research project Objectives 1 and 2. A summary of the questions raised during this workshop is given below and whether they were able to be addressed in this report is given in Appendix 2 (Summary of questions from the Foveaux Strait Oyster Management Group Workshop).

It is recommended that this report is read together with a report including conceptual models of the population (Michael et al. 2023b).

1.1 Summary from stakeholder workshop

A workshop was held with OYU 5 fishery stakeholders in Invercargill, February 2021, in which participants acknowledged the Foveaux Strait oyster fishery (OYU 5) is of customary, regional, national, and environmental significance. Most of the discussion was concentrated on fishing (dredging) interactions with the stock and oyster habitat and factors that affect the long-term productivity of the fishery, e.g., disease mortality and other effects, and thereby its ability to provide for future customary, social, economic and habitat benefits. A summary of discussions is given in Appendix 2.

This report, in part, addresses drivers of oyster productivity. The questions raised by stakeholders that could be addressed by this report and the companion report Michael et al. (2023b) are condensed into the six themes below and provided in more detail in Appendix 2.

1. Disease. What are the triggers for oyster mortality from *B. exitiosa*, including environmental factors, and what drives the cycles of mortality, e.g., oyster density? Also discussed are the effects of biogenic areas on mitigating the spread of *B. exitiosa*. There are insufficient data at present to assess the roles of co-infections of other pathogens and climate factors on disease mortality.
2. Reproduction. Reproductive processes in Foveaux Strait *O. chilensis* that drive recruitment to the oyster population are not well understood. Specifically, the key factors that initiate gametogenesis and affect spawning, fertilisation, and brooding success; drivers of sex change at size and age; and competition for settlement substrata. Some local ecological knowledge (LEK) of skippers' observations and early investigations of recruitment are useful (Cranfield 1968a, Cranfield 1968b, Hill et al. 2010).
3. Effects of fishing. A brief summary of the literature (Cranfield et al. 1999a, Cranfield et al. 2001, Cranfield et al. 2003, Cranfield et al. 2004, Cranfield et al. 2005, Michael 2010a, Michael 2019b) is briefly discussed.
4. Oyster growth. Information on growth is summarised in a companion report—Michael et al. (2023b).
5. The effects of climatic drivers, e.g., sea surface temperature (SST). There are insufficient data to quantify the contributions of key climate factors on oyster productivity. Some inferences from the data are discussed in this report and by Michael et al. (2023b). Data from the Bluff Oyster Management Company Limited (BOMC) research currently monitoring temperature are briefly summarised in this report.

2. METHODS

Available data from surveys, the literature, and fishers' logbooks are summarised. Sources of information on epibenthic taxa associated with oyster beds include direct observation methods and inferences from dredge bycatch. Direct observation such as video or photographic methods and by dive sampling are the most reliable methods for describing oyster habitat, i.e., the sedimentary structures and epifauna and flora associated with oyster beds. Inferences from the bycatch data, from dredge sampling, are less reliable because of two key issues:

1. Dredge saturation, where the dredge fills up early in the tow and ceases sampling, i.e., does not sample the entire tow, and
2. Where the dredge contents become aggregated throughout the length of tow (commercial tow lengths are usually greater than 400 m) resulting in a loss of spatial information on patchiness and the associations between oyster beds and the fauna within oyster bed boundaries.

2.1 Characterise potential drivers of productivity and long-term change in oyster abundance and fishery productivity (Specific Objective One)

The Foveaux Strait oyster fishery has a long history of research and is data rich. Research has been funded by various organisations:

- Public funding: Fisheries New Zealand, Ministry for Primary Industries predecessor organisations such as the Ministry of Fisheries, Fisheries Research Division, Fisheries Management Division; and New Zealand Foundation for Research, Science and Technology programmes.
- Industry funding: Bluff Oyster Management Company Limited (BOMC, 1999 to present) and Bluff Oyster Enhancement Company Limited (1992–1999), and Seafood Innovations Limited programmes.

Data are also available from several university studies. Metadata for these data are scant, and a relatively small proportion of these data are held on the Fisheries New Zealand Oyster database. Much of these data are owned by BOMC. Data were collated into several broad categories: survey abundance, *B. exitiosa*, population size structure, and size structure of the commercial catch and effort data; BOMC fishers' logbook data (on catch and effort, size, disease mortality, and habitat (dredge contents)), BOMC meat condition data; BOMC spat monitoring data; climate and environmental data from NIWA-SCENZ, NIWA-CliFlo, and NASA-Giovanni databases.

Key questions on potential drivers of productivity and long-term change in oyster abundance, fishery productivity, and habitat were identified from the Foveaux Strait literature. Conflicts in the literature are discussed. Key questions from the stakeholder workshop, and from expert opinion, are grouped into themes and, where undertaken, scientific methods for analysis.

Information on essential oyster habitats is summarised from the literature to give the earliest descriptions of oyster habitat and how habitat may have changed over the years. Bycatch data from logbooks (2006–2021), oyster and Bonamia surveys (1992–2021), and bycatch surveys (2019–2021) are examined to investigate whether oyster habitat has changed. If there are strong relationships between oyster productivity and habitat alone, changes in habitat should in turn be reflected by changes in oyster recruitment, oyster densities, and thereby the oyster population sizes.

Graphical summaries are used to show data on disease mortality and the relationships between non-fatal, fatal infections, new clocks (oysters that had died recently), and total deaths. Data on fatal infections from Bonamia surveys and fishing intensity (number of dredge tows) by reporting grid from fishers' logbooks are merged and plotted to investigate potential relationships. Meat quality data (percentage first grade oysters in individual vessel daily catches) from BOMC are used as a proxy for energy levels available to biological processes. These are compared graphically.

Climate data are extracted from databases and summarised graphically. Climate variables and indices were divided into two groups to avoid collinearity and to facilitate the analysis of a relatively large number of variables for a relatively short time series of recruitment, mortality, and meat quality data.

Values for group 1 variables are derived from satellite and weather stations to provide local scale conditions that change relatively rapidly. Anomaly data on sea surface temperature (SST), chlorophyll a concentration (CHL, mg/m^3), and Total Suspended Solids (TSS, g/m^3) from remote sensing satellite are from NASA's Moderate Resolution Imaging Spectrometer on the Aqua satellite (MODIS-Aqua)[3]. MODIS-Aqua data are available from mid-2002 to 2021. Anomalies are calculated as the difference between the time series and climatology. These data were extracted using NIWA's SCENZ analysis tools. Data were summarised into monthly and three-monthly rolling averages appropriate for climate data analysis. SST, CHL, and TSS data from NASA's MODIS Aqua satellite were sourced from the NOAA databases and extracted down to daily intervals from an area delimited by 46° 39.900′– 46° 46.200′ S and 168° 03.000′ – 168° 25.920′ E (around 1600 pixels) at 1 km resolution encompassing the Foveaux Strait fishery area. These data were filtered to remove images with less than 100 pixels per record (Matt Pinkerton, NIWA, unpublished data). Group 2 climate indices are measures of the difference in mean sea-level pressures between different weather stations across the Pacific Ocean, e.g., Southern Oscillation Index (SOI); and 'Trenberth' indices for New Zealand weather stations, e.g., Meridional (i.e., southerly) wind (M1), and Zonal (i.e., westerly) wind (Z2) represented regional conditions that persist for longer periods, see Hurst et al. (2012) for detailed descriptions. Southern Oscillation Index (SOI) data were downloaded from the NOAA data service[4] from January 1950. M1 and Z2 pressure indices from 1940 were extracted from the NIWA climate database.

Data handling and graphics used R software (R Core Team 2022). Exploratory data methods were used to look for relationships and patterns in the drivers of oyster abundance. Classification tree ensembles (e.g., Conditional Random Forests, described by Hothorn et al. 2006 were used to rank factors in order of importance to the variation in response variables (recruitment and disease mortality). These include climate and environmental factors and data on *B. exitiosa* infections and oyster productivity (recruitment, spawner abundance, and disease mortality). These methods provide robust variable importance measures from relatively small data sets and with large numbers of variables, especially in cases where the predictor

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[3] https://oceancolor.gsfc.nasa.gov/data

[4] https://psl.noaa.gov/gcos_wgsp/Timeseries/SOI/

variables vary in their scale of measurement and there are nonlinear and complex high-order interaction effects (Strobl et al. 2007). The effects of each predictor variable are assessed individually, as well as in multivariate interactions with other predictor variables with unbiased variable selection measures. The percentage of each explanatory variable to all the variable importance measures summed together gives a relative proxy ‘effect size’.

Data for modelling were generally sparse. A generalised linear model approach was used to estimate the contributions of key factors to indices of abundance, recruitment, and mortality. Models were constructed using the “add1” function in R. This function computes a table of the changes in fit using all variables defined in the starting model with a single significant term added to the model at each iteration until the final model includes all significant variables. This approach allows significant variables to be added without being masked by others. Initial models were constructed using main effects only because of the large numbers of variables in the data. Significant terms were added based on the largest decrease in projected AIC. Competing models that included two-way interactions were constructed and the overall best-fit model selected based on AIC. Model fits and compliance with statistical assumptions were evaluated graphically. The aim was to estimate the contribution (effect sizes) of key drivers of oyster population abundance and their relative contribution to oyster productivity.

2.2 Map long-term changes in oyster distribution in relation to habitat and identify potential drivers of any identified change (Specific Objective Two)

Changes in the distribution of oysters are inferred from early surveys, from fisher catch per unit effort (CPUE) and logbook data, and recently from stock assessment surveys. Several factors make it difficult to accurately define the extent of the fishery and how the distributions of ‘oyster beds’ have changed. The definition of ‘oyster beds’ is a generalisation that may range from an extensive area of the fishery to one or more closely aggregated patches of high oyster densities, within a relatively small area. Oyster surveys dating back to 1906 (Sorenson 1968) provide a structured approach to delimiting the fishery area. The precision of navigation has changed over time from the triangulation of landmarks and sextant bearings to radar bearings and distances and increasing levels of accuracy of the Global Positioning System (GPS). The comparability of early survey data is assessed graphically and discussed, as are the shortcomings of CPUE data.

Foveaux Strait oysters have been fished for over 155 years and there is an extensive history of surveys and catch data available. Much of the data pre-2000are summarised by Dunn (2005a) and Fu et al. (2016). A list of surveys from Dunn (2005a) is appended and updated to 2021 and is given in Table A5.1 (Appendix 5). Sorenson (1968) summarised data from surveys of Foveaux Strait oysters in 1906, 1926, and 1945 from New Zealand Marine Department records. Surveys 1960 to 1964 are reported by Stead (1971b), and 1973 and 1975 by Allen & Cranfield (1979). Regular sampling for oyster densities and *B. exitiosa* infection have been undertaken since 1986 (see Appendix 5).

Catch and effort data are available from 1948 to the present. Dunn (2005a) provides data for 1948–1971 from Marine Department Annual Reports and 1972–1981 from Ministry of Agriculture and Fisheries reports. Catch and effort data from 1982 to the present are available from Fisheries New Zealand.

Some qualitative data are available back to 1906 (Fleming 1952, Sorenson 1968, Cranfield et al. 1999a). Quantitative data on the distribution of oysters, catch and effort, and descriptions of oyster habitat are available from 1906 (Sorenson 1968), the 1960s (Fleming 1952, Cullen 1962, Cullen 1967, Sorenson 1968, Stead 1971a, Stead 1971b, Street & Crowther 1973, Street et al. 1973, Allen & Cranfield 1979, Cranfield et al. 1999a). Bycatch data have been recorded from oyster surveys since 1999 (Michael 2007). These data were recorded from surveys employing stratified random designs that are poor at describing distributions of oysters, *B. exitiosa* infections, and bycatch. Since 2019, four Fisheries New Zealand surveys have sampled bycatch in twelve strata that sampled four distinctly different regions (eastern, southern, central, and western) of the commercial fishery area, each stratified by high, moderate, and low fishing effort (Michael 2019c, 2022a, 2022b, 2023). Three fishers’ logbook grid cells were sampled in each stratum, with a single random tow in each.

2.3 Design a long-term monitoring programme for key drivers of change in oyster abundance, productivity, and habitat (Specific Objective Three)

Strategic research plans underpin the goals of the OYU 5 fisheries plan (Ministry of Fisheries 2009), provide for information needs for management, and build knowledge of the fishery. Stakeholder strategic research plans have been established for Foveaux Strait oysters since 2000 (Andrew et al. 2000, Michael & Dunn 2005, Michael 2010b). They are living documents that prioritise and schedule research and may change in response to changes in management needs, the fishery, and our knowledge of the fishery that includes its interaction with fishing, its ecosystem, and the environment. The Foveaux Strait oyster strategic research plan was last revised in 2010. Long-term monitoring programmes should be developed based on an updated strategic research plan that incorporates new information from the fishery. Critical to better inform the management of OYU 5 is the further development the stock assessment model with a capability to predict future stock size (under Fisheries New Zealand project OYS2020-02, Michael et al. 2023b). An oyster disease sub-model is required to provide this capability. To develop a disease model, an understanding of disease processes is required to structure the model, and a time series of key data from long-term monitoring is required to inform the model. Other information needs of fishery stakeholders (e.g., oyster meat condition) should also be considered in long-term monitoring programmes.

At a meeting with stakeholders in February 2023, Fisheries New Zealand communicated a preference to retain assessments of OYU 5 using a stock assessment model that integrates data from many sources, and that future development of the OYU 5 stock assessment model (Fu et al. 2016) under research programme OYS2020-02 should include a disease sub-model to estimate future oyster mortality from pathogens, primarily *Bonamia exitiosa*. Fisheries New Zealand also undertook to update the strategic research plan in collaboration with stakeholder and to present a draft plan to a Shellfish Working Group meeting in August 2023. Objective 3 will be informed by the revised strategic research plan, and research programmes OYS2020-02 (alternative stock assessment models) and gaps in our knowledge highlighted by this report (OYS2020-03).

3. RESULTS

3.1 Objective 1: Drivers of oyster productivity and long-term change in oyster abundance and fishery productivity

The Fisheries New Zealand (2021) definition of productivity, "*Productivity is a function of the biology of a species and the environment in which it lives. It depends on growth rates, natural mortality, age at maturity, maximum average age and other relevant life history characteristics*" (Fisheries New Zealand 2021) is used to guide this summary. As changes in the OYU 5 stock are primarily driven by recruitment and disease mortality, this report focuses on biological capability and the discussion around essential habitat to produce new recruits to the population and the fishery. This approach is summarised by Randall et al. (2013), and reiterated by Bradford et al. (2014), "*the production of new biomass and habitat that is essential for life cycle*". A broader analysis of fishery productivity, e.g., Wilson et al. (2019), "*how well fishery inputs produce outputs*", is out of scope for this study.

A conceptual stock model of the drivers of OYU 5 productivity is given by Michael et al. (2023b). The conceptual model assumes:

- That oysters (post settlement) are not moved by the swift tidal currents that are generated by storms.
- The recruit-sized population is primarily driven up by recruitment and driven down by disease mortality.
- Variations in growth and mortality, other than that from disease, are secondary to these two drivers.
- Variation in recruitment is dependent on successful spawning and fertilisation, brooding, and larval settlement. The percentages of brooding-sized oysters that typically brood fertilised

larvae are low (< 2%, BOMC data). Relatively high larval settlement events translate into high oyster cohort strengths. There is a lag between increases in the recruited stock and the size/age at which oysters are commercially harvested (> 65 mm in length).
- High variation in growth determines the speed at which small oysters grow to recruit-size.
- Heightened mortality from disease has the greatest effect on oyster population size in OYU 5.

The energy available (energy budget) to individual oysters and how energy is partitioned amongst biological processes (i.e., growth and reproduction) and disease processes is fundamental to oyster abundance. Climate and environment determine primary production, and thereby food available to oysters, and the frequency of large storms that mobilise sediments and bury oysters—reducing their ability to feed. How the energy budget is partitioned between biological processes is a critical knowledge gap. Energy is partitioned between shell growth and repair and somatic growth (meat condition), reproduction, and other factors affecting the susceptibility to, or the tolerance of, pathogens (disease mortality). Essential oyster habitat, especially for larval settlement and spat survival is described and discussed in context of the literature. Oyster mortality other than from disease (e.g., fishery removals, natural mortality, and incidental fishing mortality) is relatively low and is discussed by Michael et al. (2023b).

3.1.1 Drivers of oyster productivity

3.1.1.1 Essential oyster habitat

Oyster habitat varies substantially across the fishery area, i.e., a single description of habitat associated with oyster beds cannot be tightly defined. Moreover, there is an assumption that once oysters settle as spat, they are not moved by tidal currents. Storms can generate high orbital velocities and swift tidal currents that can mobilise large sedimentary particles, e.g., arrange cobbles into waves in 50–60 m depth in western Foveaux Strait (Michael et al. 2008c). Storms and tidal currents are thought to influence the shape of oyster beds, move oysters as sedimentary particles, and aggregate oysters against sandbanks and other underwater features and into depressions in the seabed (Fleming 1952, Cullen 1967, Stead 1971b, Street & Crowther 1973, Cranfield 1979, Michael 2007, Hill et al. 2010). A survey of local ecological knowledge (LEK) held at the time by retired and current oyster skippers (Hill et al. 2010) reported the main oyster beds are generally persistent over many years and are often found along the edges of underwater topographic features such as sandbanks and mullock (low profile, biogenic reefs). ‘Mullock’ is a term used to describe a range of benthic animals caught as bycatch and provides a description of macro-epibenthic communities. Stead (1966, 1971b) described mullock patches in the 1960s as small patchily distributed areas of sponges, mussels, and bryozoans with relatively few oysters. If oysters are moved by storms, there is no direct link to a specific habitat.

Early dive and photographic surveys found ‘oyster beds’ in Foveaux Strait, most of which were not exploited at the time, occurred on firm, coarse sediments which were distributed widely across Foveaux Strait (Cullen 1962, Stead 1966, Stead 1971b). Most oysters were on the surface of the substrate or lightly covered in sand (Stead 1971b). Photographs of the seabed from 20 stations sampled throughout Foveaux Strait in 1961 (Data of Cullen 1962, New Zealand Oceanographic Archive), including areas thought never to have been dredged before (Cullen 1967), showed mainly gravel and sand substrates, few show any epifauna, and only one image showed bryozoans (i.e., *Cinctipora elegans*). Photos of the seabed taken over oyster beds by divers rarely recorded biogenic reefs. Biogenic reefs recorded on a few of these images were of sponge dominant assemblages, thought to be climax assemblages (Michael 2007). Most of the dive observations on oysters and dredge performance were on sand and gravel substrates that supported high densities of oysters (Stead 1966, and author’s observations). “*At nearly all* [dive] *stations, live oysters occurred either on the surface or lightly covered by coarse sediments sometimes to a depth of about “3 inches” and occasionally to depths of “5 inches” (~13 cm) in loose pebble substrate*” (Stead 1971b). Dive observations during an extensive oyster survey between 1960 and 1964 found commercial densities of oysters (6–8 oyster/m^2) almost entirely on gravel and sand substrates, near sand ridges, in depressions, and near mullock patches (but not within them) that occurred in both fished and previously unfished areas (Stead 1971b). Many of the previously unfished areas in the central and southwestern straits had these mullock patches. There were more "young oysters"; assumed to be spat, wings, and pre-recruit-sized oysters, on exploited rather than unexploited fishery areas suggesting that recruitment and survival was higher in exploited areas. Oysters in dense mullock were often small and in poor condition and those on nearby open areas (sand and gravel substrates) were in "fat" condition (Stead 1971b).

Observations of oyster bycatch from the early to mid-1900s (Sorenson 1968) describe oyster habitat as sand gravel, clean shell, and "weed", which in the eastern fishery was probably red algae and in the southern fishery area may have been the bushy bryozoan *Othoscuticella fusiformis*. Data from Sorenson (1968) suggest that live bycatch was approximately 7% of the catch by weight. The earliest sampling of the bycatch of oyster dredging (Fleming 1952) was sampled on the 30th of May 1950 off the East Bed. The catch comprised live oysters and the shells of dead oysters, other mollusc shells, pebbles, and a little shell-sand (shell hash). The seabed comprised gravels with shell. Oysters dominated the dredge contents, followed by the ascidian *Pyura pachydermatina*, sea urchins (4 species, including kina), brachiopods, mussels (mytilids), and other bivalves as "secondary characterising species". Bryozoans and sponges were also present, including *Cinctipora elegans*; however, not enough to be recorded as a characterising species. Of the bryozoans, the *Stomatopora* spp. were the most common encrusting species (Fleming 1952). Fleming did not link oyster beds to abundant complex biogenic assemblages, unlike Cranfield et al. (1999a), "*The nearly virgin epifaunal community described by Fleming was dominated by the reef-building bryozoan,* Cinctipora elegans *Hutton, and the oyster,* T. chilensis".

Observations of oyster beds from the 1960s and 1970s are consistent with the fishers' logbook data 2006–2021 (Figure 2); relatively high densities of oysters occur on sand, gravel, and shell substrates with little epifauna. The shells of live oysters in the commercial catch are usually free of large encrusting organisms; however, the shells of dead oysters are encrusted with small bryozoans. Oyster and other bivalve shells are aggregated by the tidal currents and may be readily over-settled by a wide range of benthic taxa. Bycatch species are mostly ubiquitous mobile species predominantly associated with the less complex habitats, and characterising species vary across the fishery area (Fleming 1952, Stead 1971a, Michael 2022a).

Survey data show that Foveaux Strait has abundant and diverse bivalve communities including *O. chilensis*, *Oxyperas elongatum* (locally known as tuatua), *Tucetona laticostata* (large dog cockle), *Panopea smithae* (geoduck), *Glycymeris modesta* (little dog cockle), and *Tawera spissa* (morning star shell). Shells of dead bivalves are exposed by orbital velocities of swell and tidal currents providing an abundance of settlement surfaces for oysters and other benthic taxa. The recurrent *B. exitiosa* epizootics maintain high levels of oyster shell and their large, heavy shells persist for many years in this environment. Observations from research and from catch sampling show that oysters readily settle on any shell or clean substrata; however, abiotic mortality of settlers on small or light shells (probably from abrasion and burial; Street et al. 1973, Michael 2009) is higher than for heavy shells. In Foveaux Strait, settlement substrata comprise large, live oysters and the shells of large gastropods, e.g., *Astraea heliotropium*. An LEK survey of fishers reported that oyster spat are frequently found on the stalks of kāeo (*Pyura pachydermatina*) (Hill et al. 2010), mostly in the eastern fishery area. As the OYU 5 fishery area has an abundance of clean settlement substrata (shells), recruitment to the oyster population is dependent on successful reproduction and the abundance of competent larvae. Recruitment is highly variable (Michael et al. 2021) (Figure 3). High numbers of competent larvae (estimated from spat monitoring) translate into strong year class strengths (catch sampling and survey data) (see Figure 4).

These data and observations from the fishery show that essential oyster habitat comprises mostly stable substrates of shells, sand, and gravels with no or little other epifauna (i.e., Hypothesis 2) — not complex biogenic habitats (Hypothesis 1). Few fishers believed that oysters depend on mullock assemblages but at times are associated with these assemblages (Hill et al. 2010). Some eastern fishery areas have extensive stands of kāeo on gravel substrates. Dredge efficiency on these habitats is greatly reduced because the dredge skims above the seabed with little or no contact. These areas are not commercially fished and are not effectively sampled by surveys (Michael et al. 2021).

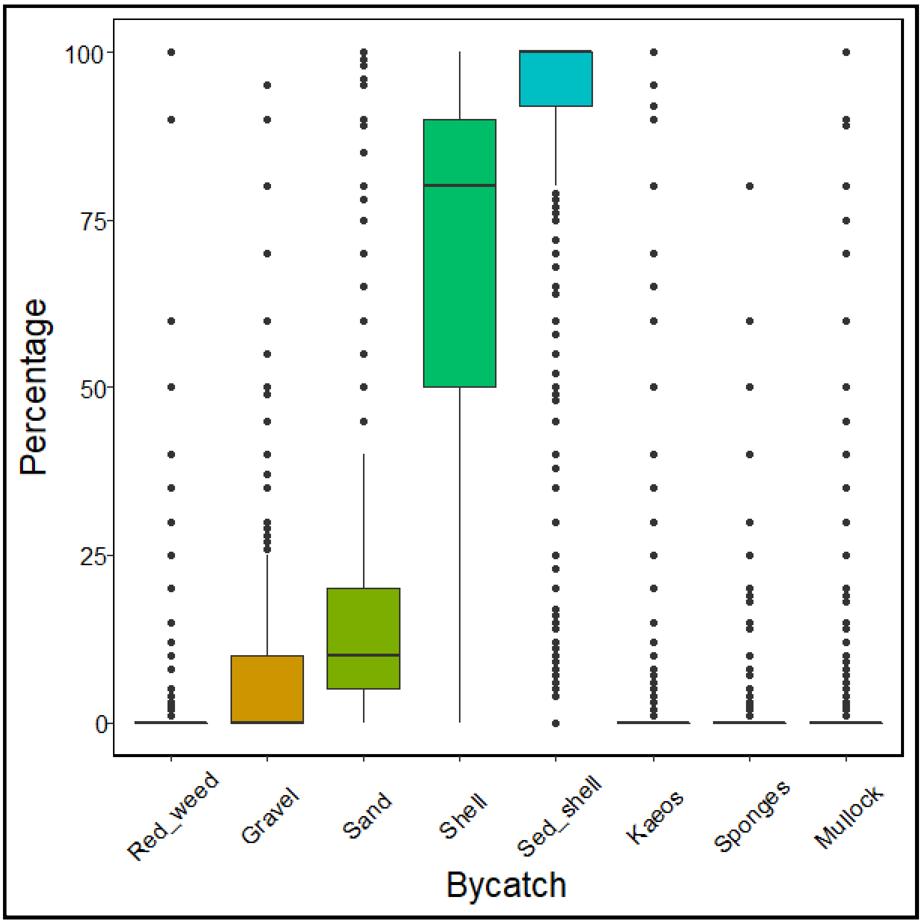

Figure 2: Boxplots of the percentage occurrences of each seabed type 2007–2021 from daily commercial catches by fishers' logbook grids. Kāeo (sea tulips, *Pyura pachydermatina*), Mullock (mixed invertebrates, mostly comprises mytilids, ascidians, and bryozoans), and 'Sed_shell' (combined percentages of sand, gravel, and shell). Box plots show median (solid lines), boxes at 25 and 75 percentiles, whiskers at 95 percentiles, and outliers shown as black circles above and below whiskers.

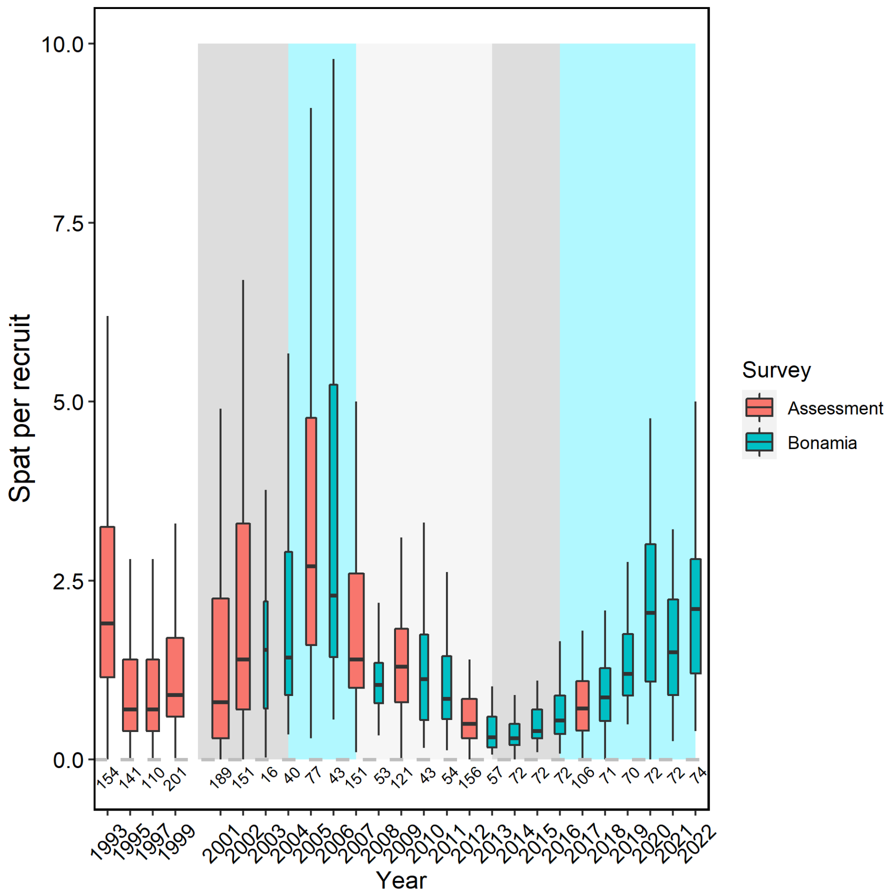

Figure 3: **The numbers of small oysters per recruited oyster sampled between 1993 and 2022 during stock assessment surveys (Assessment) and Bonamia surveys (Bonamia). Medians are shown as solid lines, boxes represent 50th percentiles (25–75%), and whiskers 90th percentiles (5–95%). Outliers smaller than 5% and greater than 95% have not been plotted for ease of visualisation. The number of stations sampled each year varied (16 lowest and 201 highest) (shown below boxes as black text and represented by box widths). Periods of mortality caused by *B. exitiosa* 1999–2022– are shown as three mortality categories of percentage annual mortality: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), high (greater than 10%, dark grey), and no detected Bonamia mortality shown in white.**

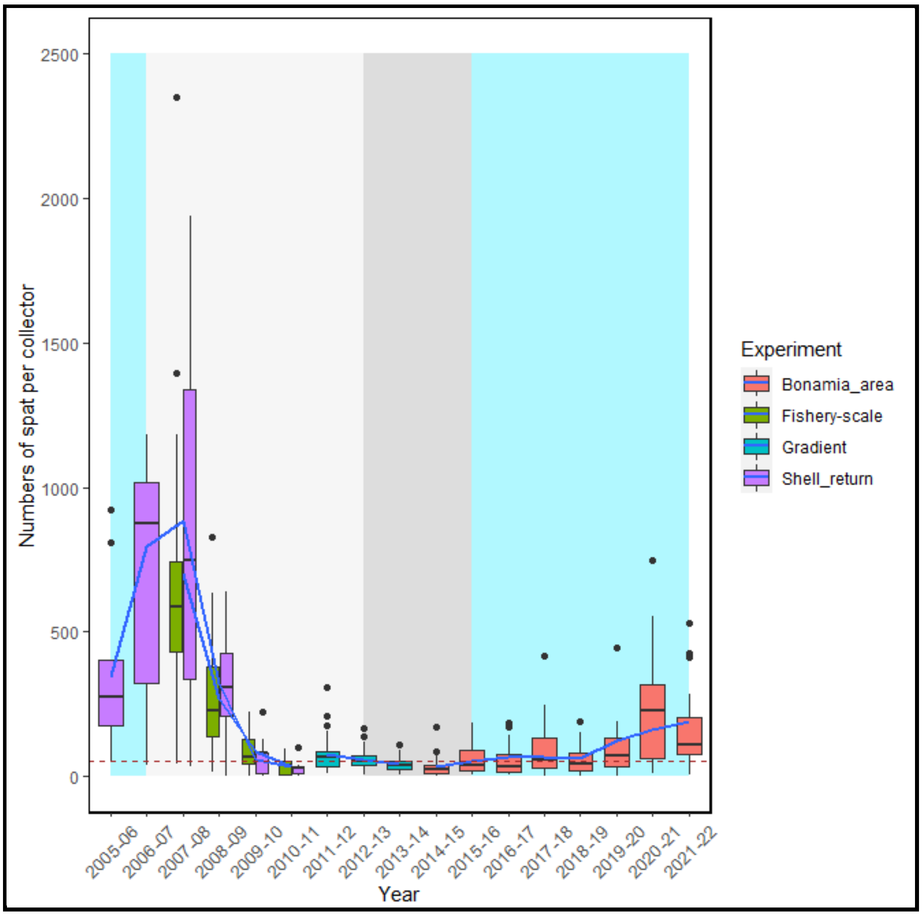

Figure 4: The total numbers of spat per collector sampled over the summers of 2005–06 to 2021—22. Spat settlement shows the success of spawning and indicates the levels of replenishment to the oyster population. Data represent four different experiments and different areas (Michael et al. 2011, Michael et al. 2022a): the shell return site and fishery scale experiments, the gradient experiment in the central fishery area and fishery scale monitoring that began over the summer of 2014–15. Brown dashed horizontal line denotes mean recruitment during the low period between 2009–10 and 2014–15. Periods of mortality caused by *B. exitiosa* 1999—2022 are shown at three mortality categories of percentage annual mortality: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), and high (greater than 10%, dark grey).

3.1.1.2 Changes in oyster habitat over time

Foveaux Strait was first dredged for oysters in 1868, see Appendix 1. The first descriptions of oyster habitat inferred from dredging were in 1950 (Fleming 1952), and first direct observations were in the 1960s (Cullen 1962, Stead 1966, Cranfield 1968a, Stead 1971b, Cranfield 1975b). These surveys found commercial densities of oysters were almost entirely on gravel and sand substrates with shell. These densities were localised patches (‘oyster beds’). Fishers’ logbook data (Figure 5) show the mean annual percentage of each bycatch category in commercial tows. The bycatch data aggregate any small spatial-scale patchiness in oysters and epibenthic communities. Fishers’ logbook data show almost all commercial fishing occurs over sand, shell, and shell sand habitats, with little change between 2007 and 2021 (Figure 5). Predominant bycatch categories per tow are shown in Figure 6. Stratified random dredge surveys are used to estimate oyster population sizes. The tows occur in fished and unfished areas and are likely to sample biogenic areas with few oysters. Figure 6 shows sponges and bryozoans have been consistently represented as dominant bycatch categories since 1990; however, this categorisation is relative to other bycatch categories and does not provide a quantitative estimate. The numbers of recruit-sized oysters per tow, by bycatch category, and percentage dredge full recorded from surveys are shown in Figures 7 and 8.

The composition of benthic epifaunal communities varies across different parts of Foveaux Strait, and are determined by the nature of the sediments, their stability, and other environmental factors (Michael 2007). Bycatch of commercial fishing reflects the annual spatial patterns of fishing.

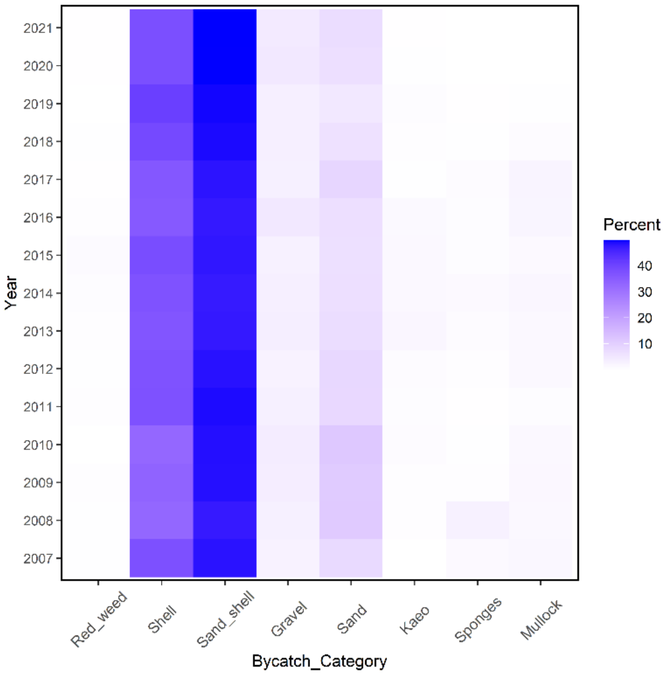

Figure 5: Heat map of the annual percentage bycatch for each oyster season (Year) between 2007 and 2021 from fishers' logbooks. Categories: 'Red_weed', algae; Shell; 'Sand_shell', sand and shell; Gravel; Sand; Kāeo (sea tulips, *Pyura pachydermatina*); only Sponges; Mullock, sponges, and bryozoans (and many other species including *Cinctipora elegans*).

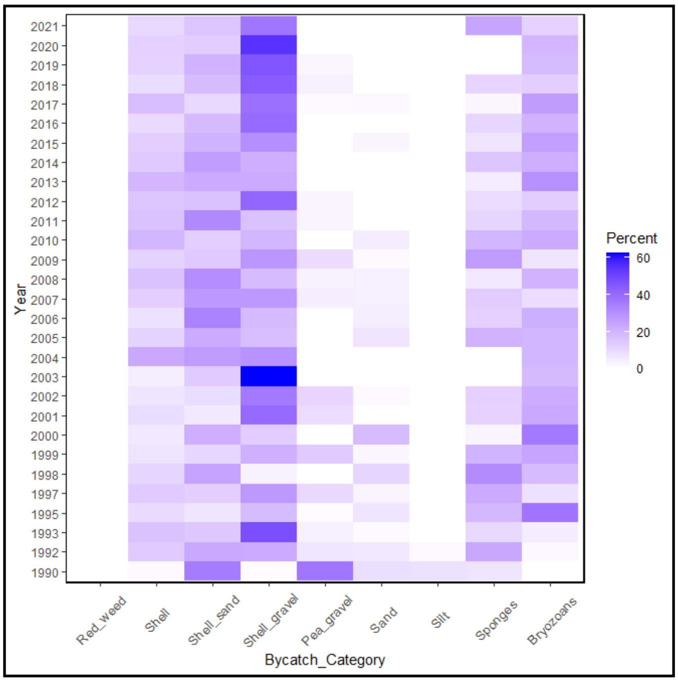

Figure 6: Heat map of the annual percentage of the most abundant of nine bycatch categories ('Red_weed', algae; Shell; 'Sand_shell', sand and shell; 'Sand_gravel'; 'Pea_gravel'; Sand; Silt; Sponges; and Bryozoans (many species including *Cinctipora elegans*) for each oyster survey between 1990 and 2021. Sampling is based on random stratified designs; tows are more likely to sample non-commercial areas.

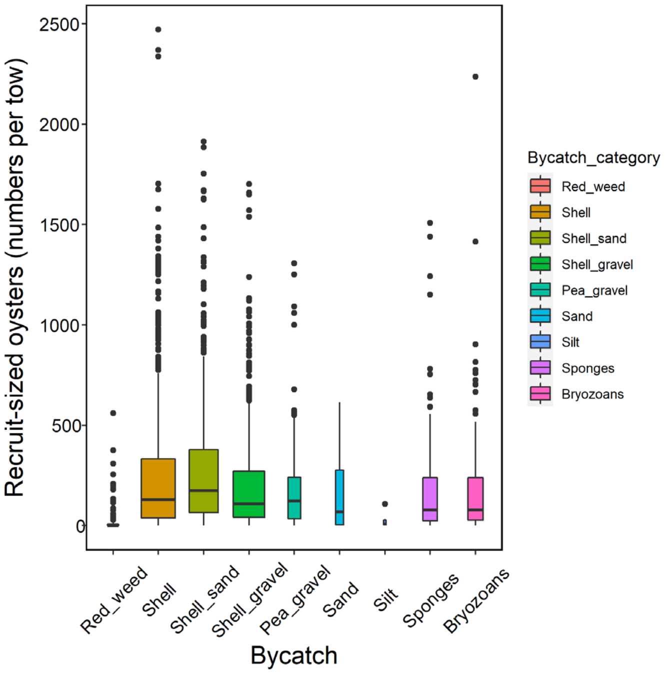

Figure 7: Boxplots of the numbers of recruit-sized oysters per tow by dominant bycatch category from oyster surveys 1990–2021. Sampling is based on random stratified designs, and tows are likely to sample non-commercial areas. Bycatch categories do not provide a quantitative estimate of bycatch. Box plots show median (solid lines), boxes at 25 and 75 percentiles, whiskers at 95 percentiles, and outliers shown as black circles above and below whiskers. Box width reflects the relative number of tows.

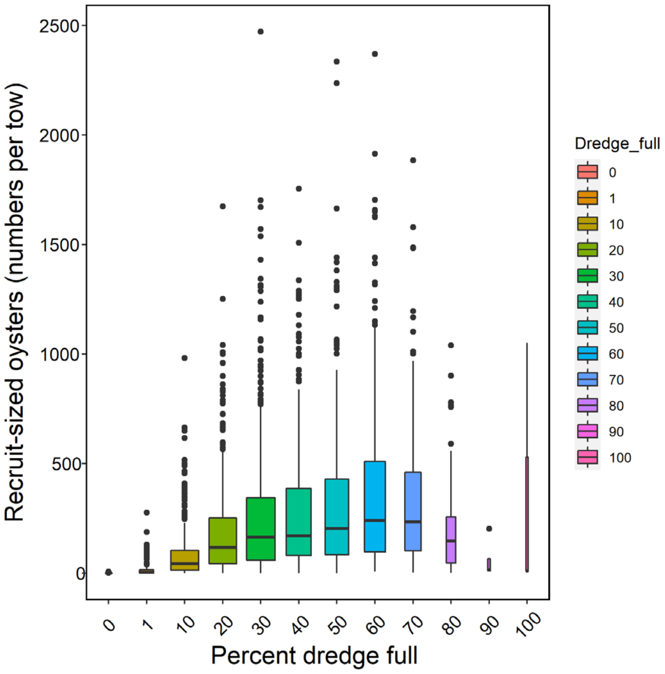

Figure 8: Boxplots of the numbers of recruit-sized oysters per tow by percentage dredge fullness from oyster surveys 1990–2021. Sampling is based on random stratified designs, and tows are more likely to sample non-commercial areas. Box plots show median (solid lines), boxes 25 and 75 percentiles, whiskers at 95 percentiles, and outliers shown as black circles above and below whiskers. Box width reflects the relative number of tows.

Surveys of bycatch (2019–2022) stratified by four OYU 5 fishery regions and three levels of fishing effort quantified benthic taxa in catches (Michael 2022a, Michael 2022b). Bycatch mostly (47.9%) comprised four species (in order of rank, *Astraea heliotropium*, *Modiolus areolatus, Ophiopsammus maculata*, and *Pyura pachydermatina*). Bycatch weight differed by region and by fishing effort. The median weights of live bycatch were higher in cells with high fishing effort and lowest in cells with low fishing effort. There were some differences in the composition of bycatch within region, which may reflect differences in benthic habitats and benthic communities rather than fishing effort per se.

The consensus of LEK from a study by Hill et al. (2010) is that dredge bycatch from the eastern portion of the strait has been similar over the 30 or more years represented by the respondents. However, bycatch in the western portion of Foveaux Strait has changed considerably, showing a decline of the complex habitats in much of this area. Some fishers noted a recent increase in bycatch of species associated with complex habitats in areas that have not been fished for more than a few years, implying some level of recovery. Cranfield et al. (2003) visually compared the distribution of benthic structures from late 1970s and late 1990s side scan sonar surveys and inferred changes to the composition of benthic communities at large scales; however, no ground truthing was done to identify those structures.

A drift underwater video survey was completed in February 2006 (see Michael 2007, including station data given in Appendix A1). The survey area was divided into the commercial oyster fishery area and the areas rarely fished for oysters outside the commercial area, but within the stock boundaries (Figure 1). The commercial and non-commercial areas were further divided in 4 strata in each. A minimum of 5 transects, sampling a minimum distance of 0.2 nautical mile or minimum duration of 20 minutes, were sampled in each stratum (see figure 11 of Michael 2007). These video samples were used to provide general descriptions of seabed composition, stability, topography, small and large spatial-scale structure and complexity, and the assemblages of epibenthic macrofauna, non-living components of the seabed sediments such as mollusc shells, and the presence of fish. No reefs of *C. elegans* were observed in either fished or unfished areas and two stations in each of commercial and non-commercial strata had bryozoans. Fourteen stations show sponges, 12 in commercial fishery areas and 2 in non-commercial areas. Video transects on or near sites that were sampled by still images in 1961 showed no discernible differences in sedimentary structures or benthic habitats (Michael 2007 and also images and video clips embedded in the report by Michael et al. 2008c).

Additionally, no consideration is given to the role of storms in mobilising and distributing sediments. Little is known about the nature of recovery after fishing and storms. Cranfield et al. (2001) proposed a model of recovery, but the secession process is likely to vary in different regions.

3.1.1.3 Enhancing oyster habitat, ‘working the oyster beds’

Fishers’ LEK suggests that constant fishing on commercial oyster ground is required to maintain oyster productivity (Hill et al. 2010). Oyster beds unfished for a time are quickly (~3 years) colonised by fouling organisms such as sponges (Sorenson 1968), mussels (*Modiolus areolatus* and *Modiolarca impacta*), and bryozoans (Cranfield et al. 2001). Fishers mostly agree that ‘working the oyster beds’ (‘harrowing’ in the northern hemisphere, Bromley et al. 2016) enhances oyster habitat in Foveaux Strait. This method is used to increase oyster productivity, meat quality, and catch rates. Fishers repeatedly dredge areas with moderate oyster catch rates, and with low to moderate bycatch, to remove epifauna and to break up clusters of oysters (Hill et al. 2010). Working the beds reportedly increases oyster growth and increases survival, especially of small oysters, by reducing predation and over colonisation of oysters (Hill et al. 2010). The premise of this practice is consistent with the characteristics of essential oyster habitat identified by this research. Dredge tracks, even in heavily fished grids, were indistinguishable on the seabed using side scan sonar and drift video four months after the oyster season (Michael 2011a).

‘Working the beds’ differs from targeting biogenic reefs. Fishers do not target complex epibenthic communities (mullock) because oyster densities are low there. When rich epifaunal areas are encountered, fishers move. Fishers at times fish along the edges of underwater topographical features such as sandbanks and biogenic areas, e.g., mullock (Hill et al. 2010). Although oyster density can be locally high on these edges, possibly aggregated there by tidal currents (Stead 1971b), most commercial oyster dredging occurs on open sand and gravel habitats (Cullen 1962, Stead 1971b). Fishers stress that working edges differs from 'working the beds'. Areas with high volumes of bycatch, especially biogenic areas, are avoided because they are uneconomic to fish. The high volumes of bycatch in these areas take longer to sort, and the rapid dredge saturation substantially reduces the numbers of oysters caught and thereby the catch rate. Oysters in complex biogenic areas tend to have poor meat condition (Stead 1971b). Fishers report that they do not fish these areas (Hill et al. 2010).

Many factors determine the daily patterns of fishing. Fishers target areas where both catch rates are acceptable and oyster meat condition is expected to be good. Other key determinants of fishing patterns include distance from port to fishing areas, weather, and the effects of tidal strength and direction on steaming time and dredge efficiency. Daily catch limits imposed on vessels by processors affect the daily numbers of tows per reporting cell as well as the broader location fished. Bycatch surveys 2019–2022 show composition and volume of bycatch in fished areas varies with the spatial patterns of fishing; however, volumes of bycatch are generally low (Michael 2022a, Michael 2022b).

Overseas, harrowing is used in muddy sheltered estuarine habitats in Europe to remove silt and increase clean settlement substrata for larval settlement of *O. edulis*. A study by Bromley et al. (2016) found that harrowing was ineffective in that habitat, and that harrowing reduced sensitive erect epifaunal species. These habitats are very different to the highly exposed habitats of coarse sediments and abundant settlement substrata of Foveaux Strait.

3.1.2 Biological drivers of the variation in oyster production

3.1.2.1 Mortality of oysters caused by disease

Large scale mortalities of oysters have been reported since the earliest surveys from 1906 (Sorenson 1968). Size dependent mortality is the most significant driver of oyster abundance in Foveaux Strait. Mortality of recently settled spat and juvenile oysters is putatively high, as it is for most marine invertebrates. During epizootics, oysters are assumed to have a 'U' shaped mortality relationship with size, where high levels of mortality are also observed in large individuals (Doonan et al. 1994). Oyster mortality can be partitioned into the following four sources, ranked in order of importance: disease mortality, fishery removals, natural mortality, and incidental fishing mortality. This section focuses on disease mortality as the primary driver of the OYU 5 stock. Catch, natural mortality, and incidental fishing mortality are briefly summarised for context and discussed in more detail by Michael et al. (2023b).

Ostrea chilensis in Foveaux Strait is infected by a range of pathogens. Sampling in 2020 found 80% of oysters had one or more pathogens (*Bonamia exitiosa*, Apicomplexan X (APX), *Alcicornis longicornutus* (previously *Bucephalus longicornutus*), *Microsporodium rapuae*, and or *Rickettsia*-like organisms (RLO), and *Endozoicomonas*-like organisms (ELO)), and 30–40% had two or more pathogens (Michael et al. 2022b). Co-infections maybe important in Foveaux Strait oysters and may have significant effects on oyster recruitment as well as on mortality (Hine 2002).

Disease mortality from *B. exitiosa* accounts for almost all the mortality of oysters in OYU 5 during epizootics; however, other pathogens may also cause mortality or exacerbate disease (e.g., APX, see Hine 2002). The effects of disease from *B. exitiosa* on oyster population size are well documented (Doonan et al. 1994, Cranfield et al. 2005, Michael et al. 2021). Host size/age, meat condition, reproductive state, co-infections, oyster densities, and climatic factors all influence *B. exitiosa* infection dynamics (Hine 1991a, Doonan et al. 1999, Hine 2002).

Bonamia exitiosa was first identified in 1985 (Dinamani et al. 1987) but observed in archived Foveaux Strait oysters collected in 1964 (Hine & Jones 1994) when elevated mortality between 1958 and 1964 was attributed (probably erroneously) to the digenean trematode *Alcicornis* (previously *Bucephalus*) *longicornutus* (Howell 1967). *Bonamia exitiosa* spread rapidly through the oyster population in 1985, indicative of a naïve host population, despite its earlier presence in the fishery (Doonan et al. 1994, Cranfield et al. 2005). Heightened mortality from *B. exitiosa* in 2000–2005 and 2013–2016 presented different patterns of infection across Foveaux Strait, which is indicative of an endemic pathogen (Dunn et al. 2003, Michael et al. 2008c, Michael et al. 2019a).

No *B. exitiosa* infection data for individual oysters from each station are available earlier than 2000. Annual trends in *B. exitiosa* non-fatal and fatal infections, their prevalence, and oyster mortality track concurrently together over time (Figure 9). Note that some oysters with fatal infections would have been removed by mortality and are accounted for by new clocks. Data available suggest that the 1985–1992 epizootic started at a single location (focal infection) and spread through the fishery. Since 2000, non-fatal and fatal infections increased in a similar pattern, contrary to the SIR (susceptible-infected-removed) model (Hethcote 1989). Potentially low-level and undetectable endemic infections are intensified in some years; some develop to fatal infections while others do not. If non-fatal infections do not progress to fatal infections at the same rate over time, and that intensification of infection is caused by a 'year effect' independent to the period of infection, non-fatal infections cannot be used as a predictor of fatal infections the following year. The abundance of new clocks gives a good signal of heightened mortality. *Bonamia exitiosa* infections are sampled over 2–3 weeks within the two or more months of peak annual mortality, with potential for some sampling variation.

3.1.2.2 Other mortality

Fishing mortality is the removal of recruit-sized oysters from the population by fishing, i.e., catch. The patterns of fishing vary within and between years, and between regions within OYU 5. The oyster fishery catches less than 2% of recruit-sized oysters in any season; however, *B. exitiosa* accounts for up to 91% of recruit-sized (legal-sized) oysters in a single heightened mortality cycle (epizootic) (Cranfield et al. 2005).

Trials in March 1997 (Cranfield et al. 1997) quantified incidental dredge mortality. The mortality of oysters left behind on the dredge track was inversely related to size. Spat (0+, ≤ 10 mm in length) were the most vulnerable size, with mortality of 11%–36%. Juvenile (10–57 mm) oyster mortality was 7%–10% which was statistically significantly greater than that for recruit-sized (≥ 58 mm in length) oysters (2%). Incidental mortality from dredging may reduce subsequent recruitment in heavily fished areas, but the relatively small area fished is unlikely to have any effect on overall recruitment to the fishery.

Natural mortality (other than disease mortality) is not well estimated (Dunn et al. 2000) but is considered low. Natural mortality is size dependent and generally low for 1+ age cohort and older oysters. Sources of natural mortality include predation, over-colonisation (smothering), poor condition, and old age (senescence), and the occasional effects of large storms that may move and bury large numbers of oysters. Mortality from intense infestations from the bio-erosive sponge *Cliona* spp. may be occasionally significant in some areas of the fishery (Stead 1971b, Cranfield 1975a), as it is for *Crassostrea virginica* in North America (Carroll et al. 2015).

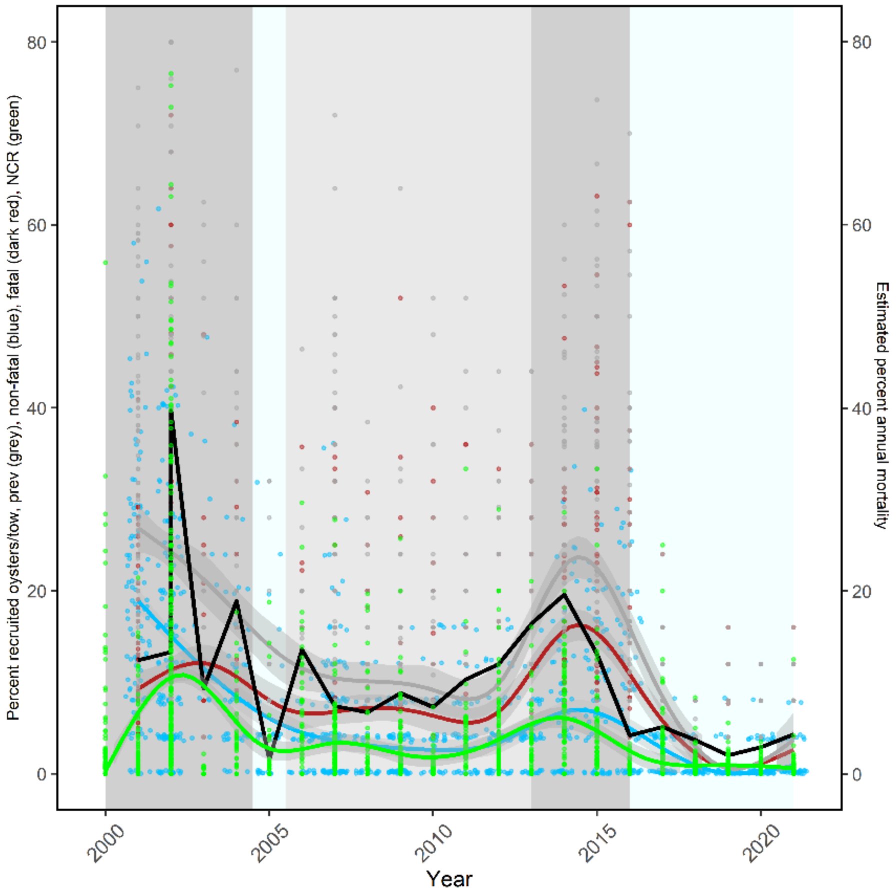

Figure 9: Annual trends of *Bonamia exitiosa* prevalence (%) of infection (grey), non-fatal (blue) and fatal infections (red), new clocks (green) by survey tow over time, points coloured by variable. Smoothed lines used a GAM function with standard error (s.e.) shown in grey fill. Annual mortality (%) in the oyster population shown as a black line. Vertical grey strips show the period of heightened oyster mortality caused by *B. exitiosa*, categories: low (0.1–4.9%, light blue), moderate (5.0–9.9%, light grey), and high (greater than 10%, dark grey) of percentage annual mortality.

3.1.2.3 Effects of dredging on exacerbating disease

Disturbance from dredging is suggested to play a critical role in physiological stress and thereby disease susceptibility (van Banning 1991, Cranfield et al. 1999a, Cranfield et al. 2005). Laboratory experiments (Diggles & Hine 2002) found constant stirring of oysters intensified *B. exitiosa* infections.

Analysis of survey and fishers' logbook data found no relationship between the percentage of fatal *B. exitiosa* infections of recruit-sized oysters (Figure 10) and pre-recruit oysters (Figure 11) and the categories of the numbers of commercial dredge tows in each of the fishers' logbook grid cells each year. Each category of the number of dredge tows is further stratified by low (0.1–4.9%), moderate (5.0–9.9%), and high (greater than 10%) categories of percentage of annual mortality from *B. exitiosa*.

Ranked variable importance measures (VIM) from classification tree modelling to predict percent fatal infections from *B. exitiosa* in recruit-sized oysters are given in Table 1. Factors include percent non-fatal infections, *B. exitiosa* (Bonamia) mortality category (low, moderate, and high percentage annual mortality in the oyster population), year effect (Year), fishers' logbook grid, number of recruit-sized oysters per tow (Recruit-sized), and the number of tows in each grid cell each year for 2007–2021. Ranks from VIMs and proxy 'effect sizes' (the percentages of effects, VIM%) were robust to the numbers of trees generated; differences in the VIMs of variables using 2000, 5000, and 9000 trees were negligible. The number of dredge tows per grid cell each season contributed very little to the percentage of fatal infections the following summer, < 2% of all variables (Table 1). Fatal infections are closely associated with non-fatal infection and with oyster mortality category caused by *B. exitiosa* , Year, and their interaction (Table 1).

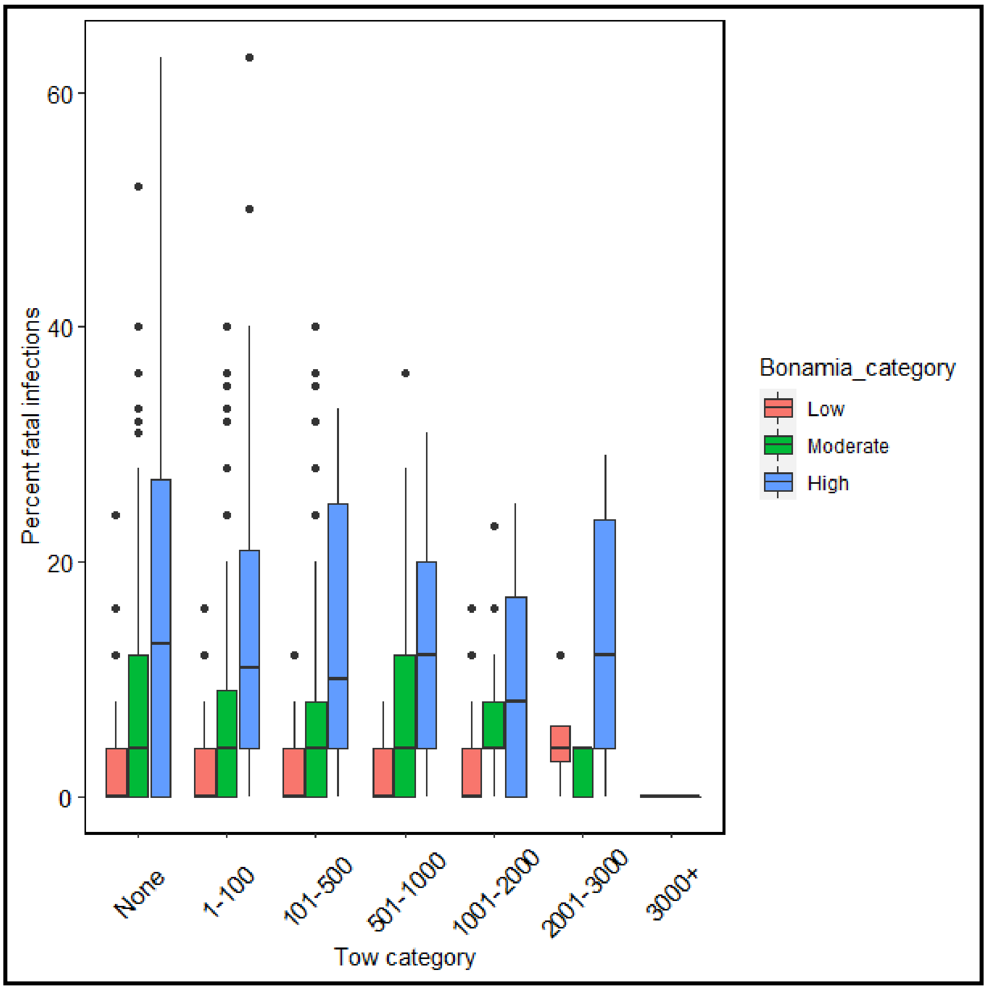

Figure 10: Boxplots of the percentage of fatal *Bonamia exitiosa* infections of recruit-sized oysters by categories of the number of commercial dredge tows in each of the fishers' logbook grid cells each year. Each dredge tows category is further stratified by low (0.1–4.9%), moderate (5.0–9.9%), and high (greater than 10%) categories of percentage of annual oyster mortality caused by *B. exitiosa*. Box plots show median (solid lines), boxes 25 and 75 percentiles, whiskers at 95 percentiles, and outliers shown as black circles above and below whiskers.

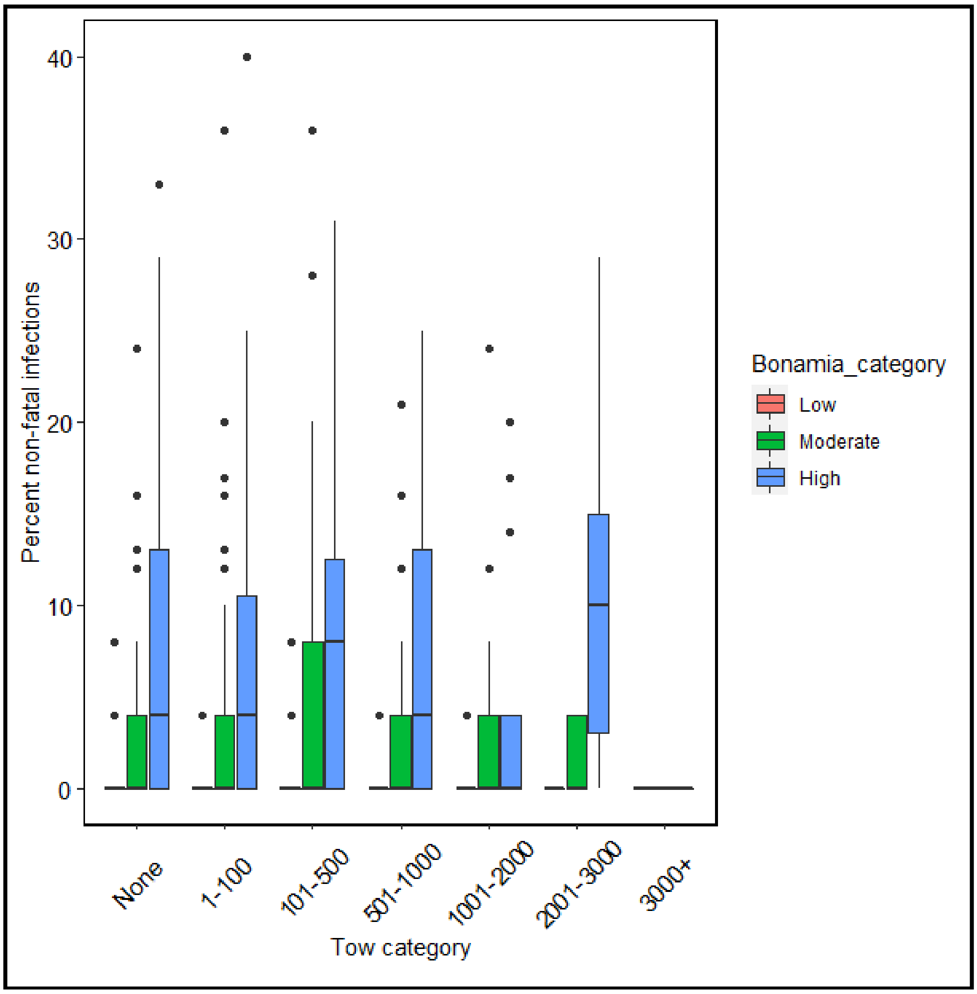

Figure 11: Boxplots of the percentage of fatal *Bonamia exitiosa* infections of pre-recruit oysters by categories of the number of commercial dredge tows in each of the fishers' logbook grid cells each year. Each dredge tows category is further stratified by low (0.1–4.9%), moderate (5.0–9.9%), and high (greater than 10%) categories of percentage of annual oyster mortality caused by *B. exitiosa*. Box plots show median (solid lines), boxes 25 and 75 percentiles, whiskers at 95 percentiles, and outliers shown as black circles above and below whiskers.

Table 1: Ranks of the relative variable importance (VIM) of percent non-fatal infections, *B. exitiosa* (Bonamia) mortality category (low 0.1–4.9%), moderate (5.0–9.9%), and high (greater than 10%) percentage annual mortality), year effect (Year), fishers' logbook grid, Numbers of recruit-sized oyster per tow (Recruit-sized), and the number of tows in each grid cell each year for 2007–2021 to predict percent fatal infections from *B. exitiosa* in recruit-sized oysters using Conditional Random Forest models (Hothorn et al. 2006). Variable importance measure (VIM) and the percentage of all importance measures combined as a proxy for effect size (VIM%). Sensitivity analyses give changes to VIM resulting from dropped variables. '-' denotes factors dropped from analysis.

Variable	**VIM**	**VIM%**		**VIM**	**VIM%**
Percent non-fatal	25.5	36.3		–	–
Bonamia category	17.5	24.9		–	–
Year	15.8	22.6		52.0	76.4
Logbook grid	8.8	12.5		–	–
Recruit-sized	1.6	2.2		7.2	10.6
Number of tows	1.1	1.6		8.9	13.0

3.1.2.4 Effects of oyster host condition on *Bonamia exitiosa* mortality

Oyster host energy may be used for the suppression of disease, usually through mounting an immune response. Thereby, the development of disease affects the energy budget of the host (Egerton et al. 2020). There are two opposing principal hypotheses:

1. High food availability, good physiological condition, and associated high energy reserves of hosts lowers the oyster's susceptibility to disease (Pernet et al. 2019), or
2. Conversely, limited food availability and poor host physiological condition limits resources available to pathogens.

There is a trade-off between oyster growth and meat condition, and mortality risk, where improved growth and metabolic rates of the host (i.e., high energy) in turn amplify replication of pathogens, and intensify infections leading to mortality, e.g., ostreid herpesvirus (OsHV-1) in Pacific oysters *Crassostrea gigas* under laboratory challenge conditions (Pernet et al. 2019). Oysters are typical r-strategists (small in size with fast development and moderate fecundity, but high reproductive success), and the transition to oysters with S-strategy life traits (slower growth, reduced reproductive output, and enhanced tolerance to disease) demonstrated by Egerton et al. (2020) suggests greater energy allocation and investment into enhanced disease response function to combat pathogens.

Oyster meat condition is a good proxy for the energy available to biological and disease processes (Michael et al. 2022b). In any one year, meat condition probably reflects food availability, ability to feed, and reproductive activity over the previous spring and summer. Meat condition data from the OYU 5 fishery (Figure 12) suggests that oyster mortality caused by *B. exitiosa* is highest in years of high meat condition, with a strong correlation (Pearson rho) of 0.61 ($p \leq 0.01$). High food availability, good feeding conditions, and good host physiological condition provide high energy resources available to pathogens, i.e., years with high meat condition and thereby high energy levels coincide with high prevalence of *B. exitiosa* infection and high oyster mortality, and years with low meat condition coincide with low prevalence and low mortality. Additionally, Hine (1991a) suggested a link between an increase in host energy available to pathogens resulting from an increase in lipids from the reabsorption of unspawned ova and the intensification of *B. exitiosa*. This intensification of *B. exitiosa* increases the production of host haemocytes as the host mounts an immune response to infection, thereby draining host energy (Hine 1991b). Coincidentally, high meat condition years also coincide with low larval production and recruitment (low reproductive output), and this raises questions around spawning cues and triggers for the reabsorption of ova. Such events may result in low recruitment and high oyster mortality caused by *B. exitiosa* in the same summer (Figure 12). The percentage of the recruit-sized population killed by *B. exitiosa* each year, percentage fatal infections, and percentage new clocks (oyster shells from recent mortality) follow similar trends to high meat condition and opposite trends to recruitment (numbers of competent larvae). The percentage fatal infection is tightly correlated to the number of recruit-sized new clocks, Kendall's rank correlation tau 0.78, $p < 0.001$.

In any one oyster season, there is variation in meat condition both within and between vessels. During oyster seasons when meat quality is high, both within and between vessel variation in meat condition is relatively low. When meat condition is low, variation is high (Figure 12). Some of this variation is driven by individual vessel fishing locations (Michael et al. 2022b).

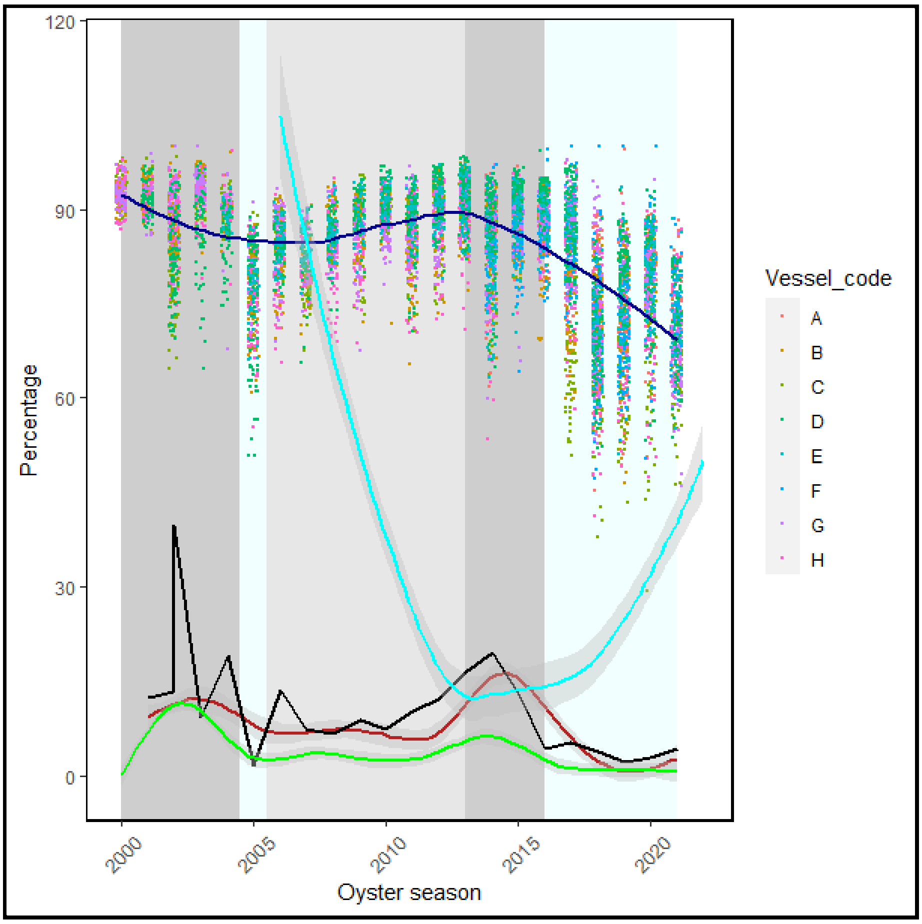

Figure 12: Scatter plot of the daily percentage of first grade oysters (i.e., those with a high level of meat condition) landed daily, for years 2000–2021 by each vessel. Each vessel (Vessel_code) is plotted in a separate colour (see legend). Dark blue line is a loess smoother applied to all data from all vessels each year. Filled grey vertical strips show the period of heightened oyster mortality caused by *Bonamia exitiosa*, categories: low (0.1–4.9%, light blue), moderate (5.0–9.9%, light grey), and high (greater than 10%, dark grey) of percentage annual mortality. Cyan line is the loess smoothed percentage recruitment per collector per year, as a percentage of the 90th percentile of all collector counts, overall years, those few percentages above 100% scaled down to 100% (2006–2022). Black line is the percentage of the recruit-sized population killed by *B. exitiosa* each year, the red line is a GAM smoothed percentage fatal infection, and the green line a GAM smoothed percentage new clocks (oyster shells from recent mortality).

3.1.2.5 Effects of climate variables on oyster mortality caused by *Bonamia exitiosa*

The Bluff Oyster Management Company Ltd initiated a programme to monitor seawater temperatures in 2021, using wet tags (ocean temperature and pressure sensors) provided by the Moana Project[5] funded by the Ministry for Business, Innovation and Employment. Temperature data are automatically transmitted to a remote database. A wet tag fitted to the survey dredge showed temperature varied < 4 °C between the surface and the seabed. Wet tags were also fitted to spat collectors and deployed across the fishery area (Figure 13) for the duration of spat monitoring (November 2021–February 2022). The bottom temperature profiles recorded over this period show variation in bottom temperature, especially from mid-January 2022, that may reflect the effects of a large weather system (Figure 14). Because of these differences, all the wet tags deployed together at a site by Dog Island found temperature records between wet tags were very similar (Figure 15). Although in situ recording of temperature is likely to give the most accurate data for Foveaux Strait, satellites derived SST has high

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[5] https://www.moanaproject.org/temperature-sensors

utility given it can be extracted from different regions in Foveaux Strait, and at high frequency for a long time series back to mid-2002.

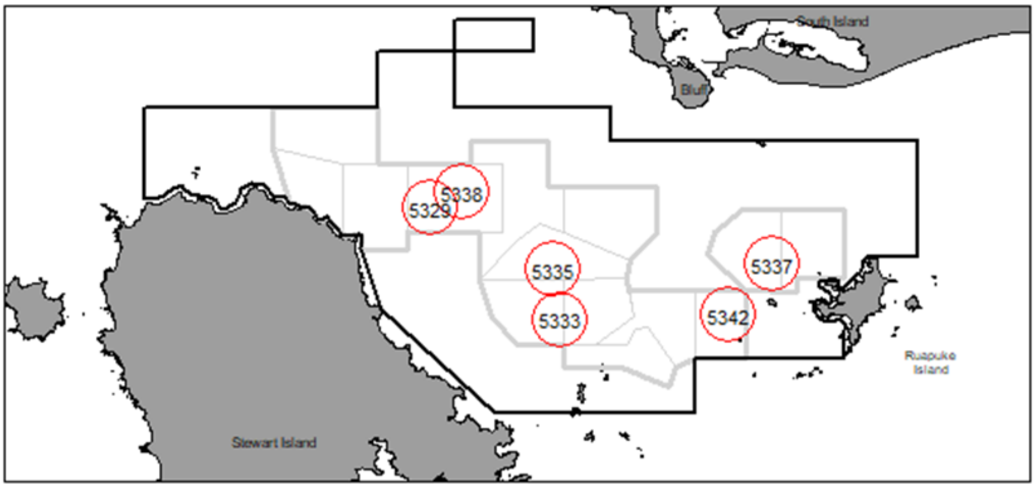

Figure 13: The six site sites where wet tags were deployed on spat collectors between November 2021 and February 2022.

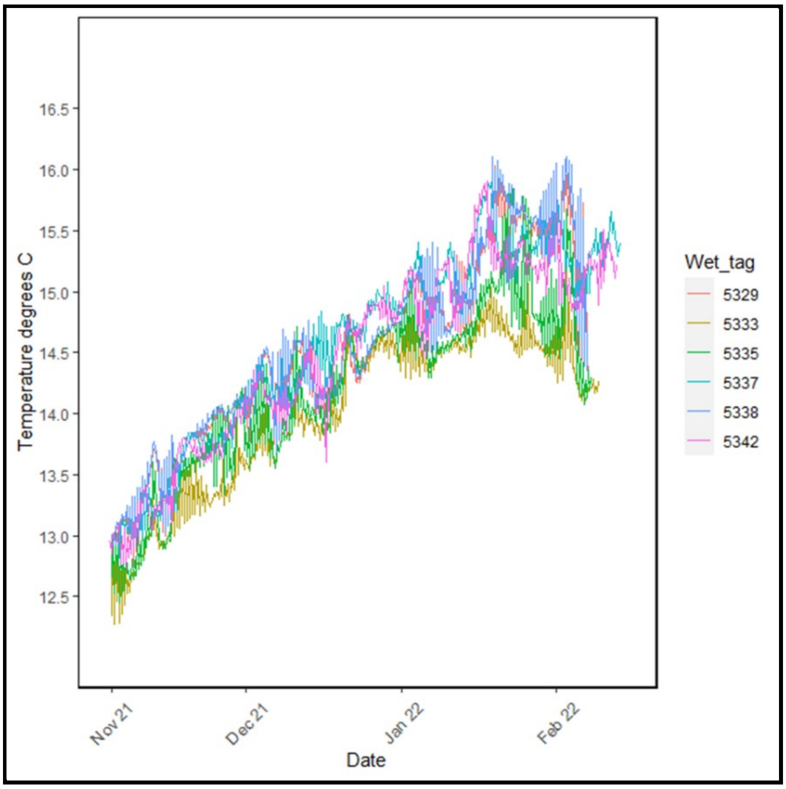

Figure 14: The temperature recordings from wet tags on six spat collectors between November 2021 and February 2022.

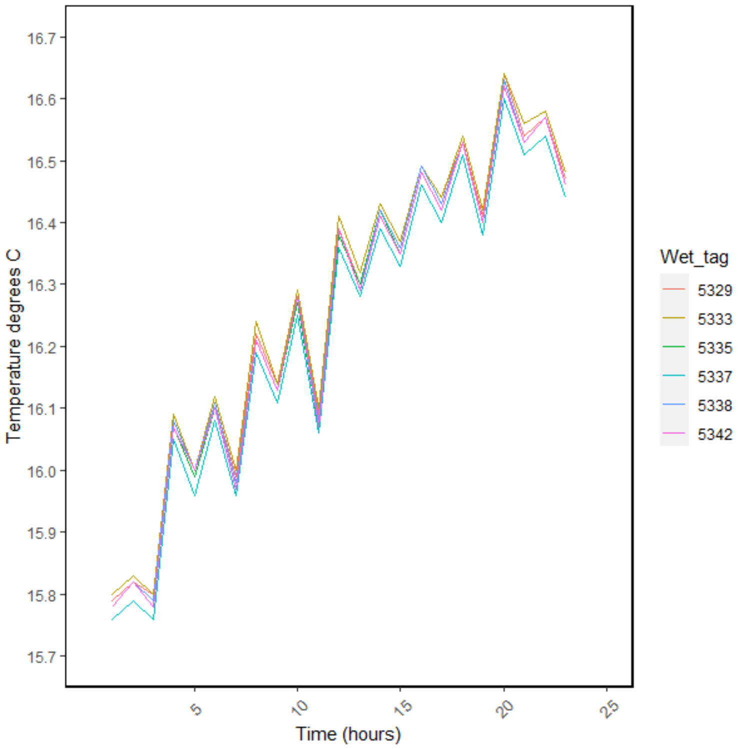

Figure 15: The temperature recordings from all six wet tags deployed to a site at Dog Island over a 24-hour period in February 2022.

Climate anomaly data for sea surface temperature (SST), chlorophyll a (CHL), and Total Suspended Solids (TSS) are shown in Figure 16. Higher than average summer and autumn temperatures (SST, panel a, Figure 16) occur during periods of low oyster mortality caused by *B. exitiosa* and are also associated with higher reproductive success, and lower meat condition (i.e., energy) the following winter (Figure 12). Years where SST anomalies in the summer and autumn are near long-term average or below are associated with years of moderate and high mortality. Periods of mortality occur when winter SST anomalies on average are similar to or higher than summer SST anomalies. Primary production (CHL, panel b, Figure 16) fluctuates around the long-term average without trend, except for 2019 and 2020 when winter, spring, and summer production was relatively high. There may be a disconnect between food availability and the ability of oysters to feed. CHL does not appear to have a strong relationship with mortality, except for periods of moderate and high mortality which are proceeded by years of seasonal low summer and autumn CHL. The correlation between SST and CHL in any given year is insignificant, Kendall's rank correlation tau -0.21, p = 0.55. Total suspended sediment (TSS, panel c, Figure 16) includes both algal (phytoplankton) and non-algal particulates and also fluctuates around the long-term average without trend.

Trends in the data suggest relationships between disease mortality and climatic variables, such as SST. However, the likelihood of complex interactions, and a relatively short time series of data with only two cycles of high and low oyster mortality caused by *B. exitiosa*, suggest that the reliability of Conditional Random Forest models and generalised linear models is unknown. Additionally, the relatively short time series of climatic, fishery, and disease data constrain any robust analysis. Candidate variables for these models were identified from MODIS-Aqua data products using Kendall's rank correlations (see Figure A3.2–A3.5, Appendix 3). Ranked variable importance measures (VIMs) for variables 5th and 95th percentile of the Z2 pressure differential, 95th and average M1 pressure differential, 5th and 95th Southern Oscillation Index (SOI), primary production (CHL), and temperature (SST) to predict percent fatal infections from *B. exitiosa* in recruit-sized oysters are given in Table 2. Ranks from variable importance measures (VIMs) and proxy ‘‘effect sizes’ (the percentages of effects VIM%) are reportedly robust. The most important variables were global climatic factors SOI, M1, and Z2 (Table 2).

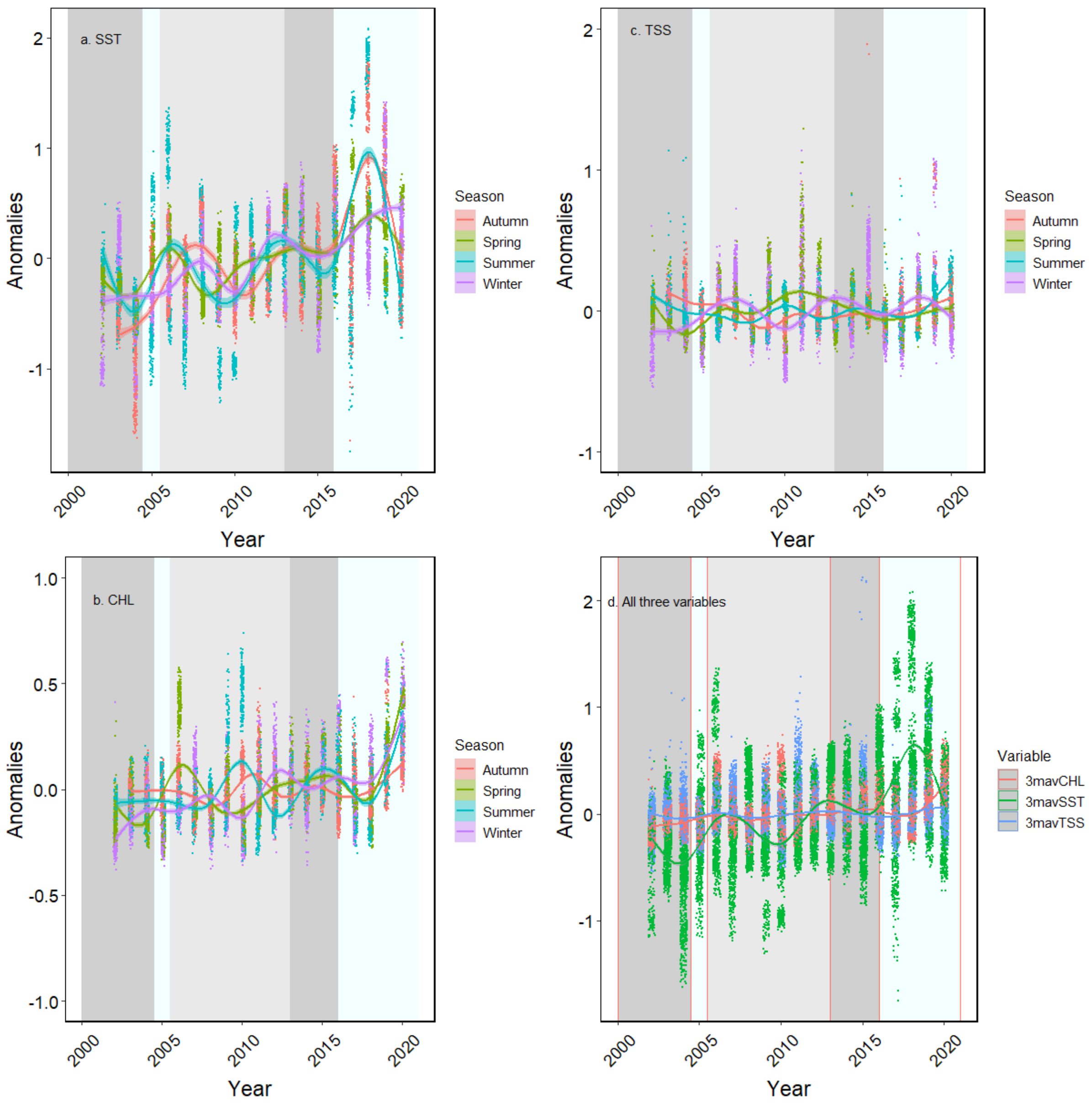

Figure 16: Climate anomalies by year and season plotted for sea surface temperature (a. SST), primary productivity shown as chlorophyl a (b. CHL), total suspended solids (c. TSS), and all climate variables together (d.). Trend lines are coloured by season, data smoothed using GAM. Filled grey vertical strips show the period of heightened oyster mortality caused by *Bonamia exitiosa*, categories: low (0.1–4.9%, light blue), moderate (5.0–9.9%, light grey), and high (greater than 10%, dark grey) of percentage annual mortality. The red line is a GAM smoothed percentage fatal infection, and the green line a GAM smoothed percentage new clocks (oyster shells from recent mortality).

The SOI is associated with El Niño (SOI ≤ -0.5) and La Niña (SOI ≥ 0.5) climate patterns (Figure 17). There is no definitive pattern between SOI and oyster mortality caused by *B. exitiosa* (Figure 17). Generally, but not always, mortality was highest in periods when the Southern Oscillation Index was increasing from negative values (2000—04 and 2010–15), i.e., from a strong El Niño; however, mortality caused by *B. exitiosa* has remained low between 2018 and 2022 when the SOI is decreasing towards negative values.

During El Niño events, winds are stronger or more frequent from the west in summer, from the south in winter, and south-westerly winds in the spring and autumn. El Niño events are known to enhance upwelling off the west coast of the South Island (Hurst et al. 2012) and thereby increase food for oysters in the water column. North-easterly winds are common during La Niña events and are characterised by warmer than average sea temperatures. Periods of high oyster mortality from *B. exitiosa* tend to occur following El Niño events and increasing SOI; and both decrease following La Niña events when SOI is decreasing (Figure 17).

Table 2: Ranks of the relative variable importance (VIM) of numbers of recruit-sized new clocks per tow (NC_rec), 5th and 95th percentile of the Z2 pressure differential (Z2_5 and Z2_95), 95th and average M1 pressure differential (M1_95 and M1_AVG), 5th and 95th Southern Oscillation Index (SOI)(SOI_05 and SOI_95), primary production (CHL), and temperature (SST) to predict percent fatal infections from *B. exitiosa* in recruit-sized oysters using cforest (Hothorn et al. 2006). Variable importance measure (VIM) and the percentage of all importance measures combined as a proxy for effect size (VIM%). Sensitivity analyses give changes to VIM resulting from dropped variables. '-' denotes factors dropped from analysis.

VARIABLE	VIM	VIM%	VIM	VIM%
NC_REC	17.51	21.80	–	–
Z2_95	15.67	19.52	24.74	37.69
M1AVG	15.08	18.77	26.72	40.70
M1_95	14.00	17.38	–	–
Z2_5	7.33	9.13	–	–
SOI_95	5.11	6.37	10.03	15.29
SOI_05	4.77	5.94	–	–
CHL	0.50	0.63	1.96	2.98
SST	0.36	0.45	2.19	3.34

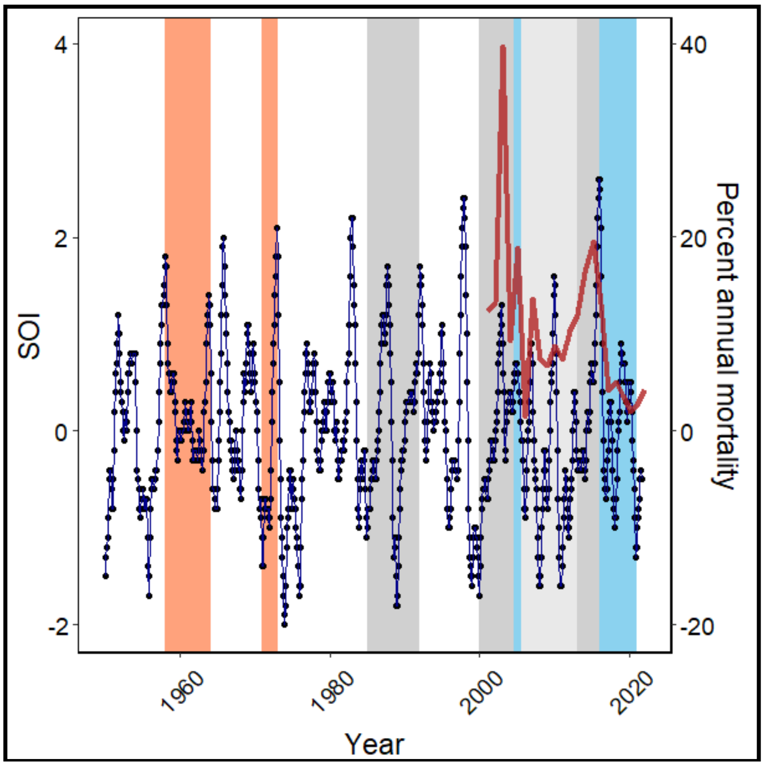

Figure 17: Southern Oscillation Indices by year 1949 to 2021. Filled polygons show periods of heightened oyster mortality. The salmon-coloured vertical strip 1958–1964 shows a period of disease mortality attributed (probably erroneously) to the digenean trematode *Alcicornis* (previously *Bucephalus*) *longicornutus* (Howell 1967), but possibly *Bonamia exitiosa*, and another suggested heightened mortality period 1968–1972 when catch rates inexplicably fell to between 6.6 and 7.7 sacks per hour (Dunn 2005b). Periods of oyster mortality caused by *B. exitiosa* 1985–2016 are shown at three mortality categories of percentage annual mortality: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), and high (greater than 10%, dark grey), and no detected Bonamia mortality shown in white. The red line shows percentage annual mortality of recruit-sized oysters.

The connection between SOI and sea surface temperatures is not well understood (Stanton 2001), as cited by Hurst et al. (2012); however, cross correlation analysis between the smoothed SOI and SST data from Leigh in northern New Zealand shows a coefficient of 0.62 (see figure 11 of Hurst et al. 2012). The El Niño phase of the Southern Oscillation (ENSO) tends to produce increased westerly and south-westerly winds, cooler sea surface temperatures, and enhanced upwelling off Fiordland and western Foveaux Strait. This has been found to be related to increased nutrient flux and phytoplankton growth in these areas (Hurst et al. 2012). Periods of enhanced westerlies, with associated cooler air and sea temperatures, an enhanced west-east precipitation gradient (wetter than normal in the west and south, and drier than normal in the east and north). Increased rain in south-western New Zealand increases freshwater input into Foveaux Strait via Fordland and the Waiau River in Southland, further increasing nutrient input. There were significant correlations with SOI including M1 (r=0.25, p=0.035), CHL (r=0.29, p=0.012), and SST (r=-0.34, p=≤0.01.

Figure 18 shows M1 and Z2 pressure indices by season. Z2 is the monthly mean sea level pressure difference between Christchurch and Campbell Island and measures (approximately) the strength of the westerly wind that may affect SST, CHL, and TSS. M1 measures differences between Hobart, Australia, and the Chatham Islands. A positive M1 means more southerly winds and a negative value indicates more northerly winds that may also affect both SST and CHL (Hurst et al. 2012). Periods of high oyster mortality caused by *B. exitiosa* that appear to coincide with both M1 and Z2 indices are neutral (near 0), i.e., one index trending from positive to negative while the other trends from negative to positive (Figure 18).

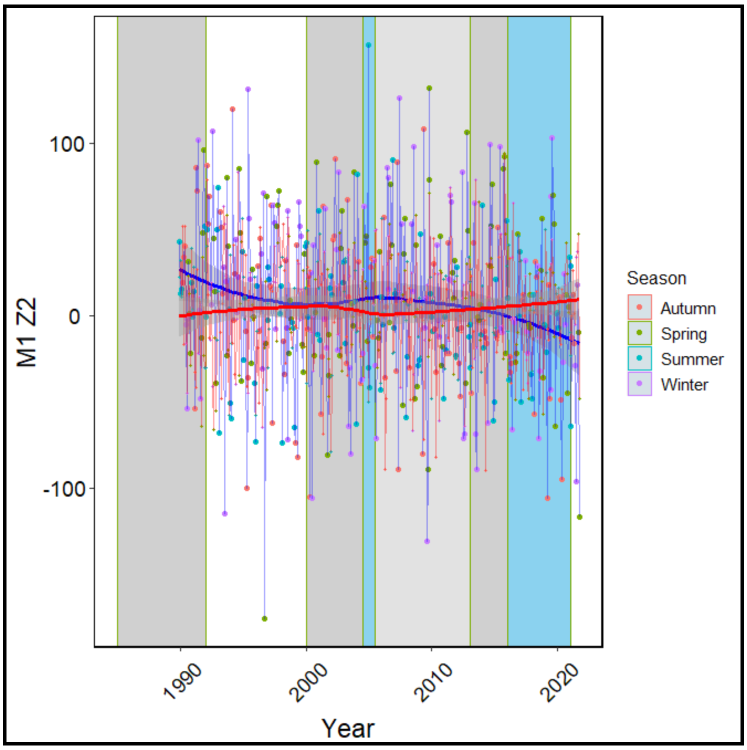

Figure 18: Meridional (M1 southerly wind, blue line) and Zonal (Z2 westerly wind, red line) 'Trenberth' pressure indices by year and season. Z2 is the monthly mean sea level pressure difference between Christchurch and Campbell Island and measures (approximately) the strength of the westerly wind that may affect sea surface temperature (SST), chlorophyl (CHL) and Total suspended solids (TSS) as measures of primary production. M1 measures differences between Hobart and the Chatham Islands. A positive M1 means more southerly winds and a negative value indicates more northerly winds that may affect both SST and CHL (Hurst et al. 2012). Periods of *Bonamia exitiosa* mortality1985-2016 are shown at three mortality categories of percentage annual mortality: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), and high (greater than 10%, dark grey), and no detected Bonamia mortality shown in white.

Generalised linear models with factor means, 5th and 95th percentiles (SST, CHL, Z2_95, Z2_5, SOI_05, SOI_95, M1_95, M1avg), and their interactions were modelled to predict fatal infections. All models showed poor fits with sensitivity analyses suggesting overfitting of data, and so results are not reported.

3.1.2.6 Reproduction and recruitment

Recruitment to the population and the fishery is a fundamental measure of fishery productivity. The OYU 5 fishery has shown a continued ability to produce high levels of recruitment to the population (spatfall) that has driven relatively quick rebuilding of the oyster stock. High recruitment to the populations has occurred after each mortality event caused by *B. exitiosa* (epizootic), when spawner stock size is low; and these events demonstrate that the nature of essential habitat for successful recruitment still exists, that the stock is productive, and can rebuild from low spawner densities. However, when oyster spawner densities and population sizes are high, recruitment can be very low. Several factors such as oyster condition, climatic variables, and the effects of pathogens on reproductive processes probably interact to reduce recruitment to the population. Thereby, factors other than spawner densities and essential habitat may play key roles in driving the variation in recruitment. See Michael et al. 2022b for detailed discussion.

Variation in the recruitment to the population

Several characteristics of the reproductive biology of *O. chilensis* in Foveaux Strait have the potential to cause substantial variations in annual recruitment to the population (see Figure 4) and thereby to the fishery. These characteristics include gametogenesis and synchrony in the release of male and female gametes, levels of brooding (fertilised larvae) in the population and extent of larval development, the dispersal of larvae, and the settlement of larvae and survival of spat. Oyster condition (energy levels), oyster densities and size structures, climatic factors, and pathogens all reportedly contribute to successful recruitment.

Gametogenesis and synchrony in the release of male and female gametes

Temperature and food rations have marked effects on oyster gametogenesis (Westerskov 1980, Buroker et al. 1983, Joyce et al. 2015). *Ostrea chilensis* produces large, lecithotrophic (maternally provisioned) ova; gametogenesis requires high levels of energy to develop female gametes. Temperature cues are thought to initiate gametogenesis. Temperature minima (below 12 °C) synchronize female spawning in *O. chilensis* (Jeffs 1998a) and initiate a switch in energy utilisation from somatic and shell growth to glycogen stores and maternal provisioning in *O. edulis* (Joyce et al. 2013). However, low temperatures may increase variability in synchrony amongst male and females (Jeffs 1998a, Jeffs 1998b, Jeffs & Hickman 2000, Joyce et al. 2015). At high temperatures (≥ 20 °C), the gonad cycle may advance rapidly and asynchronously to phagocytosis, and thereby reduce fertilisation and brooding (Jeffs & Hickman 2000).

Synchronized spawning occurs when sperm is released into the water at the same time when viable ova are present in the mantle cavity of female and hermaphrodite oysters. Asynchronous gonadal development and spawning of males and females reduce fertilisation success (Joyce et al. 2015). A rapid increase in temperature of about 2 °C in September–October initiates spawning. Joyce et al. (2015) suggested a spawning threshold 17–18 °C for *O. chilensis*. Ripe ova are transferred to the inhalant chamber of the mantle and spermatozoa into the exhalent chamber of the mantle. Sperm from neighbouring oysters is drawn through the inhalant chamber for fertilisation of the brood. Self-fertilisation is possible (Jeffs 1998a).

It is not known whether individual oysters spawn as either males or females each year, or how synchronous the release of sperm is with the presence of viable ova.

Brooding and larval development

Levels of brooding are a key productivity indicator as they determine the levels of competent larvae for recruitment to the population. Brooding occurs throughout the year and consistently peaks in November–December in Foveaux Strait. Brooding period (Chaparro 1990, Toro & Morande 1998) and the stage of development when larvae are released (Joyce et al. 2015) are affected by temperature.

Larval size affects settlement success (Cranfield & Michael 1989, Chaparro 1990, Utting et al. 1991). *Ostrea chilensis* in Foveaux Strait exhibits the extreme end of brooding strategies in Ostreinae (flat oysters). Large (448 to 541 µm) larvae (Cranfield & Michael 1989) brooded to pediveliger with eyespots (Hollis 1962, Stead 1971a) are fully competent and ready to settle immediately on release (minutes to hours) (Cranfield 1979, Westerskov 1980). Release of smaller larvae (~230 µm) has been reported from hatchery production (Joyce et al. 2015). Larvae can feed during development to boost the energy available for metamorphosis and settlement.

The percentages of brooding-sized individuals brooding in Foveaux Strait was between 7% and 18% in the 1960s and 1970s (Hollis 1962, Stead 1971a, Cranfield 1979, Jeffs & Hickman 2000) and 1–2% in 1996–2000 (Bluff Oyster Enhancement Company unpublished data). The decline in brooding percentages occurred post the 1985 *B. exitiosa* epizootic; however, no link has been established.

As larval size increases with development, a small proportion of larvae may be forced out of the pallial cavity by space limitation caused by growing larvae and may be released early (Cranfield & Michael 1989) or ejected from the mantle. Whether significant percentages of broods are released early or ejected is not known. Larvae released early continue to develop ex-parent to full competency (Hickman 2000). Larvae can disperse throughout the fishery and may be advected out of the fishery area by the strong tidal currents.

Recruitment to the oyster population in Foveaux Strait differs to other commercial oyster fisheries in that it is not limited by settlement substrata. Within a given year, spatial patterns of spat settlement are similar across the commercial fishery area (Michael & Shima 2018). Larval availability is not related to spawner densities (Michael & Shima 2018). Survey data show high spatfall translates to large year class cohorts and eventually high recruitment to the commercial oyster fishery. The relative abundance of competent larvae available for settlement is monitored annually by a Bluff Oyster Management Company Ltd spat monitoring programme. Almost all settlement in Foveaux Strait occurs between November and February (Michael & Shima 2018).

Current brooding percentages are not well estimated. Even if brooding percentages have declined since the mid-1980s, recruitment to the oyster population is high enough to drive rapid rebuilding of fishery areas affected by high levels of disease mortality (see Figures 19 and 20).

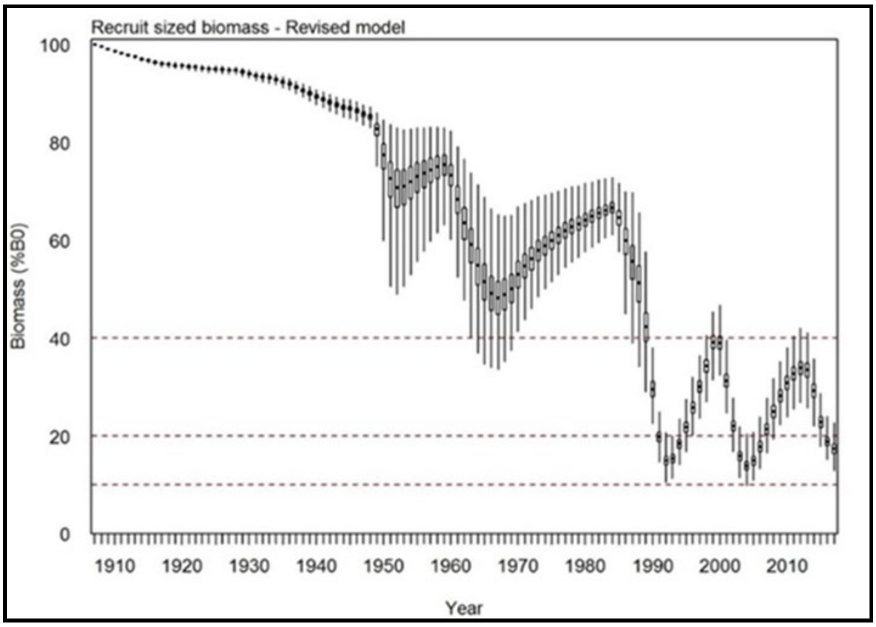

Figure 19: Recruit-sized (legal-sized oyster) population size as a percentage of B_0 (the population before fishing began) from the last (2017) Foveaux Strait oyster stock assessment. Horizontal dashed lines show 40%, 20%, and 10% B_0. The rapid declines of population size from three *Bonamia exitiosa* epizootics can be clearly seen from 1985, 2000, and 2011. Figure from Large et al. (2021).

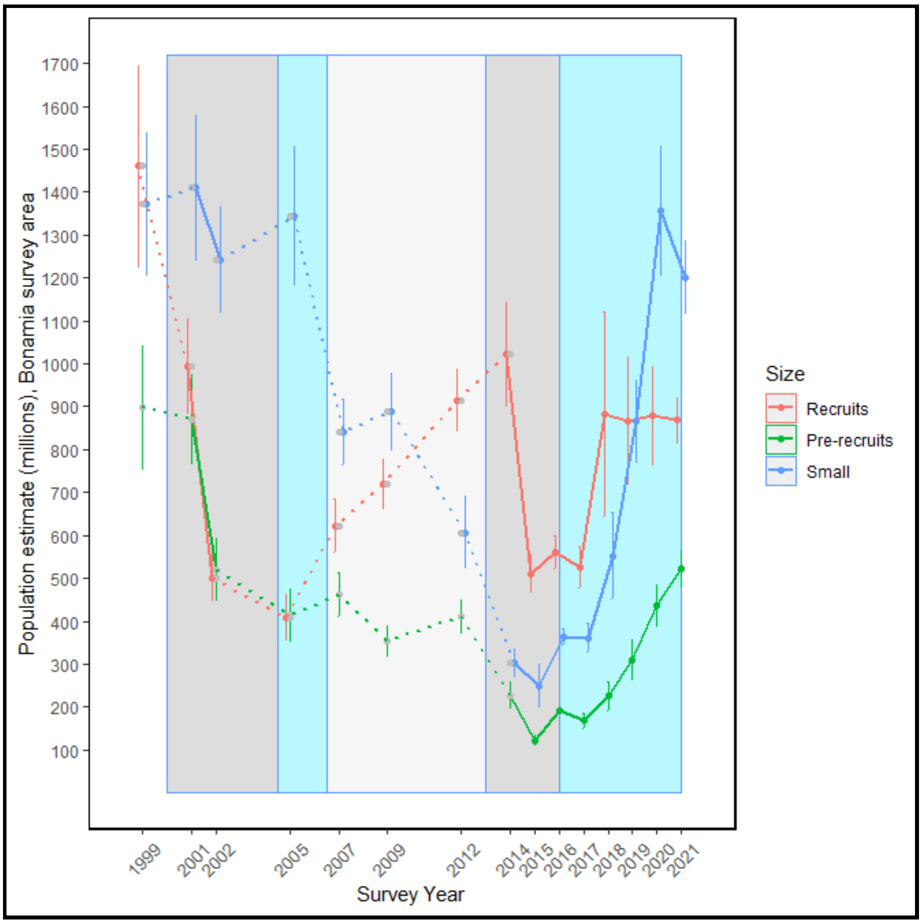

Figure 20: Mean population sizes with 95% confidence intervals from survey s.d. (solid lines) for recruit-sized (red), pre-recruit (green), and small (blue) oysters in the OYU 5 stock assessment survey area between 1999 and 2021 from stock assessment and Bonamia surveys. Only five survey tows were undertaken in 54% of the stock area during Bonamia surveys, and these estimates are likely to be low. The trends in mean population sizes for years with no surveys between 1999 and 2021 have been interpolated (dotted lines). Periods of oyster mortality caused by *Bonamia exitiosa* 1999–2021 are shown at three mortality categories of percentage annual mortality: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), high (greater than 10%, dark grey), and no detected Bonamia mortality shown in white.

The putative effects of pathogens on energy partitioning and gametogenesis

Pathogens may have a range of effects on oyster reproduction from direct parasitism of gonad material to the indirect effects of reducing the energy available for gametogenesis and maternal provisioning (Egerton et al. 2020). Parasitism by the trematode *Alcicornis longicornutus* castrates the host (Howell 1967). Apicomplexan infections may reduce energy available for gametogenesis, e.g., an apicomplexan has been shown to disrupt reproduction in the Iceland scallop *Chlamys islandica* (Kristmundsson et al. 2011).

A hypothesis that pathogens compete with the host and other pathogens for the host's energy is proposed by Michael et al. (2023b). Concurrent, non-fatal infections may cause a reduction in, or complete cessation of, gametogenesis through energy limitations.

The two principal alternative hypotheses discussed by Michael et al. (2023b) are:

1. high meat condition as a proxy for high energy reserves of hosts lowers their susceptibility to disease, or
2. high levels of energy are used to intensify replication of pathogens, and intensifying infections leading to mortality.

Hypothesis 2 is supported by the fisheries data (see Figure 12). Energy partitioning in oysters can locally adapt in response to pathogens. European flat oysters *O. edulis* grown in areas in Ireland where *Bonamia ostreae* is enzootic grow more slowly with lower reproductive activity than oysters from areas without *B. ostreae* (Egerton et al. 2020). A decrease in the percentage of brooding oysters was recorded after the 1985 *B. exitiosa* epizootic in Foveaux Strait. The drivers of this change are conceivably from a difference in energy partition or trade-offs associated with a response to disease. Data demonstrating a change in energy partitioning or cues for switching energy to and from reproductive processes are scarce and are an important knowledge gap in our understanding of *O. chilensis* in Foveaux Strait.

All pre-recruit and most recruit-sized oysters sampled from Foveaux Strait in 2020 infected with *Alcicornis longicornutus* were castrated. *Alcicornis longicornutus* prevalence across the fishery is not known. Howell (1967) reported a prevalence of up to 40% in Foveaux Strait in the 1960s. *Alcicornis longicornutus* prevalence is likely to be strongly influenced by stargazers (*Kathetostoma giganteum*) (Howell 1966), the putative definitive host of these parasites, which are at times common in Foveaux Strait. Apicomplexan X and *B. exitiosa* are also thought to severely affect gametogenesis (Hine 2002) and, thereby, recruitment.

The contribution of biotic and abiotic factors to recruitment variability

Recruitment to the oyster population indicated by oyster spat settlement was negatively correlated to spawner density ($r=-0.57$, $P \leq 0.01$). None of the climatic variables alone were correlated to oyster recruitment.

Ranks from variable importance measures (VIMs) and proxy effect sizes (VIMs) in Conditional Random Forest models show spawner density as the most important predictor of recruitment to the oyster population (Table 3). Dropping spawner density highlighted the importance of interactions between oyster meat quality and oyster mortality from *B. exitiosa* (see Figure 12 and Table 3), storms, and SST and CHL anomalies. Dropping the pressure indices M1 and Z2 increased the importance of meat quality, mortality, and SST (Table 3).

Table 3: Ranks of the relative variable importance (VIM) of variable spawner densities (Spawner), mortality caused by *Bonamia exitiosa* (Mortality), oyster meat quality (percentage grade 1 oysters in catch (Quality)), atmospheric pressure indices Z2 and M1, and sea surface temperature (SST) and chlorophyll (CHL) anomalies to predict recruitment to the oyster population using *cforest* (Hothorn et al. 2006). Variable importance measure (VIM) and proxy for effect size (VIM%). Sensitivity analyses give changes to VIM resulting from dropped variables.'-' denotes factors dropped from analysis.

Variable	VIM	VIM%	VIM	VIM%	VIM	VIM%
Spawner	78373.86	80.3	–	–	–	–
SST	4982.01	5.1	4912.46	16.4	9004.91	19.9
CHL	4135.34	4.2	2148.24	7.2	3775.08	8.4
Mortality	3551.79	3.6	7676.02	25.6	12894.42	28.5
Storms	-2627.09	2.7	-4255.86	14.2	-6148.39	13.6
Z2	-1557.52	1.6	-2043.02	6.8	–	–
M1	1337.23	1.4	1225.46	4.1	–	–
Quality	990.74	1.0	7743.75	25.8	13381.77	29.6

Spat data include two periods of high settlement and a prolonged period of low settlement. The low numbers of cycles from low to high are too few to model the contributions of variables describing long-term climate patterns such as SOI.

The bio-erosive sponge *Cliona* spp. is widespread in Foveaux Strait oysters. A study by Michael et al. (2022c) investigated the effects of *Cliona* spp. on *O. chilensis* reproduction and growth). In the US, *Crassostrea virginica* colonised by *Cliona celata* diverts significant energy from shell and somatic growth, and presumably reproductive processes, to shell maintenance and repair (Carroll et al. 2015).

There was a negative correlation between *C. celata* infestation and *C. virginica* meat condition. Michael et al. (2022c) did not detect any effects on reproduction in their study; however, oyster meat quality was inversely related to *Cliona* colonisation. Oysters with higher *Cliona* colonisation had significantly lower meat condition indices, especially recruit and pre-recruit sizes ($p < 0.001$). Generally, the bio-erosive sponge *Cliona* spp. is more prevalent in the shells of live oysters in the western and southern fishery areas, and meat quality can be lower in these regions (BOMC data).

3.1.2.7 Growth

Growth rates determine the transition of small oysters to recruit and commercial sizes, and thereby contribute to the productivity of the stock. Growth rates of *O. chilensis* are not well estimated and constitute an important knowledge gap for estimating productivity and for stock assessment. Growth was last estimated in the 1970s (Dunn et al. 1998). There are no data on interannual and spatial variation in growth. Growth increment data are from 1970 and 1981, from caged experiments at a single site in the eastern fishery area. Growth is highly seasonal, with all growth occurring over the summer. Marked differences in growth (i.e., 'good' and 'bad' years) are apparent from the observations of summer resource surveys (author's observations). Better estimates of growth will greatly benefit OYU 5 stock assessments because low growth can be problematic as the proportion of large oysters in the population size structure informs the upper limit to B_0 in Markov chain Monte Carlo estimation. Uncertainty in the estimates of B_0 have flow-on effects in the interpretation of stock status and spawning population size reference points used for management of the fishery.

Unlike some other species of oysters (e.g., *O. edulis*, Richardson et al. 1993), oysters from Foveaux Strait cannot be aged from their shells. Growth lines from the umbo do not extend to the shell margins to give size at age (Michael et al. 2000). Without length at age data, stock assessments rely on a length-based model (Fu et al. 2016). Putative spatio-temporal variation in growth makes it difficult to track year class strengths in the population. In summers with large growth increments, small oysters (< 50 mm) may grow through the pre-recruit size group (50–57 mm) to recruit-size (≥ 58 mm). The two-dimensional measure of size used in the stock assessment may overestimate the proportions of sexually mature individuals in the population, with flow-on effects on modelled estimates of disease selectivity (see Michael et al. 2023b).

Different regions of the OYU 5 fishery area have different habitats and environmental drivers and the maximum size of oysters differs; generally, oysters grow to a larger two-dimensional size east to west. Oysters reach maximum size in length and height relatively quickly, and continue to increase in depth, sometimes for many years. Three-dimensional measures of size may better represent size at age, maturity, and disease susceptibility.

3.2 Objective 2: Long-term changes in oyster distribution in relation to habitat

Changes in oyster abundance, localised densities of oysters ('oyster beds'), the distribution of oyster beds, and changes in essential habitat associated with oyster production (see section 2.1) are used to investigate changes in productivity of the OYU 5 stock.

A key measure of how the Foveaux Strait oyster fishery has changed is the change in spatial extent of the fishery area over time. Oyster beds are considered by fishers as local entities, patches of relatively high densities of harvestable-sized oysters separated by areas of low oyster density or no oysters. At times several of these 'patches' may also be considered an 'oyster bed'. Allen & Cranfield (1979) and Stead (1971b) suggested the oyster fishery comprised more than 50 discrete oyster beds found in depths of 20–50 m.

The navigation issues of early surveys (1906, 1926, and 1945) are illustrated by a quote from Young's report of the 1926 survey given by Sorenson (1968), "*The Government survey of 1906 tested the Strait pretty thoroughly as far as commercial working goes, but it is worthy of mention that from the positions marked they missed the Saddle Bed altogether. They also show an extensive bed, further out which has* *yet to be rediscovered*". Location and extent of named beds such as the Saddle Bed occurred in different locations on maps (Knight 2008).

Fishers' data such as catch and effort landings data have been recorded at the spatial scale of the Foveaux Strait oyster statistical reporting areas since 1960 (see Figure A4.1). Fisher behaviour and not the distribution of oysters determined the early patterns of fishing. The distance from port to fishing areas was important in the early days of the fishery, few vessels rarely ventured to western oyster beds (Sorenson 1968). As sailing cutters were replaced by steam vessels, and then by diesel vessels, daily fishing range increased. The weather and tidal strengths and direction that determine steaming time and affect dredge efficiency determined the areas fished. Historical catch rates and oyster densities are difficult to compare because the minimum legal size (MLS) is defined by the internal diameter of a reference ring that has changed several times over the history of the fishery. The MLS before 1929 was 1.75 inches (44.45 mm), 2.0 inches (50.80 mm) in 1929, 2.125 inches (53.98 mm) in 1941, and has remained at 2.25 inches (57.15 mm, unable to pass through a 58 mm diameter ring) since 1969 (Dunn 2005a). The precise locations where fishing occurred are not well recorded. Since 1985, disease mortality from *B. exitiosa* changed the spatial and temporal distribution of oysters in any one year and thereby the availability of relatively high densities of oysters to fishers. Since 2010, daily catch limits imposed on vessels by processors and fiscal incentives for large-sized oysters and high meat quality often determined the areas fished, and high-grading has reduced the catch rates.

3.2.1 Changes in the distribution of oysters

A historical record of the spatial extent of the oyster fishery is shown in Appendix 4. The original survey maps are shown, because it is not known how accurately they illustrate the location and extent of 'oyster beds'. Figures A4.2–A4.9 (Appendix 4) show that the spatial extent of the fishery has not changed. Figure A4.7 (Appendix 4) shows the footprint of commercial fishing for 2006–2019 is very similar to that of the oyster fishery defined by Stead (1971b) in 1960–1964 (Figure A4.3, Appendix 4). Fine spatial and temporal data to investigate long-term ('generational') changes in oyster distribution are not available.

A Marine Department survey of oysters in Foveaux Strait (Hunter 1906) found that the oyster beds were patchily distributed and extended over 25 miles from 11 miles west-south-west of Waipapa Point to 10 miles east-south-east of Centre Island (Figure A4.2 Appendix 4). Twelve oyster beds were identified ranging in length from 0.5–7.0 miles (down tide) to 0.5–2.0 miles wide, and in depths from 10 to 20 fathoms. Of the 12 oyster beds, the Saddle Bed and West Bed were the largest. Hunter reportedly stated that "*beds at a greater distance than those already located [in the eastern fishery] were never likely to become popular*" (Sorenson 1968). The 1906 survey (16th–30th January) established the extent of the commercial oyster fishery that has remained similar 155 years later (see Appendix 4). Howard (1940) reports that after more than 50 years of intensive fishing, the beds showed no sign of diminishing.

A survey between March 1926 and January 1927 using commercial oyster vessels confirmed the presence of known commercial oyster beds in Foveaux Strait (Sorenson 1968). Some new beds were also discovered by this survey; however, they were generally small in area. Oyster beds considered of commercial importance were those close to Bluff, especially those around Ruapuke Island. Oyster beds to the west were extensive. The West Bed and Saddle Bed reportedly merged with the Port William Bed to the east and Lucky Beach Bed to the west and extended well into the strait. This survey did not reach western and eastern extent of the oyster fishery; however, any oyster beds beyond the survey area were not deemed important as their distance from port and weather conditions probably precluded them being fished. The Saddle Bed and the East Bed were the most productive at that time. The Saddle Bed had the highest catches, but oyster quality was poor. Generally, oyster condition was poorest in August, probably due to spawning. Little has changed in 2022.

The 1945 survey was compromised by navigational difficulties, chart inaccuracies, and uncooperative charter vessels. Most of the time was spent fixing tow positions instead of recording biological data. Only 'worthwhile' catches of oysters were recorded from known oyster beds, catches of oysters were very low outside these areas (Sorenson 1968). These comments suggest that the extent of the fishery was known in the early 1900s.

A summary of surveys 1960–2022 is given in Table A5.1 (Appendix 5). Most of these surveys use a two-phase stratified random design (Francis 1984), which produces the best estimates of population size but are not good for mapping the distribution of oysters. Survey data show the OYU 5 fishery comprises many localised areas with relatively high densities of oysters (oyster beds). The spatial distribution and locations of these oyster beds have remained constant through time. Oyster densities in these localised populations wax and wane, mostly determined by mortality from *B. exitiosa* and by recruitment to the population and the fishery (Figures A4.8 & A4.9, Appendix 4). At low *B. exitiosa* infection and mortality, the oyster population rebuilds quickly in the fishery areas that have been fished for many years, suggesting that any changes in habitat have not reduced the productivity of oysters.

3.2.1.1 Changes in oyster densities

If the spatial extent of the fishery and numbers of oyster beds within it have not greatly changed, any long-term (generational) changes in oyster distribution, regardless of habitat, can be inferred from changes in oyster densities and population sizes. Two key sources of information include fishery independent survey data and fishers' CPUE and logbook data. The earliest reliable surveys of the oyster population were those of Stead (1971b) in 1960–64 and Allen & Cranfield (1979) in 1975–76. These surveys act as a pre-epizootic reference point and are pivotal to investigations of long-term changes in the fishery. However, these data have been standardised for comparability with later standard surveys from 1992. Some issues with their standardisation are discussed below. CPUE reflects fisher behaviour but, at small spatial scales, commercial catch reporting can also provide a measure of localised oyster density. The time series of CPUE data dating back to 1948 requires interpretation and should not be used as standalone proxies for oyster densities. The 1985 *B. exitiosa* epizootic caused a regime shift in the ability of the fishery to rebuild. Because oyster beds are disproportionately affected by mortality, cyclic disease mortality from *B. exitiosa* prevented high oyster densities and population size from rebuilding to pre-epizootic levels.

Surveys

Surveys during 1906–2005 were summarised by Dunn (2005b), updated by Large et al. (2021), and further updated to 2022 in Table A5.1, Appendix 5. Catches from surveys of Stead (1971b) during 1960–1964 (assigned as the 1962 survey by Dunn 2005a) have been adjusted and incorporated into a time series of survey data for stock assessment. Surveys for 1960–1964 estimated the number of recruits (≥ 58 mm), and from 1990 pre-recruit (≥ 50 mm to <58 mm) and small (<50 mm) oysters. Sampling over the time series (1962–2021) used four different dredges; and catches were adjusted to a standard tow length (0.2 nautical mile) from timed dredge tows without vessel speed data and for measured tows using different position fixing systems with different levels of precision. These surveys were undertaken using different designs and areas, with vastly different sampling effort (Table 4). Adjustments include scaling catches to absolute densities using several dredge-specific efficiencies. Mean estimates of dredge efficiency were similar: 0.11 (95% CI 0.08–0.16) for dredge 'E' (Dunn 2005a), 0.16 (95% CI 0.04–0.42) for dredge 'F' (Allen & Cranfield 1979), and 0.17 (95% CI 0.11–0.24) for dredge 'D' (Doonan & Cranfield 1992) (Table 4). These adjusted estimates and dredge efficiencies are used to estimate absolute population sizes, which are a key component of the OYU 5 stock assessment model and are assumed to be comparable.

Surveys pre-1990 are likely to overestimate populations sizes and may have an undue influence on the posterior projections of B_0 and the degree to which the OYU 5 stock has recovered from the 1985–92 *B. exitiosa* epizootic; the '1962' estimate may be a gross overestimate of recruited population size (3059 million, CV 0.21, Dunn 2005a). The volume of recruit-sized oysters in some of the high adjusted catches (Table 4) would not fit in a commercial dredge, let alone any pre-recruit and small oysters, and other bycatch. This survey period coincides with low catch rates in the fishery (6.0–10.6 sacks per hour, 1962–72, Dunn 2005a) and a marked decline in landings between 1962 and 1964 (53.4–73.5 million oysters, Dunn 2005a). A marked decline in the oyster population was reported from 1958 to 1964 by Howell (1967); up to 40% of oysters were infected with *Alcicornis longicornutus*, most of which would have reportedly died. *Bonamia exitiosa* was also identified in preserved oyster tissue in 1964 (Hine & Jones 1994). These anecdotal data suggest the 1962 population size may have been grossly overestimated.

The 1975–76 surveys also used a small dredge and a high level of sampling effort on a relatively small area (~35% of the 2007 stock assessment survey area) of high oyster densities, the commercial fishery area at the time. Adjustments of survey catch are like those for the 1962 survey. However, landings at that time were relatively high (88.8–89.0 million recruit-sized oysters) as were catch rates (10.8–11.9 sacks/hour). The survey estimate of population size was scaled up to the stock assessment survey area and may also be an overestimate because of earlier reports of low densities of oysters beyond the known oyster beds of the time (Sorenson 1968).

The 1962 and 1975–76 surveys (if the mark recapture estimates are omitted, see Dunn 2005a) are the only abundance surveys before the 1985–1992 *B. exitiosa* epizootic. If these surveys overestimate population size, the shift in oyster productivity suggested pre- and post-epizootic may not be as marked as currently given by the OYU 5 stock assessments. Stock assessments assume *B. exitiosa* is an endemic parasite (Hine & Jones 1994) and has caused mortality prior to 1985. The pattern of mortality during1985–1992 (Cranfield et al. 2005) suggests that the *B. exitiosa* epizootic was either a reintroduction, a new infection, or was exacerbated by the introduction or increase in prevalence of another pathogen, e.g., APX (Hine 2002). The continuing mortality from *B. exitiosa* does not appear to have affected productivity (recruitment to the population); however, it has limited the upper level of population size (see Figures 19 and 20).

Surveys between 1960 and 2021 sampled different sized survey areas, with different numbers of stations and with different sized dredges and, it can be assumed, different tow lengths. Dredge details and the numbers of stations sampled are given in Table 4. Catches were standardised to be comparable between surveys and to allow a time series of population estimates to be calculated. Standardised catches for surveys between 1962 (1960–64) and 2021 are binned by numbers of oysters per two categories: zero oysters, 1–99, 100–399, 400–999, 1000–1999, 2000–2999, 3000–4999, and more than 5000 recruit-sized oysters per tow (Table 4). A heat map of oysters in each category across surveys (Figure 21) shows most tows in each of the surveys caught less than 400 oysters per standard tow, with similar densities of oysters across the surveys. Notably the 1960–64 (assigned 1962) survey had a lot of tows with no oysters caught.

Table 4: Summary of adjusted dredge catches from survey tows 1962 (1960–64) to 2021. Catches are binned by number of oysters per tow: zero, 1–99, 100–399, 400–999, 1000–1999, 2000–2999, 3000–4999, and more than 5000 oysters per tow. Numbers in the cells represent the number of tows in each catch bin. Dredge type denotes the survey dredge: 'D' 3.35 m-wide and about 530 kg; 'E' 0.91 m-wide with a rigid mesh catch bag; 'F' 1.25 m-wide, double-bit, and double ring bag; and 'G' 3.32 m-wide, double-bit, and double ring bag and weighing 400 kg.

Year	Dredge	Zero oysters	1–99	100–399	400–999	1000–1999	2000–3000	3000–4999	5000+	Total number of stations towed
1962	E	275	67	89	47	36	9	10	9	542
1975	F	16	237	200	82	4	0	0	0	539
1976	F	15	77	103	78	19	0	0	0	292
1986	F	0	4	17	5	1	0	0	0	27
1987	F	0	24	32	10	1	0	0	0	67
1990	D	61	276	117	48	5	0	0	0	507
1992	D	75	238	87	2	1	0	0	0	403
1993	D	15	101	45	8	0	0	0	0	169
1995	D	20	78	80	28	6	1	0	0	213
1997	D	13	39	47	20	4	0	0	0	123
1998	D	0	5	10	8	7	0	0	0	30
1999	D	10	48	63	64	26	0	0	0	211
2000	D	0	10	38	24	0	0	0	0	72
2001	G	9	45	62	65	16	1	0	0	198
2002	G	8	86	98	35	2	0	0	0	229
2003	G	0	3	8	5	0	0	0	0	16
2004	G	0	14	21	5	0	0	0	0	40
2005	G	2	56	20	2	0	0	0	0	80
2006	G	1	21	21	1	0	0	0	0	44
2007	G	2	81	62	8	0	0	0	0	153
2008	G	1	20	28	5	0	0	0	0	54
2009	G	8	56	48	17	1	0	0	0	130
2010	G	0	5	18	16	3	1	0	0	43
2011	G	0	14	22	13	5	0	0	0	54
2012	G	2	67	55	26	8	0	0	0	158
2013	G	0	11	26	18	1	1	0	0	57
2014	G	0	19	41	11	1	0	0	0	72
2015	G	0	32	33	7	0	0	0	0	72
2016	G	0	28	37	7	0	0	0	0	72
2017	G	8	50	48	8	0	0	0	0	114
2018	G	1	25	31	15	0	0	0	0	72
2019	G	2	23	36	9	2	0	0	0	72
2020	G	1	21	38	11	1	0	0	0	72
2021	G	0	20	27	25	0	0	0	0	72

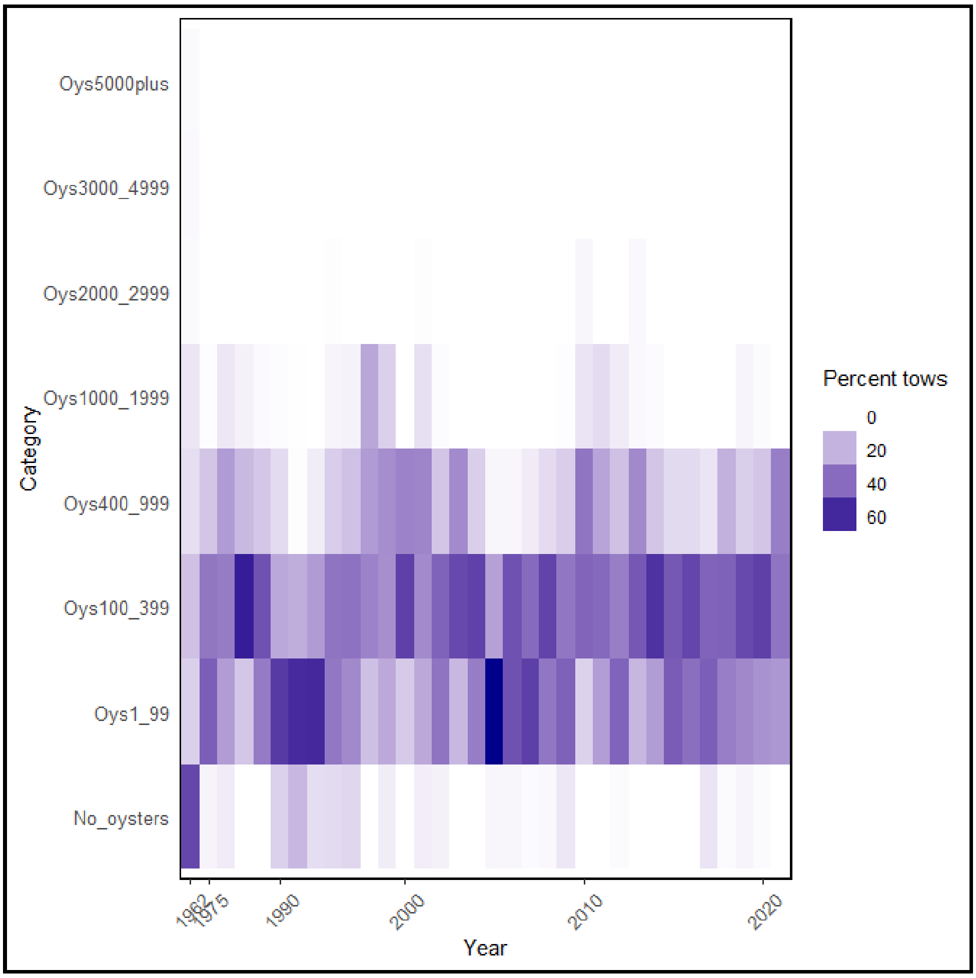

Figure 21: Heatmap of the percentage of tows for each survey between 1962 (1960–64) and 2021, binned by number of oysters per tow (categories): Zero oysters, 1–99, 100–399, 400–999, 1000–1999, 2000–2999, 3000–4999, and more than 5000 per tow. Dredge details and the numbers of stations sampled are given in Table 4.

Given the adjustments and uncertainties above, one simple way of visualising the survey data is to shows how the distribution of individual adjusted dredge catches for each tow, by survey (Figure 22). For this, catches were capped at 2500 per tow, which only affected the 1962 survey data (see rationale above). The 50th percentile range of the boxes in the boxplots shows the relative oyster densities between surveys. The size groups vulnerable to mortality from *B. exitiosa* (recruits and to a lesser degree pre-recruits, Figures 22–24) show recurrent cycles with declines during and immediately after mortality from *B. exitiosa* and increases in trend in periods of absence of disease, as do the population estimates (Figure 20). The ranges of highs and lows before and after the 1985–92 *B. exitiosa* epizootic are similar, unlike the population estimates. Small oysters are not thought to be vulnerable to *B. exitiosa*, unless near a large mortality event and exposed to lethal infection pressure (see Cranfield et al. 2005). Trends in the densities of small oysters (Figure 25) also show similar cyclic trends with mortality from *B. exitiosa* (with a time lag), and low densities of small oysters in 2014–17 following a period of low spat settlement in 2010–14 (Bluff Oyster Management Company data). The numbers (Figure 25) and population sizes (Figure 20) of small oysters increase quickly during periods of low oyster mortality from *B. exitiosa* and low spawner densities. No loss in productivity of the stock can be detected from these data.

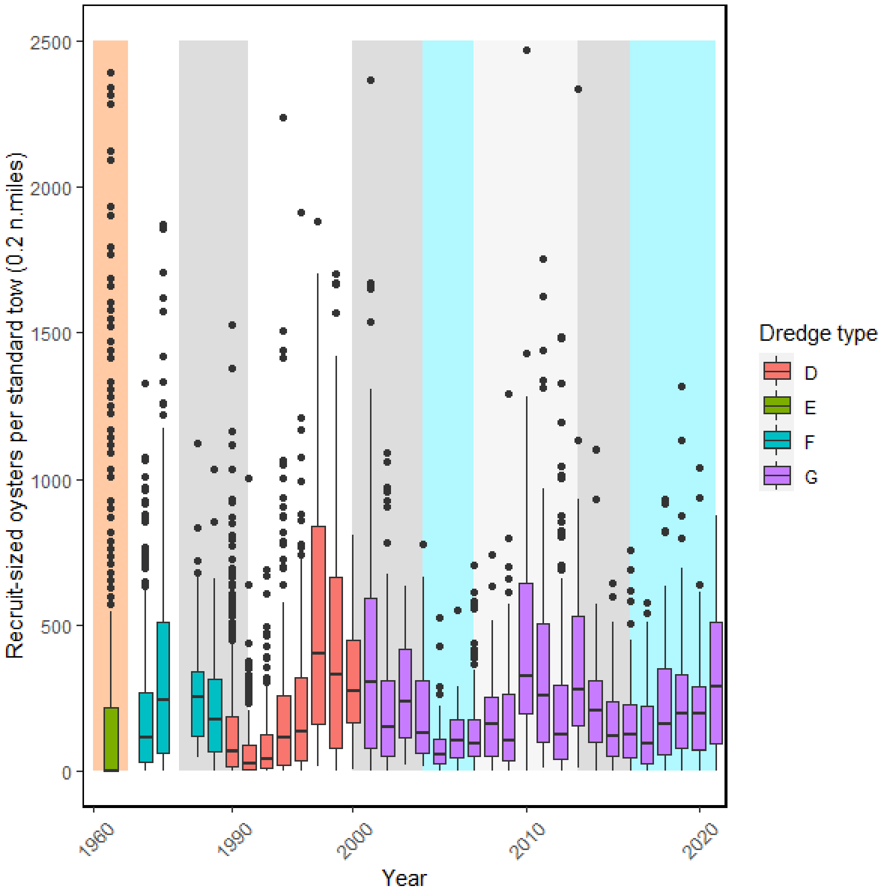

Figure 22: Boxplots of adjusted catches of recruit-sized oysters per tow for each survey between 1962 (1960–64) and 2021. Catches are capped at 2500 recruit-sized oysters per tow. Medians are shown as solid lines, boxes represent 50th percentiles, whiskers 95th percentiles, and outliers as filled black circles. Periods of heightened disease mortality are shown as shaded rectangles. Mortality attributed to *Alcicornis longicornutus* between 1960 and 1964 is shown as a salmon rectangle. Percentage of annual mortality from *Bonamia exitiosa* (1999–2021) is shown at three categories: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), high (greater than 10%, dark grey), and no detected Bonamia mortality is shown in white. Dredge details and the numbers of stations sampled are given in Table 4.

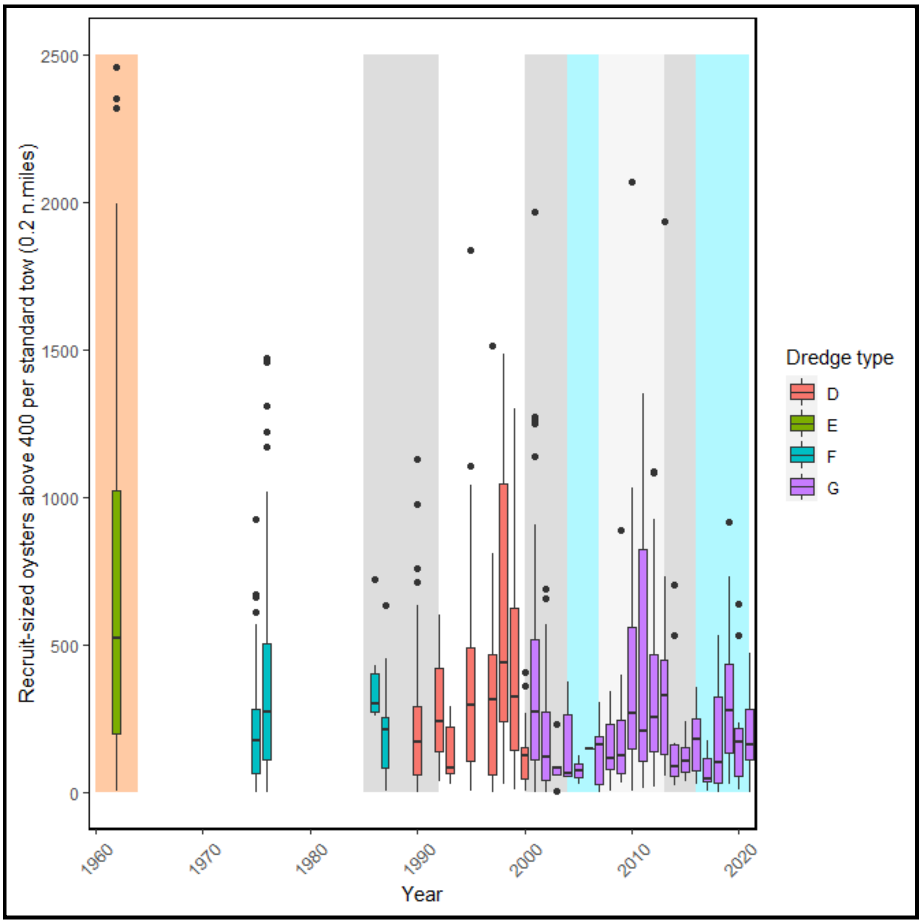

Figure 23: Boxplots of adjusted catches of recruit-sized oysters above 400 oysters per each tow (i.e., commercial densities) for each survey between 1962 (1960–64) and 2021. Catches are capped at 2500 recruit-sized oysters per tow. Medians are shown as solid lines, boxes represent 50th percentiles, whiskers 95th percentiles, and outliers as filled black circles. Periods of heightened disease mortality are shown as shaded rectangles. Mortality attributed to *Alcicornis longicornutus* between 1960 and 1964 is shown as a salmon rectangle. Percentage of annual mortality from *Bonamia exitiosa* (1999–2021) is shown at three categories: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), high (greater than 10%, dark grey), and no detected Bonamia mortality is shown in white. Dredge details and the numbers of stations sampled are given in Table 4.

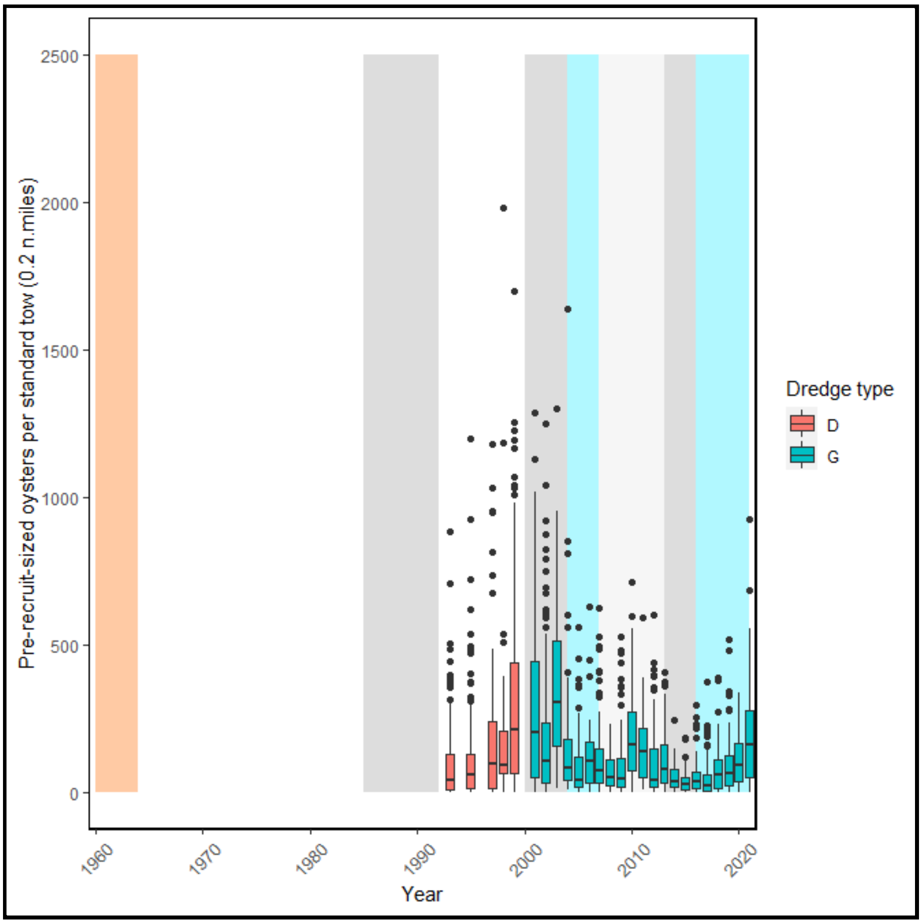

Figure 24: Boxplots of adjusted catches of pre-recruit oysters each tow by survey 1962 (1960–64) to 2021. Catches are capped at 2500 per tow. Medians shown as solid lines, boxes represent 50th percentiles, whiskers 95th percentiles, and outliers as filled black circles. Periods of heightened disease mortality are shown as shaded rectangles. Mortality attributed to *Alcicornis longicornutus* between 1960 and 1964 is shown as a salmon rectangle. Percentage of annual mortality from *Bonamia exitiosa* (1999-2021) is shown at three categories: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), high (greater than 10%, dark grey), and no detected Bonamia mortality is shown in white. Dredge details and the numbers of stations sampled are given in Table 4.

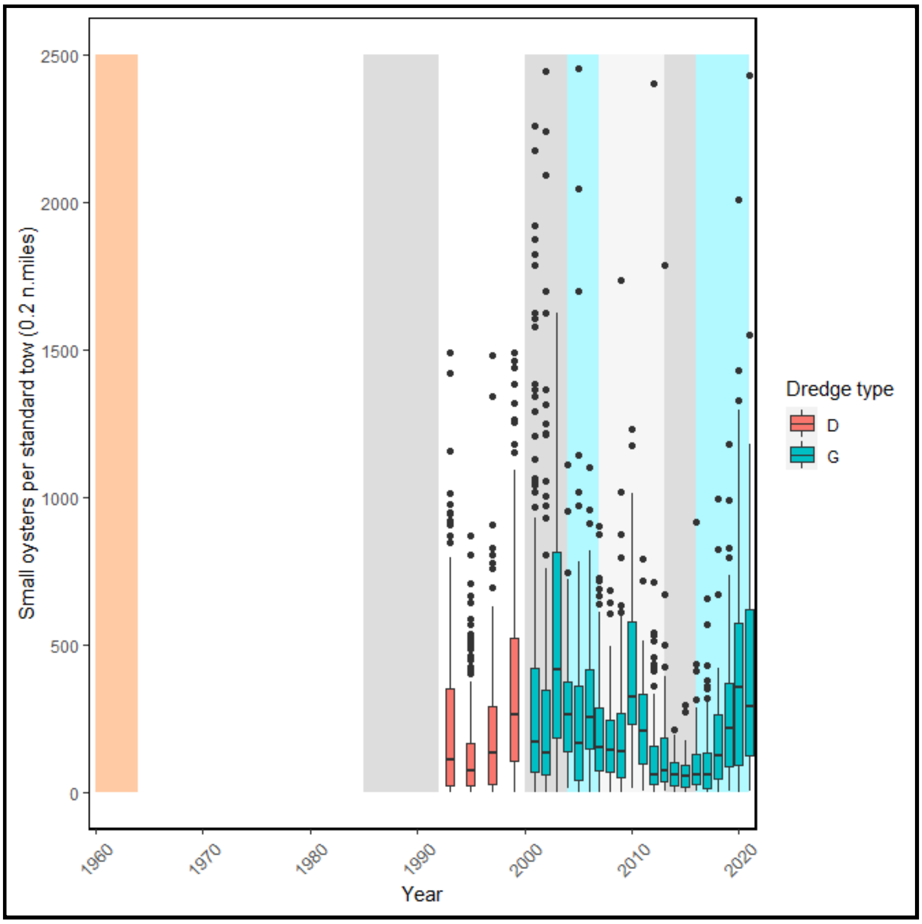

Figure 25: Boxplots of adjusted catches of small oysters each tow by survey 1962 (1960–64) to 2021. Catches are capped at 2500 per tow. Medians shown as solid lines, boxes represent 50th percentiles, whiskers 95th percentiles, and outliers as filled black circles. Periods of heightened disease mortality are shown as shaded rectangles. Mortality attributed to *Alcicornis longicornutus* between 1960 and 1964 is shown as a salmon rectangle. Percentage of annual mortality from *Bonamia exitiosa* (1999-2021) is shown at three categories: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), high (greater than 10%, dark grey), and no detected Bonamia mortality is shown in white. Dredge details and the numbers of stations sampled are given in Table 4.

Catch per unit effort (CPUE)

Sources of catch per unit effort (CPUE) data, their compilation, and their use in stock assessment are described by Dunn (2005a). CPUE data are influenced by many factors in addition to fisher behaviour. CPUE is used as an index of relative recruit-sized oyster abundance and, along with survey abundances, show how oyster densities and the population size are changing; however, the spatial resolution at which CPUE is recorded does not allow long-term (intergenerational) changes to oyster beds or localised areas to be determined. No spatial information was reported for CPUE between 1948 and 1959. Reporting of CPUE by Foveaux Strait oyster statistical areas began in 1960. These statistical areas were too large to allow an assessment of the response of individual oyster beds to fishing. A pilot voluntary fishers' logbook programme begun in 1999 and was established for all vessels in 2006. The logbook programme accounts for almost 100% of fishing and records CPUE at the spatial scale of one nautical mile squares (Michael et al. 2012a). The Fisheries New Zealand Integrated Electronic Monitoring and Reporting System (IEMRS) adopted this reporting grid and reporting became mandatory at this spatial-scale in 2019.

The numbers of vessels fishing have varied substantially over time from 5–12 vessels in the 1940s and 1950s, 30 vessels (some working outside the stock assessment survey area) between 1962 and 1969, 23 vessels between 1970 and 1993, and 11–13 vessels between 1996 and 2021. Since 1985, the effects of annual oyster mortality caused by *B. exitiosa* on the distribution of oyster beds, their densities of commercial-sized oysters, and more recently their meat quality has concentrated fishing on a subset of oyster beds available to fishers.

CPUE and landings from the fishery are shown in Figure 26. CPUE is shown as sacks per hour and landings shown in millions of oysters, converted from an average of 774 oysters per sack (Cranfield et al. 1999b). CPUE data are represented by four series: A (1948–1968), B (1969–1984), C (1985–2009), and D (2010–2021). These are based on different minimum legal sizes (MLS, i.e., the legal takeable size) of oysters and different oyster dredges used in the fishery:

- Series A, MLS was 2.125 inches (54 mm), and the typical commercial dredge was about 3.35 m-wide with single-bit and single ring bag and weighing ~150 kg,
- Series B, MLS was 2.25 inches (57 mm), and the typical commercial dredge was about 3.35 m-wide with double-bit and double ring bag and weighing ~ 400 kg,
- Series C, the typical commercial dredge was modified by increasing its weight to about 530 kg (Dunn 2005a), and
- Series D, uses the same dredge as for series C; however, fisher behaviour changed from fishing to maximise catch rate to target oyster beds with high meat condition and usually lower catch rates, and there was increased high-grading of oysters for larger sizes and fishing to catch limits imposed by processors.

It is unlikely that CPUE indices are comparable over the full time series, i.e., between series, and CPUE may not reflect oyster abundance consistently. Figure 26 clearly shows that rapid, substantial, and long-term declines in both CPUE and landings occurred during disease mortality events.

CPUE data from fishers' logbooks (Figure 27) show a similar trend and rate to the CPUE data from catch and effort landing returns (Figure 26). Catch rates increase between 2006 and 2012 despite an annual oyster mortality from *B. exitiosa* of 8–12%, decrease between 2013 and 2016 when oyster mortality from *B. exitiosa* increased, and slowly began to increase again between 2017 and 2021. Several other factors including recruitment failure and slow growth (Michael et al. 2021) have slowed increases in the densities of commercial-sized oysters.

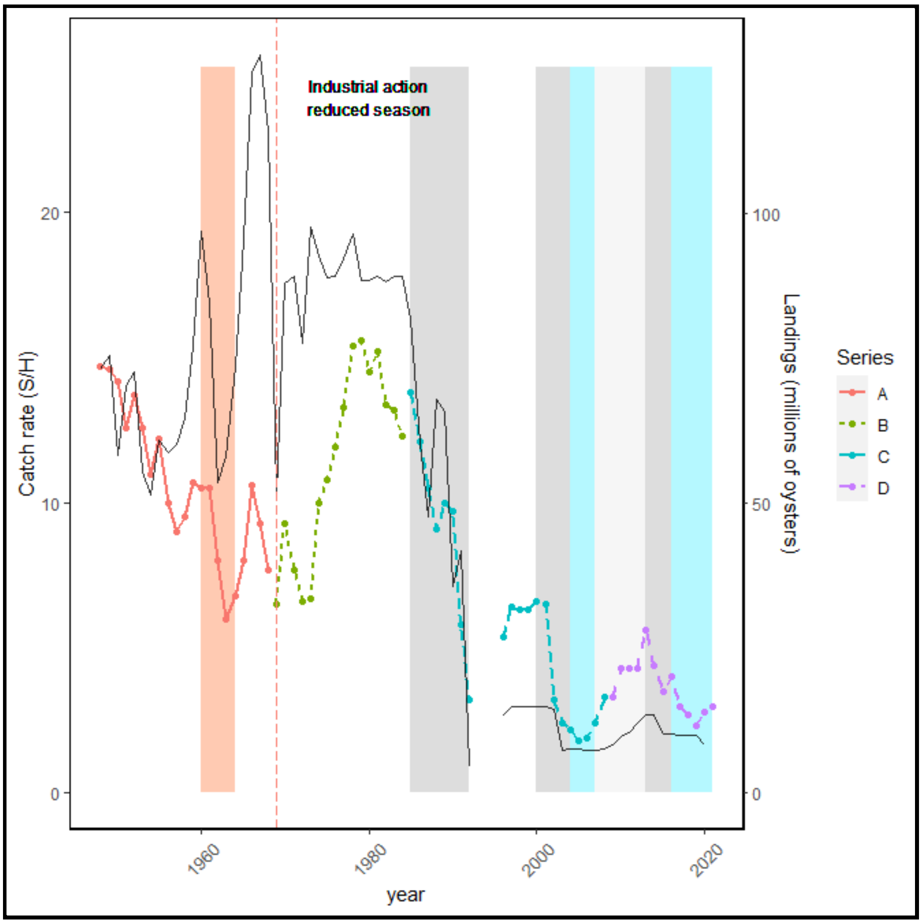

Figure 26: Catch per unit effort (CPUE) in sacks per hour. CPUE represents four series: A (1948–1968), B (1969–1984), C (1985–2009), and D (2010–2021). Landings (black line) shown in millions of oysters, converted from an average of 774 oysters per sack (Cranfield et al. 1999b). OYU 5 fishery was closed most of the 1969 season due to industrial action by oyster boat skippers. Periods of heightened disease mortality are shown as shaded rectangles. Mortality attributed to *Alcicornis longicornutus* between 1960 and 1964 is shown as a salmon rectangle. Percentage of annual mortality from *Bonamia exitiosa* (1999–2021) is shown at three categories: low (0.1–4.9%, sky blue), moderate (5.0–9.9%, light grey), high (greater than 10%, dark grey), and no detected Bonamia mortality is shown in white.

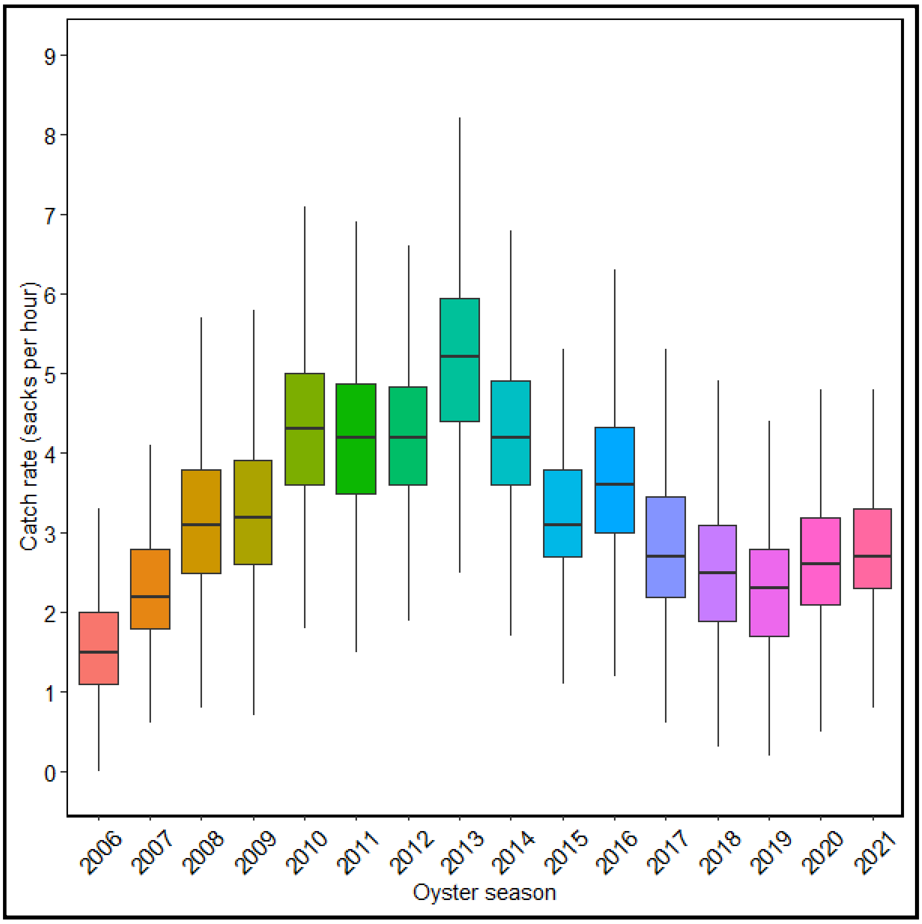

Figure 27: Catch rate in sacks per hour for 2006–2021 from fishers' logbook data.

3.3 Objective 3: Long-term monitoring programme and strategic research

A review of the OYU 5 strategic research plan will be undertaken by Fisheries New Zealand, and a stock assessment technical working group will be convened in 2023. A draft long-term monitoring programme should be completed as part of the strategic research plan.

The OYU 5 fishery is data rich, in part because BOMC has invested heavily in industry research since 1992. These data could be used to better design long-term monitoring programmes. Currently, few of these research data are in databases or have documented metadata. Some of the longer time series data and readily available data are summarised in Table 5.

Long-term monitoring needs to be prioritised to provide the highest priority research for better management and understanding of the fishery, to provide confidence beyond stock assessment of the sustainability of the oyster population, oyster habitat, and the sustainability of fishing. Hypotheses that underpin monitoring or research and sampling designs will be collaboratively developed with stakeholders. A list of suggested long-term monitoring programmes for consideration is given below, and ranked in order of priority:

1. Of primary importance to the stock assessment model, and any development of a disease model, are revised estimates of disease selectivity, i.e., new data from spatial temporal sampling of oysters for *B. exitiosa* and other important pathogens, together with data on oyster sex, reproductive state, and meat condition over the population size range.
2. Other research required to improve stock assessments:

    a. Updated estimates of growth from across the fishery (from sequential population length frequency distributions and or tagging). A decision on whether a move from two-dimensional growth to three dimensions is required.
    b. More regular estimates of population size frequency.
    c. Assess the most effective (cost versus data quality) index of recruitment from spat monitoring, estimates of 0+ from annual dredge sampling, or data from shed sampling.
    d. The dredge selectivity, persistence, fouling and erosion of new clocks as a measure of mortality.
3. Research to better understand how disease effects oyster mortality, growth, and recruitment.
4. Further investigations of the temporal relationship between non-fatal and fatal infections as predictors of oyster mortality. Are there any time lags between non-fatal and fatal infections and, if not, are there other trigger points (oyster density, climate (SST and CHL), and storm frequency)?
5. Validate remote sensing and environmental data (SST, CHL, storms), using continued BOMC SST monitoring and observation.
6. Low priority, but a good thesis topic. Quantify brooding of fertilised larval and unfertilised ova percentages. Develop laboratory experiments to determine the effects of sex ratios, temperature, and food levels on brooding success. There are some data already available in the literature but not for *O. chilensis* in Foveaux Strait.

Depending on the outcomes of the stakeholder workshops and, specifically if the previously polarised opinions on the effects of fishing on oyster productivity have been reconciled, high priority research may additionally include:

7. Publish updates of essential oyster habitat in Foveaux Strait, the effects of fishing, and the effects of *B. exitiosa* on the oyster population in the primary literature.
8. A programme to map the spatial extent of complex habitats (side scan sonar, drift camera, and video to validate) for avoidance strategies.
9. Investigate the effects of storms on sediment movement (field-based) and on energy, condition, reproduction, and disease (laboratory-based experiments)
10. Field trial to determine differences in oyster spat settlement, survival, growth, and mortality on different habitats.

Table 5: A summary of readily available long-term data sets for the OYU 5 fishery, data ranges where available and data source or ownership: FNZ, Fisheries New Zealand; BOMC, Bluff Oyster Management Company Ltd; FRD, Fisheries Research Division; FMD, Fisheries Management Division; SIL, Seafood Innovations Ltd; FRST, Foundation for Research Science and Technology; NZOI, New Zealand Oceanographic Institute; and Otago, Otago University.

Data type	Date range	Owner
Fishery independent surveys, estimates of: oysters, new and old clock densities in up to four size groups	1960–2022	FNZ, BOMC
Fishery independent survey data on presence/absence of bycatch taxa	1999–2022	FNZ, BOMC
Fishery independent survey catch images	1999–2022	FNZ, BOMC
Fishery independent bycatch surveys	2019–2022	FNZ
Catch and effort (CELR), and landing data (LFR)*	1972–2022	FNZ
Bonamia exitiosa prevalence, intensity, and oyster mortality data	1986–2022	FNZ, BOMC
Spat monitoring data estimating densities of competent larvae	1965–1968, 2006–2022	FRD, BOMC
Catch sampling for 0+ and 1+ age spat	2002, 2003, 2005–2022	BOMC
Catch sampling for the size structure of the commercial catch	2002, 2003, 2005–2022	BOMC
Population length frequencies	1960–1962, 1970–1773, 1990, 1999, 2001, 2017	FMD, FRD, FNZ
Fishers’ logbook data†	1999–2002, 2006–2022	BOMC
Monitoring SST, vertical profiles during oyster season, and moored sensors	2022	BOMC
Co-infections of different pathogens in oysters	2004, 2005–2022	BOMC, SIL
Meat condition data	2000–2022	BOMC
Oyster brooding percentages‡	2011	BOMC
Shell return to enhance spat settlement and habitat	2005–2007	BOMC, SIL
Dredge selectivity	2008–2011	BOMC, SIL
Side scan sonar surveys	1977–1979, 1998	FRD, FRST
Sediment sampling, grabs, and photography	1960, 1999	NZOI FRST
Quadrat sampling of macrofauna	1999	FRST
Growth increments from tagging	1978–1980	FRD
Estimates of mortality from tagging	1974–1986	FRD
Reproductive state and sex	1970–1971, 2004 2017–2018	FRD, FNZ, Otago

* CELR is Catch Effort Landing Return and LFR is Licensed Fish Receiver.

† Fishers’ logbook data that record catch and effort data from the fishery, bycatch information on the substrate composition and fauna encountered by the dredge, the proportions of recruit and pre-recruit oysters and wings, the proportions of new clocks in the catch, and fishing conditions.

‡ Sampled during an extended season (September–October 2011) for the Rugby World Cup.

4. DISCUSSION

There have been concerns of over-exploitation in the Foveaux Strait oyster fishery since the 1870s (Sorenson 1968). To guard against any collapse of the oyster fishery, oysters from Foveaux Strait were translocated to Cloudy Bay to establish new commercial beds in 1917 (Anon 1917). These concerns have recurred periodically since then. The Foveaux Strait oyster fishery has been dredged for over 150 years, more intensely since the 1960s (Cranfield et al. 1999a). A *Bonamia exitiosa* epizootic caused the recruit-sized population to decline by more than 90% between 1986 and 1992, and the fishery was closed in 1993 (Doonan et al. 1994, Cranfield et al. 2005). At the time *B. exitiosa* was thought to be an endemic pathogen of Foveaux Strait oysters and also suspected as the main cause of periodic mortality in oysters since early reports in 1906 (Cranfield et al. 2005). *Bonamia exitiosa* has a worldwide distribution (Hill-Spanik et al. 2015), and anecdotal evidence suggests that the 1985 *B. exitiosa* epizootic may have been a reintroduction of this pathogen.

The oyster fishery was reopened in 1996 and oysters were introduced into the Quota Management System (QMS) in 1997 (Ministry for Primary Industries 2016). Under the QMS, the number of oyster vessels in the fleet declined from 23 to 11 (Ministry for Primary Industries 2016). Since then, concerns over over-exploitation and effects of fishing have intensified and continued. Opinions on the status of the Foveaux Strait oyster fishery and its drivers of long-term change are polarised and politicised. The fundamental positions fall between the effects of disease and the effects of dredging on essential oyster habitat as the key drivers of oyster abundance. Climatic, environmental drivers such as storms, succession processes in benthic communities, over-colonisation of habitats, and disease mortality have not been considered in the relationships between the effects of fishing and the oyster population. These factors and their interactions are likely to play a significant role in the productivity of the oyster fishery. This report summarises the available information on the status of the fishery and its key drivers. Specifically, new data on trends in oyster abundance, oyster mortality caused by *B. exitiosa*, recruitment of oysters to the population, and bycatch data from the last 30 years of research are used to assess changes in productivity.

Fundamental to any assessment of the oyster fishery productivity is whether oysters are moved by storms. Although localised densities of oysters (oyster beds) wax and wane in density, they remain distributed in the same general locations over time and are assumed to be spatially stable entities. It is believed that oyster beds are self-recruiting sub-populations, and that recruitment is regular and dependent on densities of spawners (Cranfield 1979). Recent data suggest oyster larvae disperse more widely (Michael 2019a), and the highest recruitment occurs when spawner density is low (Michael & Shima 2018). The spatially stable distribution of oyster beds has facilitated fine-spatial scale rotational fishing (Hill et al. 2010). Whether oysters are moved by the high orbital velocities and swift tidal currents generated by the frequent large storms in Foveaux Strait (Gorman et al. 2003), as are other heavy sedimentary elements such as cobbles, is an important knowledge gap. If oysters are moved and reaggregated by large storms, albeit to consistent locations, the key drivers of oyster bed productivity are likely to differ. This discussion assumes oysters are not moved by storms.

Fishery data since 1986 show the principal driver of oyster availability to the commercial fishery, i.e., large numbers of oyster beds with high densities of oysters, is mortality from *B. exitiosa*. The productivity of the oyster fishery is high and is not likely to have changed much over time. Essential habitat to maintain oyster production is low complexity habitat that comprise mainly stable sediments of pea gravel and coarse calcareous sand, and the shells of dead bivalves. *Ostrea chilensis*, *Oxyperas elongatum*, *Tucetona laticostata*, *Panopea smithae*, *Glycymeris modesta*, and *Tawera spissa* shells are abundant and ubiquitous in Foveaux Strait. These shells provide an abundance of settlement substrata for *O. chilensis* larvae and the larvae of other benthic taxa. There are relationships between meat condition, disease mortality, and recruitment to the population (see Figure 12); however, it is not clear how these factors interact, or what role winter and summer sea water temperatures play in the variation observed in annual recruitment. Prolonged low recruitment during periods of high oyster mortality from *B. exitiosa* has flow-on effects to numbers of smaller oysters spawning as males (≤ 4-year-olds, Cranfield 1979), potentially limiting sperm availability and fertilisation success. The requirements for periodic high recruitment to the population exist in the fishery, and high recruitment events (Figures 3 & 4) translate to high densities of small, pre-recruit and recruit-sized oysters (Figure 20). The extent of the oyster fishery area described in 1906 (Sorenson 1968) has not been reduced by fishing (see Michael et al. 2019a).

Attempts to adjust long time-series of disparate data, e.g., survey data and CPUE, to be comparable since 1948 may have overestimated both the productivity of OYU 5 before the 1985 Bonamia epizootic. These putative overestimates of productivity will have marked effects on estimates of B_0 used as the reference point for the fishery, which in turn has clear management implication for the setting of fishery (Total Allowable Commercial Catch) and stock targets and limits as prescribed by the Harvest Strategy Standard as Fisheries New Zealand's implementation of the Fisheries Act 1996. However, managers recognise that the currently low harvest levels have no detectable effect on future oyster abundance and that future stock size is determined by disease mortality, recruitment, and a reliance on long-term average growth. Doonan (cited by Michael et al. 2023b) found that survey population sizes provide the primary abundance 'targets' for stock status during assessments. CPUE does not contribute significantly to model fits; however, CPUE is used because of the early time series for which there are no survey data.

CPUE data are now recorded by the Integrated Electronic Monitoring and Reporting System (IEMRS) programme at the spatial scale of 1 n.mile grid cells (the same grid used in fishers' logbooks); however, fishing is often concentrated in a relatively small proportion of the overall grid cell area. There are currently insufficient data to investigate temporal, especially long-term, changes to oysters and benthic communities at the fine spatial scale of oyster beds. The elliptical dredge tows employed by oyster vessels could enable individual fishing events and areas swept to be precisely delimited from vessel tracks recorded by IEMRS. Increasing the resolution of vessel dredge tracks from the relatively low current ping rate used by the Electronic Vessel Reporting System to a higher ping rate, to precisely identify the location of the small and numerous fishing events will be useful to design robust future research on the effects of fishing on oysters and their habitats, and especially their recovery.

Heightened mortality from *B. exitiosa* causes declines in recruit-sized oysters and in fisher catch rates (see Figures 20 and 26, respectively). *Bonamia exitiosa* has persisted in the fishery since 1985 and, at times, at low prevalence, e.g., 4.5% in 1995 (Cranfield et al. 1996), 0.2% in 1997 (Cranfield et al. 1998, Cranfield et al. 1999b), and 5.8% in 2005 (Michael et al. 2006). In most years since 1985, there has been some level of associated mortality, with heightened mortality events in 2000 and 2013 lasting up to 3 years. Years of heightened mortality from *B. exitiosa* may be difficult to predict because of the lack of a cyclic nature of mortality events and the lack of an adequate lag (one or more years) between non-fatal and fatal infections (Figure 9). Cranfield et al. (2005) suggested that dredging exacerbated mortality from *B. exitiosa* and that the removal of epifaunal reefs may reduce the sequestration of free *B. exitiosa* propagules, reducing disease transmission. Fishery and logbook data show no relationship between dredging or increasing categories of dredging intensity during the winter oyster season and levels of fatal infections of *B. exitiosa* the following summer (Figures 10 and 11). Fatal infections were higher in high mortality years and low in low mortality years regardless of the intensity of dredging. There may be high levels of sequestration of free *B. exitiosa* propagules; however, these reservoirs are more likely to provide alternative hosts and vectors for *B. exitiosa* and thereby increase the risk of spread of infection and recurrent mortality (e.g., mytilids and ascidians, after Costello et al. 2021).

4.1 Essential oyster habitat

Cranfield et al. (1999a) proposed a hypothesis that oyster recruitment is dependent on complex biogenic habitats, dominated by the bryozoan *Cinctipora elegans.* These habitats once reportedly covered the entire fishery area; oyster beds only occurred on these biogenic reefs (Cranfield et al. 1999a). When these reefs were removed by fishing, the oyster beds were abandoned, and the fishery area contracted. Additionally, disease mortality increased, and overall productivity of the OYU 5 greatly declined (Cranfield et al. 1999a). This hypothesis is based on an assumption that biogenic reefs may provide better conditions for settlement and post-settlement survival and growth as is the case in other complex habitats, such as the maerl ground habitat of scallops (*Aequipecten opercularis* and *Pecten maximus*) in Scotland (Hall-Spencer & Moore 2000) and oyster (*Crassostrea virginica*) reefs in the USA (Schulte et al. 2009), and on LEK from some fishers' observations of dredge bycatch (Hill et al. 2010) (see Introduction section on inferences from dredge bycatch). Mullock is a term used by fishers to describe bycatch of oyster fishing and has been used in LEK and survey observations to provide a description of macro-epibenthic communities. Stead (1966, 1971b) described mullock patches from dive observations in the 1960s as small patchily distributed areas of sponges, mussels, and bryozoans with relatively few oysters.

The Foveaux Strait oyster and fishery bycatch data (presented above) do not support this hypothesis, that oyster production is dependent on complex biogenic habitat, nor that oyster beds have been abandoned or that the fishery area has been reduced (see Appendix 4). Data from the 1960s and from 1992 to the present show that oysters are much more productive in areas with very little epifauna and where sediments are occasionally mobile. In these areas, oysters are likely to have less competition for available settlement substrata and less predation and over colonisation by other benthic taxa than on complex epifaunal reefs. Oysters on simple habitats with occasionally mobile sediments are therefore likely to have better recruitment to the population and better survival and growth, including meat condition, allowing high density localised populations to develop. Other than coralline algae (Twist 2019), *O. chilensis* is rarely covered by epifauna. Cranfield et al. (2001) found between 1993 and 1996, i.e., in three years, that "*Evidence from blue cod fishers and oyster surveys suggests that the benthic habitat of some oyster beds regenerated in the absence of dredging and that the relative density of blue cod, and then oysters, rebuilt to commercial levels*". Additionally, complex biogenic areas, especially those with large, sessile, erect epibenthic fauna such as *Crella incrustans*, *Chondropsis* spp., *Pyura pachydermatina*, *Cinctipora elegans,* and *Modiolus areolatus* are avoided by fishers (Hill et al. 2010). These areas are not considered oyster fishery areas; dredge saturation is instantaneous, filling the dredge with high volumes of bycatch with few, if any oysters, that take much longer to sort and therefore the areas are uneconomic to fish. Moreover, oysters in complex biogenic areas tend to have poor meat condition (Stead 1971b) and therefore are of lower commercial value.

4.1.1 Biogenic reefs

Biogenic reefs are not important to oyster production; however, oysters may be important to biogenic reefs. Oyster shells and the shells of other shellfish contribute substantially to the development of biogenic reefs. Lenticular structures comprising shells, sand, and gravel accumulated by hydrological forces provide stability and height (see Cranfield et al. 2004 for further detail on this hypothesis). These structures are often the foundations for settlement and succession of sessile benthic invertebrates and are the genesis of biogenic reefs (Figure 28). The colonisation of the structures depends on sources of reproductive propagules and delivery mechanisms (Caddy & Defeo 2003). Colonising propagules could be transported considerable distances in the swift currents of Foveaux Strait and spatial and temporal patterns of colonisation are likely to vary depending on the species of larvae or propagules available for settlement. Differences in the composition of benthic taxa (other than oysters) that settle on spat collectors in fishery areas suggest the composition of the communities will differ amongst fishery areas (Michael et al. 2012a).

Benthic habitat, sediments, tidal current strengths, depths, exposure to oceanic swells, and environmental factors vary across the fishery area, and there are at least four regions with distinct benthic assemblages. Surveys of bycatch (Michael 2022a) found benthic assemblages were dominated by *Cinctipora elegans* (southern region), *O. fusiformis* (western region), *Crella incrustans* (central region), and *Pyura pachydermatina* (eastern region). There is an assumption that these benthic communities are static and that only dredging disturbs the seafloor. Mobile sediments that cover fishery areas including oyster beds are a constant feature of Foveaux Strait (Sorenson 1968, Cranfield 1979, Michael 2011a), and the effects of storms on oysters, oyster habitat, and biogenic reefs is a key knowledge gap.

Cinctipora elegans is an early colonising species and was one of the first species to colonise returned shell (Figure 29, Michael 2011b). *C. elegans* is readily over colonised by other benthic taxa (Figure 30). It is considered the dominant structure-forming species (Cranfield et al. 1999a). It is possible that the abundance of *C. elegans* in the 1970s may have been related to unusually large recruitment events and extensive recovery of fished habitat from the intense dredging of the mid-1960s to the mid-1980s (Cranfield et al. 1999a). Climax communities in the area studied in the 1970s (Allen & Cranfield 1979, Cranfield et al. 1999a) are sponge dominant. Sponges readily overgrow *C. elegans* colonies, as is the case in the tropical systems (Lopez-Victoria et al. 2006). Allelo-chemicals released on the surfaces of sponges for defence prevent other larvae from settling, e.g., ascidian larvae do not settle on *Crella incrustans* (Davis et al. 1991), and some sponge species deter grazing by urchins (Wright et al. 1997). *Crella incrustans*, *Chondropsis* spp. are abundant in Foveaux Strait (Cranfield et al. 2004).

Biogenic reefs are not essential oyster habitat, and, thereby, how the composition biogenic reefs may have changed over the 150 years of fishing in Foveaux Strait is beyond the scope of this study. Long-term changes are unlikely to be known. There are no long-term temporal data at fine enough spatial scales for quantitative assessment of the changes in distributions of biogenic reefs, what changes have occurred in areas regularly fished over many generations, and what role fishing and other factors may have played in any changes, in the high energy environment of Foveaux Strait. Local Ecological Knowledge (Hill et al. 2010) suggests there have been changes. The levels and compositions of bycatch may have declined. This LEK conflicts with reports over the history of the fishery that commercial densities of oysters are found on simple habitats of sand, gravel, and shell. Qualitative data suggest that any changes may not have been substantial across the different benthic habitats of the fishery area (see Figures 31–33).

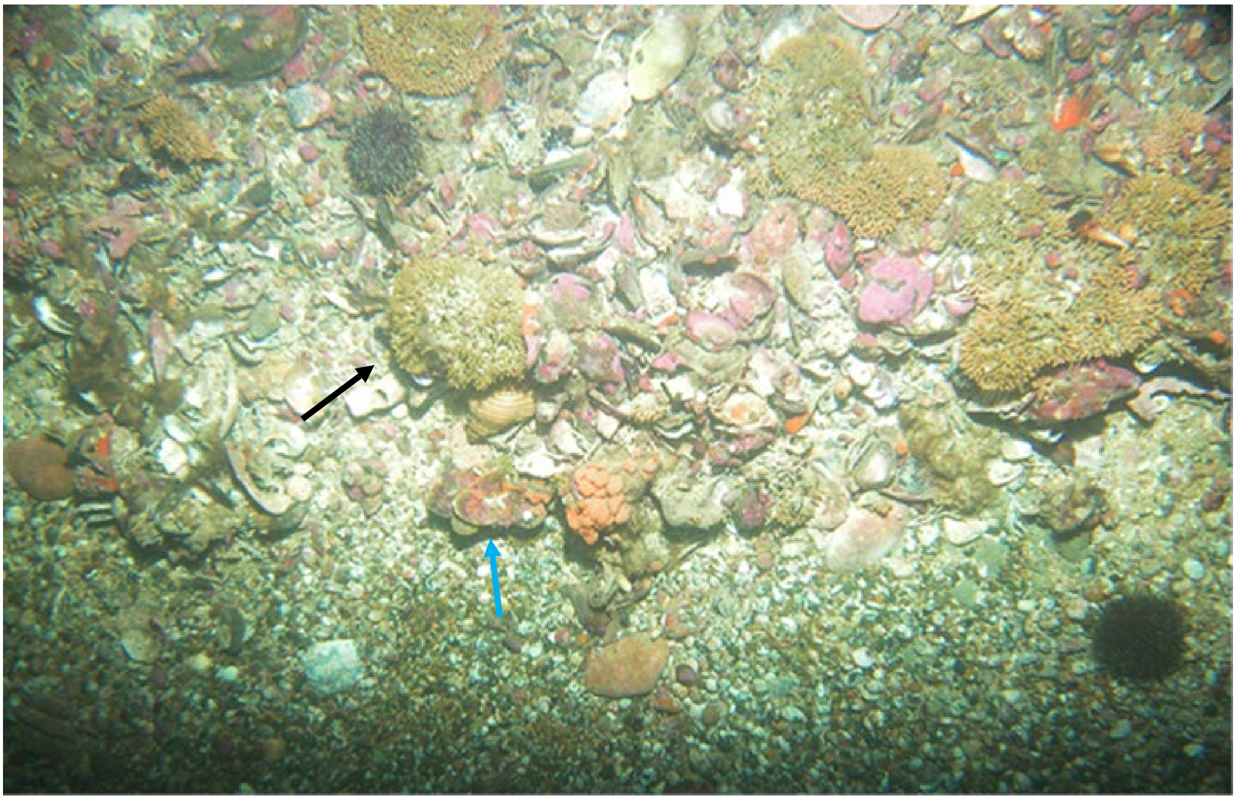

Figure 28: Lenticular structures comprised sediment and shell, formed by hydrographic forces along the current axis south of Bluff Hill (see Cranfield et al. 2004). These structures provide the genesis for complex biogenic habitat (reefs). *Cinctipora elegans* (black arrow) and *O. chilensis* (blue arrow) are among the early colonisers above the flat gravel seabed and beginning to become overgrown.

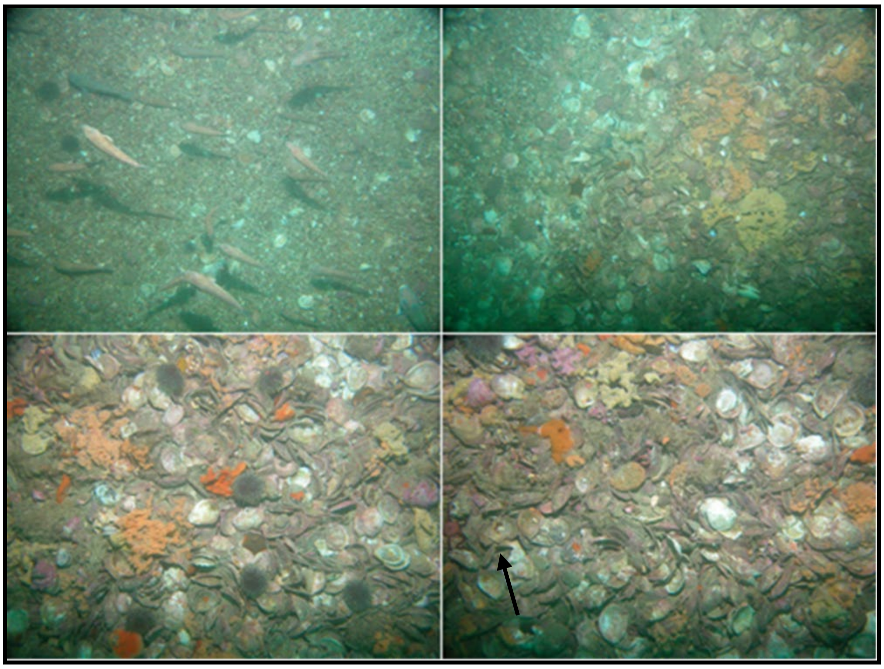

Figure 29: Colonisation of heaps of returned shell during a Bluff Oyster Management Company enhancement trial. *Cinctipora elegans* (black arrow) is amongst the early colonisers.

Figure 30: *Cinctipora elegans* overgrown and killed by benthic taxa.

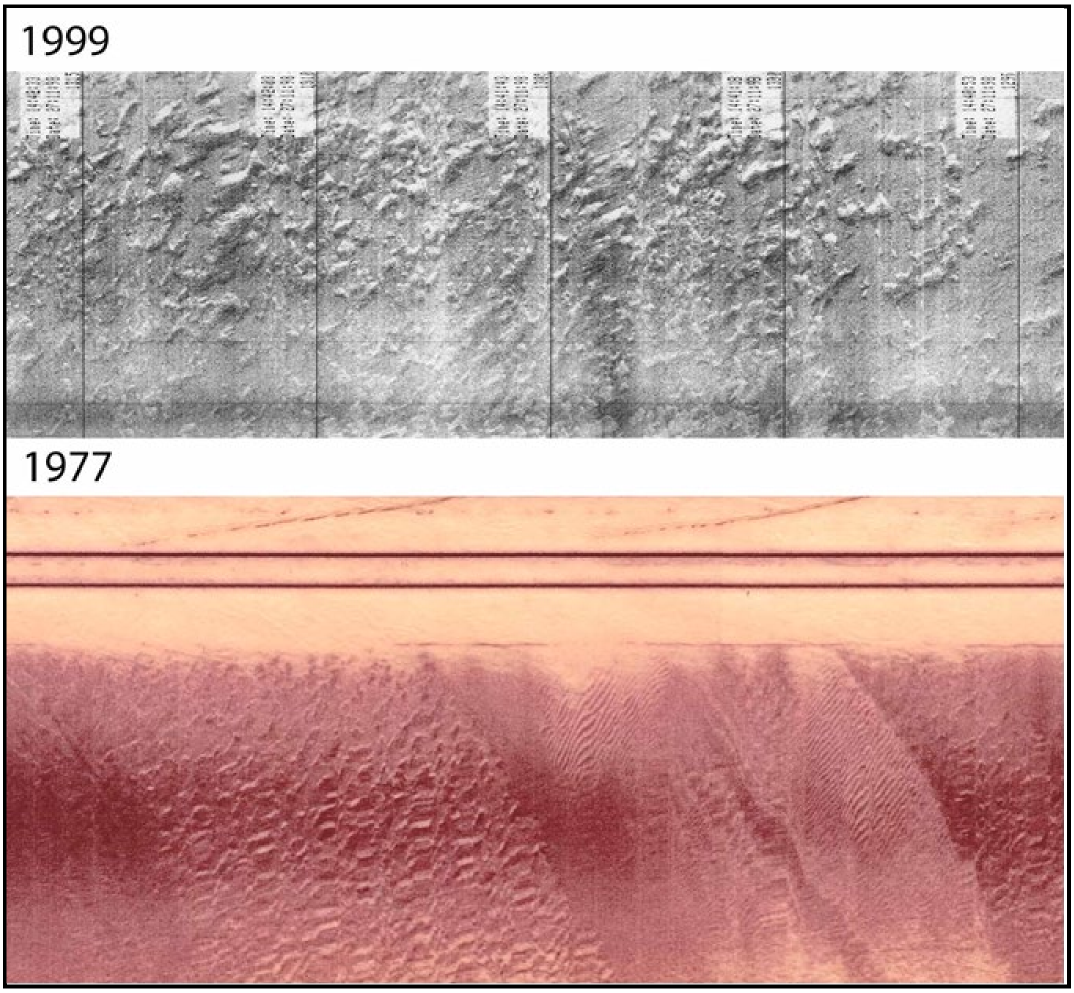

Figure 31: **Side-scan sonar images taken in 1999 and 1977 from similar sites and showing similar structural features.**

Figure 32: **Biogenic reef in the western fishery, 1960 and 1999.**

Figure 33: **Close up of biogenic reef in 1960 showing a sponge dominant benthic community and the soft red bryozoans, *Othoscuticella fusiformis*.**

4.2 Co-infections of other pathogens as potential drivers of mortality and recruitment.

The Bluff Oyster Management Company Ltd, fishers, and resource managers recognise that mortality of oysters from *B. exitiosa* is by far the most important driver of oyster densities, population sizes, catch rates, and thereby economic benefits from the fishery. Research has been primarily focused on annual surveys of the distribution of prevalence and intensity of *B. exitiosa* infection, and the effects of fatal infections on the oyster population, and thereby fishery prospects for the following season, see (Michael et al. 2023a) for an example.

Studies on the effects of pathogens on shellfish-like oysters have largely considered only single pathogens and rarely environmental variables (Maynard et al. 2016). The synergistic effects of co-infections are implicated in the intensification of infection (Hine 2002), which challenges the one pathogen-one disease paradigm (Hine 2002, Vayssier-Taussat et al. 2014, Bass et al. 2019). The incidence of shellfish diseases is determined by a three-way interaction between host, pathogens, and environmental variables. Infection intensity is made worse by unfavourable climatic variables such as warmer water temperatures (Okamura 2016, see Michael et al. 2023b).

In a recent study by Michael et al. (2022b), 30–40% of oysters had co-infections of two or more pathogens, and many were co-infections with *B. exitiosa*. Oysters infected with *Alcicornis longicornutus* were castrated, reducing recruitment severe infections reportedly cause mortality, which may be significant if prevalence is similar to the 40% prevalence reported in the 1960s (Howell 1967). Apicomplexan X (APX) may increase the susceptibility of *O. chilensis* to mortality from *B. exitiosa* (Hine 2002) and severely affects gametogenesis (Diggles & Hine 2002). Similar effects have been observed in European flat oysters *O. edulis* grown in areas in Ireland where *B. ostreae* is enzootic. *Ostrea edulis* grew more slowly with lower reproductive activity than oysters from areas without *B. ostreae* (Egerton et al. 2020). Pathogens are also likely to affect meat quality through the diversion of energy from somatic growth and meat condition, shell growth and repair, and for reproduction. Infected hosts allocate energy for the suppression of disease, usually through mounting an immune response (Egerton et al. 2020). Additionally, when the hosts are in good condition high levels of energy, especially when ova are being reabsorbed, fuel the rapid proliferation of *B. exitiosa* (Hine 1991a,b) causing death and, in less extreme cases, deprive the host of vital energy reserves and condition.

4.3 The effects of climate on key biological processes

It is difficult to tease out climatic variables that drive biological processes because of complex interactions. The low numbers of cycles, and time between peaks and lowest levels in these data make it difficult to identify climatic variables that influence meat quality, recruitment, and disease mortality. Bluff Oyster Management Company Ltd meat quality data from 2000 cover two periods when meat quality was high, recruitment data from 2006 cover two peaks in settlement, and data for annual oyster mortality caused by *B. exitiosa* from 2002 also include two heightened mortality events. The lack of strong correlation with individual climatic variables may be due to complex interactions of several variables and changes in these interactions from year to year.

Of all the climatic factors, SST appears to be a key driver of oyster meat condition, mortality from *B. exitiosa*, and recruitment to the population (Figure 12). Since 2016, seasonal SSTs, especially summer temperatures, have been higher than long-term trends, and oyster meat condition and mortality from *B. exitiosa* have been low, and recruitment high. Spawning, especially for those oysters breeding as females, has high energy requirements. Successful spawning, as indicated by higher recruitment, would normally result in spent individuals the following summer, with less reabsorption of ova to fuel intensification of *B. exitiosa* infections and thereby lower mortality. Temperature and food rations have marked effects on gametogenesis (Westerskov 1980, Buroker et al. 1983, Joyce et al. 2015) and may play an important role in conditioning, initiating gametogenesis, and synchronising gonadal development (Joyce et al. 2015). However, at high temperatures (≥ 20 °C), the gonad cycle may advance rapidly and asynchronously to phagocytosis, and thereby reduce fertilisation and brooding (Jeffs &

Hickman 2000). Additionally, in New Zealand, the percentage of brooders (as a measure of reproductive success) increases with a decrease in latitude, which suggests that temperature may be a primary determinant of successful spawning and fertilisation, and therefore brooding. Brooding percentages increase from less than 20% in Foveaux Strait (46° S) to 55–78% in Tasman Bay (41° S) (Brown et al. 2010), and to 78–90% in northern New Zealand (36° S) (Brown et al. 2010). Low seawater temperatures rather than warm years may trigger heightened mortality from *B. exitiosa* — the opposite to the findings of a laboratory study by Diggles & Hine (2002) that found warm temperatures exacerbated disease.

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APPENDIX 1: Origins and early history of the Foveaux Strait Oyster (*Ostrea chilensis*) fishery (OYU 5)

Oysters (tio) were a taonga to Rakiura Māori living in Port Adventure (Waipuna) and environs, and these oysters were also utilised by the early settlers on Stewart Island (Howard 1940). Oysters covered a considerable area of shallow estuary in Oyster Cove. Commercial exploitation of oysters in Port Adventure which began in the early 1860s is considered the genesis of the OYU 5 fishery. Oysters were shovelled into sailing cutters that were propped on the seabed at low tide. The vessels were filled to capacity in three tides. By 1867, the oyster population had declined with small oysters of no market value remaining. Attempts to establish new oyster beds in the Heron River through translocation were not successful. Port Adventure was closed to commercial oyster fishing in 1872 (Howard 1940).

In 1868, extensive ‘deepwater’ oyster beds were discovered off Port William, Foveaux Strait. Large numbers of vessels fished these beds until mid-1869 when an amendment to the 1866 Oyster Fisheries Act awarded the discoverer of a new oyster bed an exclusive licence (i.e., monopoly) for up to five years. Oyster beds were discovered off Halfmoon Bay (Oban) between Fish Rock and Bench Island in 1872; these extended more than two miles, with an average width of half a mile (Figure A4.2). These beds became the focus of oyster dredging. Eight cutters (8–16 t) from Halfmoon Bay and Bluff fished these beds between 1873 and 1874. Crews of three men could catch 250–500 dozens of oysters per day, though the average return was half that (3–6 sacks). These populations also declined, and fishers requested the fishery be closed from August 1877 to February 1879. Howard (1940) reports “*Under wise government supervision and restriction the beds in the Foveaux Strait area prospered, and the industry continued to progress*”, suggesting these oyster beds had rebuilt.

Oysters were found scattered over a wide area in Foveaux Strait between Stewart Island and Bluff Harbour in the 1880s. The larger vessels, fishing the deeper, exposed oyster beds of Foveaux Strait were based in Bluff. A survey by Hunter (1906) found that the oyster beds were patchily distributed throughout Foveaux Strait from Waipapa Point to Centre Island (see Figure A4.2). This survey established the extent of the commercial oyster fishery reported in Sorenson (1968).

Oysters from Foveaux Strait were exported to Australia earlier than 1900. By 1941, exports ranged from 1.5 million to 2 million oysters per year. In 1931, an oyster cannery was established in Bluff and oysters exported to England (Howard 1940).

APPENDIX 2: Summary of questions from the Foveaux Strait Oyster Management Group Workshop, February 2021

A workshop was held with the following OYU 5 fishery stakeholders including participants from: Allen Frazer, Marine Pomarède, Ian Tuck, Jean Davis (Fisheries New Zealand), David Skeggs and Graeme Wright (Bluff Oyster Management Company Ltd), Rodney Tribe (Ngāi Tahu), Alistair Dunn (Ocean Environmental Ltd), Craig Marshal (Otago University), Bryony Miller (e3Scientific), and Keith Michael, Ian Doonan, and Samik Datta (NIWA). The workshop was held on Wednesday, 24 February 2021 at the MPI Office, 137 Spey Street, Invercargill.

Summaries from workshop discussions

The participants acknowledged the Foveaux Strait oyster fishery (OYU 5 stock) is of customary, regional, and national significance. The discussion was concentrated on fishing (dredging) interactions with the stock and oyster habitat, and factors that affect the long-term productivity of the fishery, and, thereby, its ability to provide for future customary, social, economic and habitat benefits. Key research needs, themes, and questions are summarised below.

Oyster mortality

Oyster mortality from *B. exitiosa* is seen as the most important issue by most stakeholders. Many of the stakeholder questions relating to disease and natural mortality have been addressed in this report. These include:

1. Investigate Bonamia epidemiology, triggers for outbreaks, environmental factors, and, if a new incursion or reintroduction, whether the 1985 variant of *B. exitiosa* is now endemic in Foveaux Strait and whether it will continue to cause cyclic mortality. Further research includes:
    - 1.1. Update data on oyster size, sex and reproductive state, and disease status to better define the disease selectivity ogive for stock assessment.
    - 1.2. Compare histological samples before 1985 *Bonamia exitiosa* epizootic (Jeffs & Hickman 2000) and after 1985 histology from Bonamia surveys to investigate the roles of co-infections, especially APX.
    - 1.3. Investigate the roles of co-infections of other pathogen and climate factors such as SST on disease mortality, reproductive success, and meat quality. In part addressed other research programmes (Michael et al. 2022b).
    - 1.4. Investigate the spatial temporal patterns of Bonamia prevalence and absence.
    - 1.5. Update estimates of mortality including natural mortality (biotic e.g., predation and abiotic) and incidental mortality from dredging, e.g., differences between heavy and lighter dredges.
    - 1.6. Investigate the effects of biogenic areas on the spread of Bonamia (particle sequestration or reservoirs of disease) and what effects any changes in benthic habitat have had on oyster mortality. Such an investigation should include the general life history of Bonamia, alternative hosts, and vector's hosts (e.g., mytilids and ascidians, after Costello et al. 2021).
    - 1.7. Develop eDNA methods to better understand Bonamia.

2. Review biosecurity, especially for other oyster pathogens in Foveaux Strait.

Oyster recruitment

A better understanding of recruitment to the population was the highest priority knowledge gap. Core questions included:

3. Increase understanding of reproduction, gametogenesis, spawning, fertilisation and brooding, drivers of sex change at size and age, settlement surfaces for oyster larvae, and competition for settlement substrata.
    3.1. The relative abundance of competent larvae available to the fishery each year is monitored by a BOMC spat monitoring programme. The reproductive process is not well understood.

4. Use field experiments to determine differences in spat settlement and survival of 0+ and 1+ oysters on biogenic habitats versus simple habitats of live oysters and shell.

5. Use LEK to summarise what is known about recruitment.
    5.1. This is in part addressed by (Cranfield 1968a, Cranfield 1968b, Hill et al. 2010).

6. Investigate larval predation and new settler predation, i.e., characterise and investigate significance on different habitats.

Habitats

7. Undertake a camera survey (stills and video) in conjunction with side-scan sonar or swath mapping to investigate oyster habitat, i.e., the relationship between complex biogenic habitat for larval settlement and spat survival, and for adult abundance.
    7.1. Some information is summarised in this report, further sampling and experiment could provide some quantitative data.

8. Delimit productive areas of the oyster fishery and their habitats. What creates or contains these localised densities of oysters (‘oyster beds’).
    8.1. Compare fished and unfished areas with dredge sampling, video and images, quadrats.
    8.2. Check if Otago University has any of these data from the fishery area.

9. Investigate the potential contaminants of oysters and oyster habitat from the Tiwai smelter discharges, harbour channel dredging by Southport, and any historic discharges from Ocean Beach.
    9.1. Out of scope for this programme.

Oyster growth

10. Updated estimates of oyster growth and growth variability are required. Determining a better measure of size that better tracks age cohort should be part of this research.

11. Do oysters grow best on complex biogenic habitats? Some anecdotal evidence provided in this report that they do not.

12. Investigate the drivers of growth and energy partitioning, i.e., nutrients and inputs, food items range (phytoplankton species in oyster diets), stable isotope analysis (tissues and shells), and feeding studies simulation burial by sediments. Relationships with storms and year effects?
    12.1. Summarise data from other studies?
    12.2. In part addressed by this report and by Michael et al. (2023b).
13. Investigate if dredging retards growth, especially in juveniles?

Climate effects

14. The effects of climate and environmental factors (ocean acidification (OA), temperature (SST), storm frequency and severity on oyster processes (recruitment, growthy and mortality). In part addressed by this report and by Michael et al. (2023b).
    14.1. Investigate primary production (CHL), and the effects of reduced inputs from the Wairau.
    14.2. Investigate the effects of environmental stress on oysters using laboratory experiments.

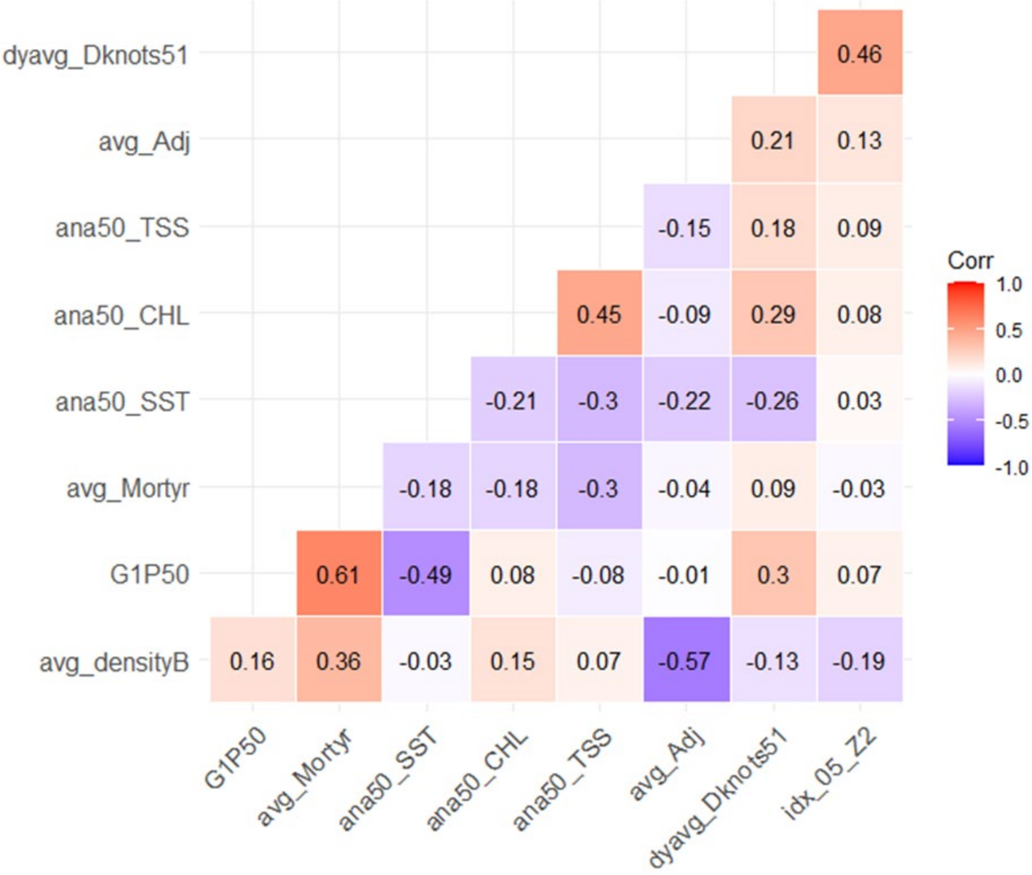
15. Establish monitoring programme to record climate and environmental data. BOMC research is currently monitoring temperature.
    15.1. Develop remote sensing data.

Oyster population dynamics

16. Has there been a reduction in the fishery area? At a large spatial scale, this is addressed by this report.

17. Investigate stock genetics, i.e., is the fishery comprised by localised genetic stocks or single genetic stock? In part addressed by Thomas (2015).
    17.1. Investigate if there any relationships with other New Zealand oyster stocks?

APPENDIX 3: Pearson correlation matrix of climate variables, host factors, and disease



	G1P50	avg_Mortyr	ana50_SST	ana50_CHL	ana50_TSS	avg_Adj	dyavg_Dknots51	idx_05_Z2
dyavg_Dknots51								0.46
avg_Adj							0.21	0.13
ana50_TSS						-0.15	0.18	0.09
ana50_CHL					0.45	-0.09	0.29	0.08
ana50_SST				-0.21	-0.3	-0.22	-0.26	0.03
avg_Mortyr			-0.18	-0.18	-0.3	-0.04	0.09	-0.03
G1P50		0.61	-0.49	0.08	-0.08	-0.01	0.3	0.07
avg_densityB	0.16	0.36	-0.03	0.15	0.07	-0.57	-0.13	-0.19

Figure A3.1: Pearson correlation matrix of median anomalies for climatic variables chlorophyl (CHL), sea surface temperature (SST), total suspended sediment (TSS), the Z2 pressure differential, and percentage grade 1 oysters each year (G1P50). Also shown are mean time adjusted oyster settler densities on collectors (avg_adj), mean percentage mortality caused by *Bonamia exitiosa* (avg_mortyr), the numbers of days per month when wind speed was greater than 51 knots (dyavg_Dknots51), and the mean percentage grade 1 oysters each year (avg_G1). R values shown in colour (see legend) and text.

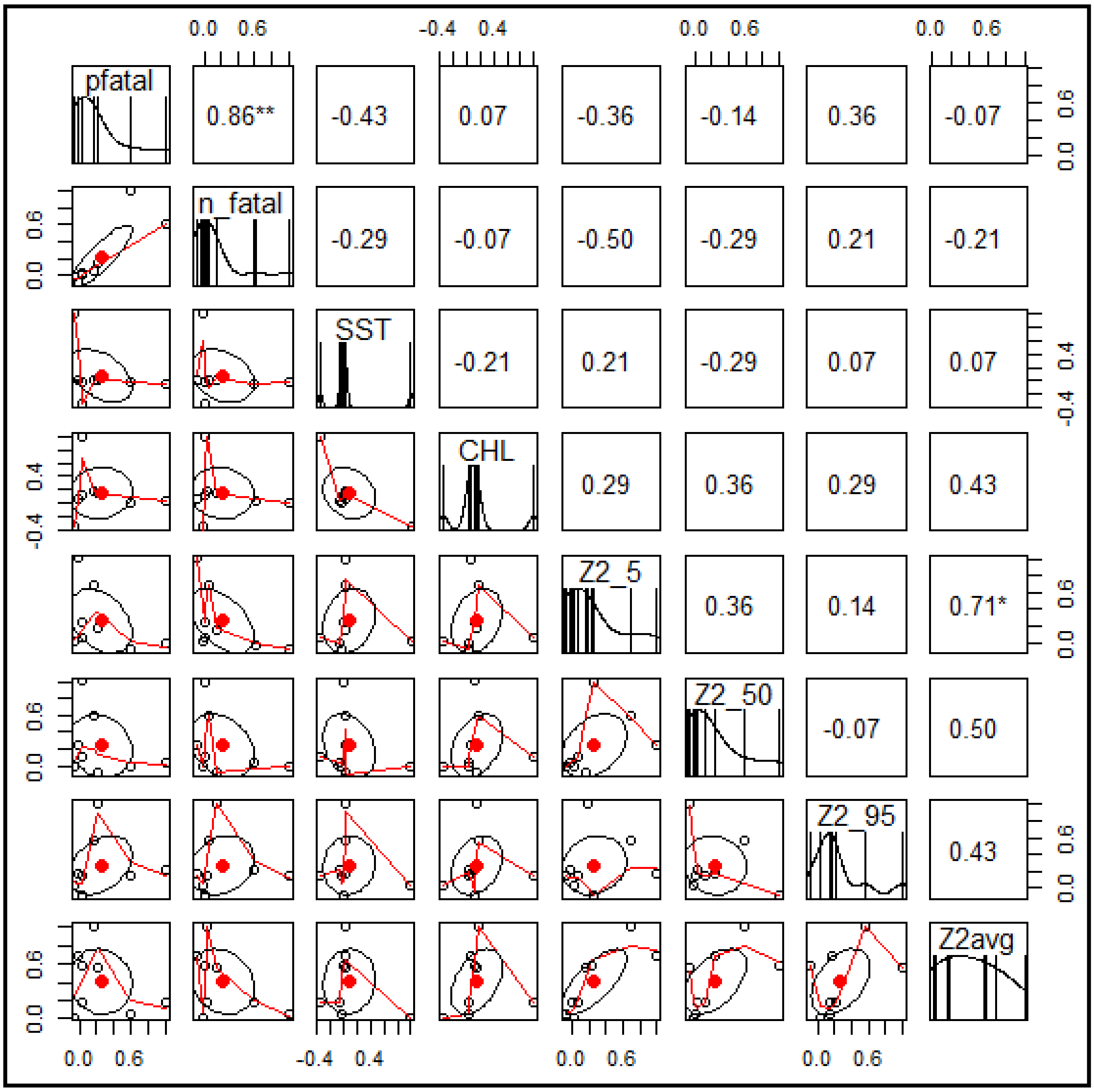


Figure A3.2: Kendall's rank correlation matrix of percentage fatal infection with *Bonamia exitiosa* and numbers of fatal infections per tow with climatic variables chlorophyl (CHL), sea surface temperature (SST), the Z2 pressure differential (5th, 50th, 95th and average indices). Kendall's tau shown as black text. For each variable, panels show 1. the variable name and histogram (diagonal); 2. jittered data, loess smother and correlation eclipse (below the diagonal), and 3. the Kendall's tau and significance level with stars (above the diagonal).

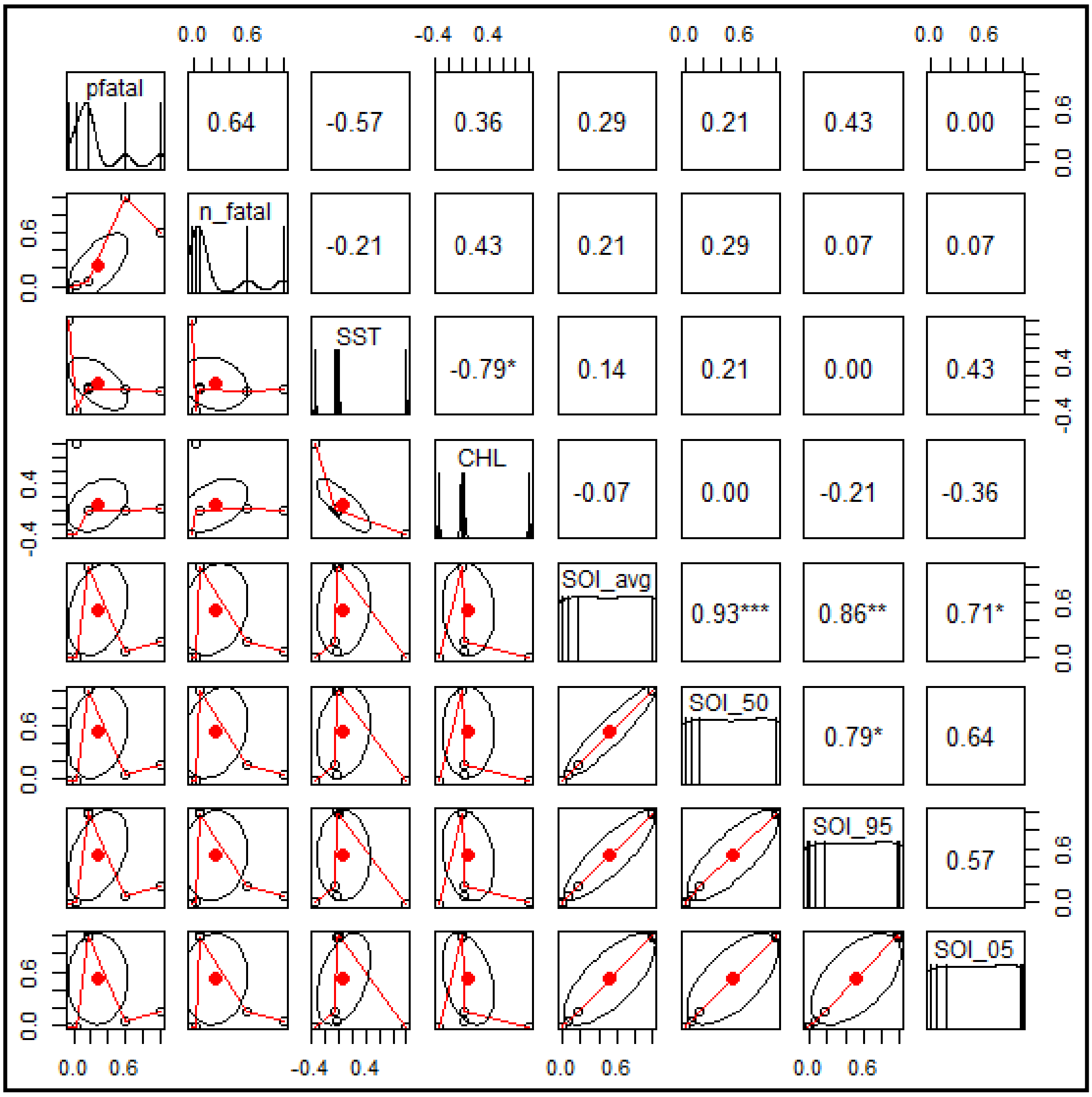


Figure A3.3: **Kendall's rank correlation matrix of percentage fatal infection with *Bonamia exitiosa* and numbers of fatal infections per tow with climatic variables chlorophyl (CHL), sea surface temperature (SST), the Southern Oscillation (SOI) index (5th, 50th, 95th and average indices). Kendall's tau shown as black text. For each variable, panels show 1. the variable name and histogram (diagonal); 2. jittered data, loess smother and correlation eclipse (below the diagonal), and 3. the Kendall's tau and significance level with stars (above the diagonal).**

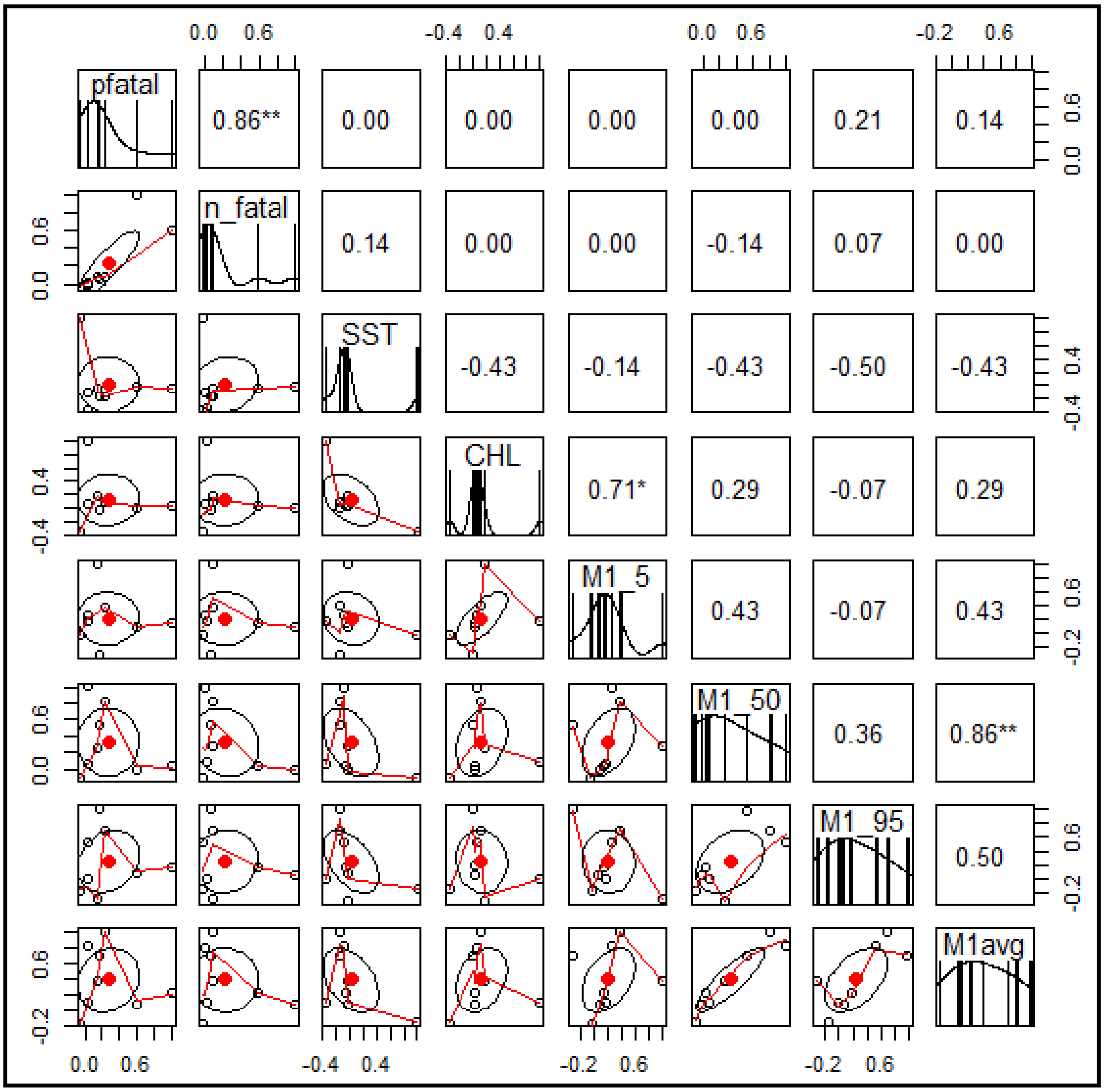


Figure A3.4: Kendall's rank correlation matrix of percentage fatal infection with *Bonamia exitiosa* and numbers of fatal infections per tow with climatic variables chlorophyl (CHL), sea surface temperature (SST), the M1 pressure differential (5th, 50th, 95th and average indices). Kendall's tau shown as black text. For each variable, panels show 1. the variable name and histogram (diagonal); 2. jittered data, loess smother and correlation eclipse (below the diagonal), and 3. the Kendall's tau and significance level with stars (above the diagonal).

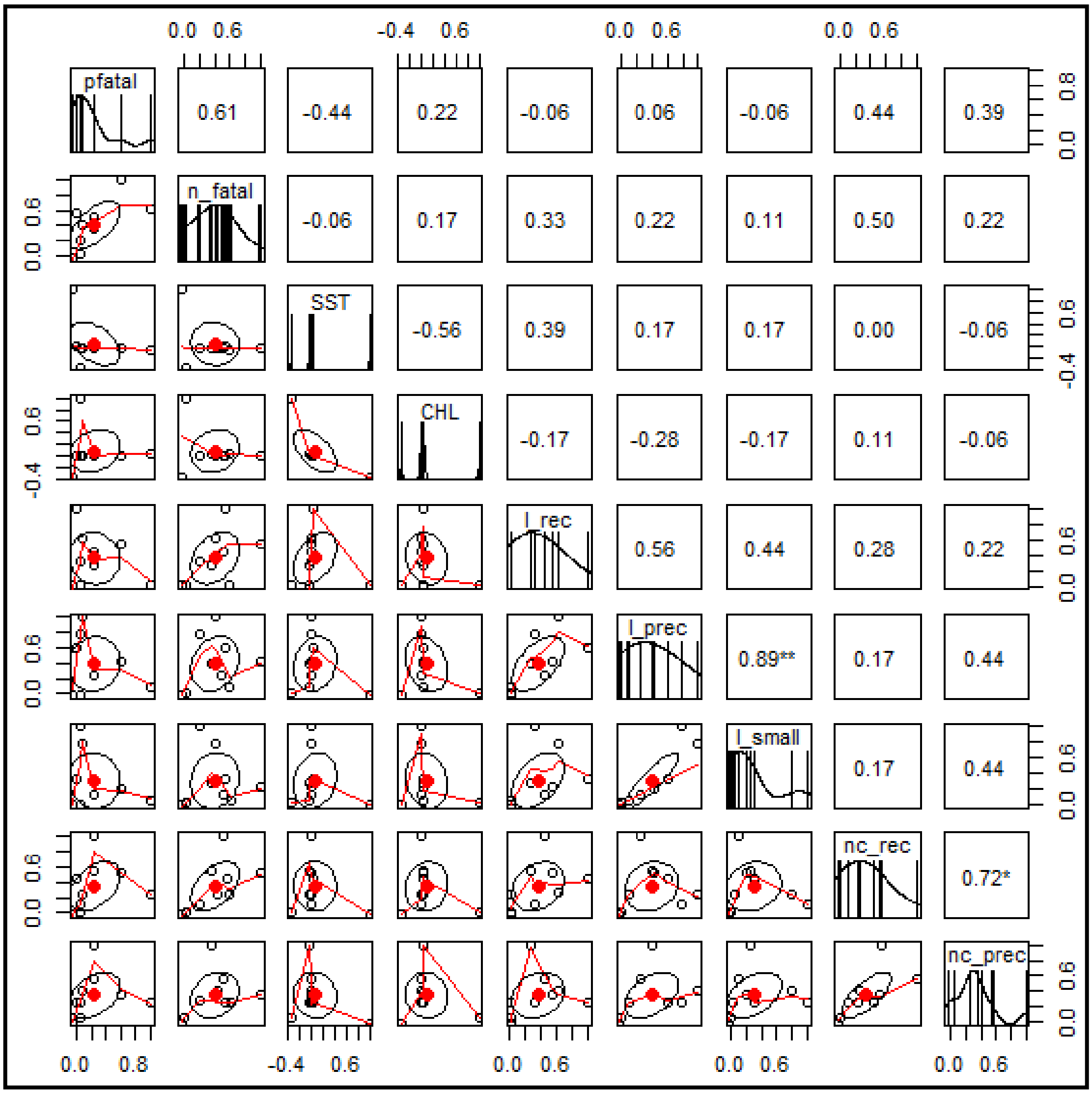


Figure A3.5: Kendall's rank correlation matrix of percentage fatal infection with *Bonamia exitiosa* and numbers of fatal infections per tow with climatic variables chlorophyl (CHL), sea surface temperature (SST), live recruit-sized, pre-recruit and small oysters, and recruit-sized and pre-recruit new clocks. Kendall's tau shown as black text. For each variable, panels show 1. the variable name and histogram (diagonal); 2. jittered data, loess smother and correlation eclipse (below the diagonal), and 3. the Kendall's tau and significance level with stars (above the diagonal).

APPENDIX 4: Maps of fishery and survey areas

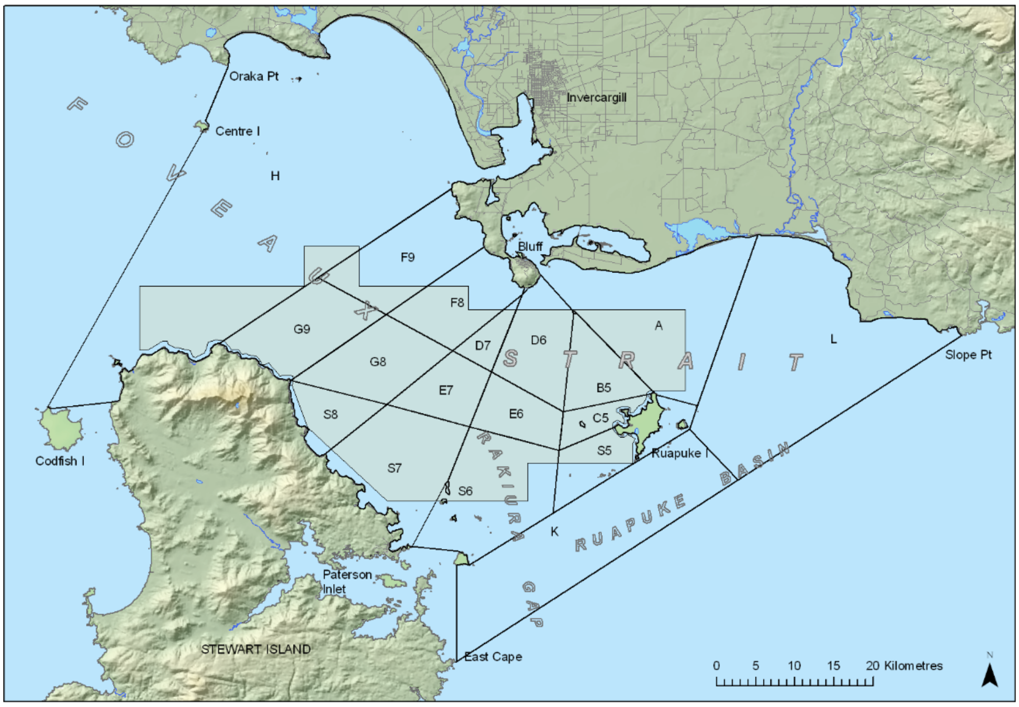


Figure A4.1: Foveaux Strait (OYU 5) stock boundary and outer boundary of the 1999 dredge survey area (shaded) encompassing almost all the commercial fishery, and the Foveaux Strait oyster statistical reporting areas.

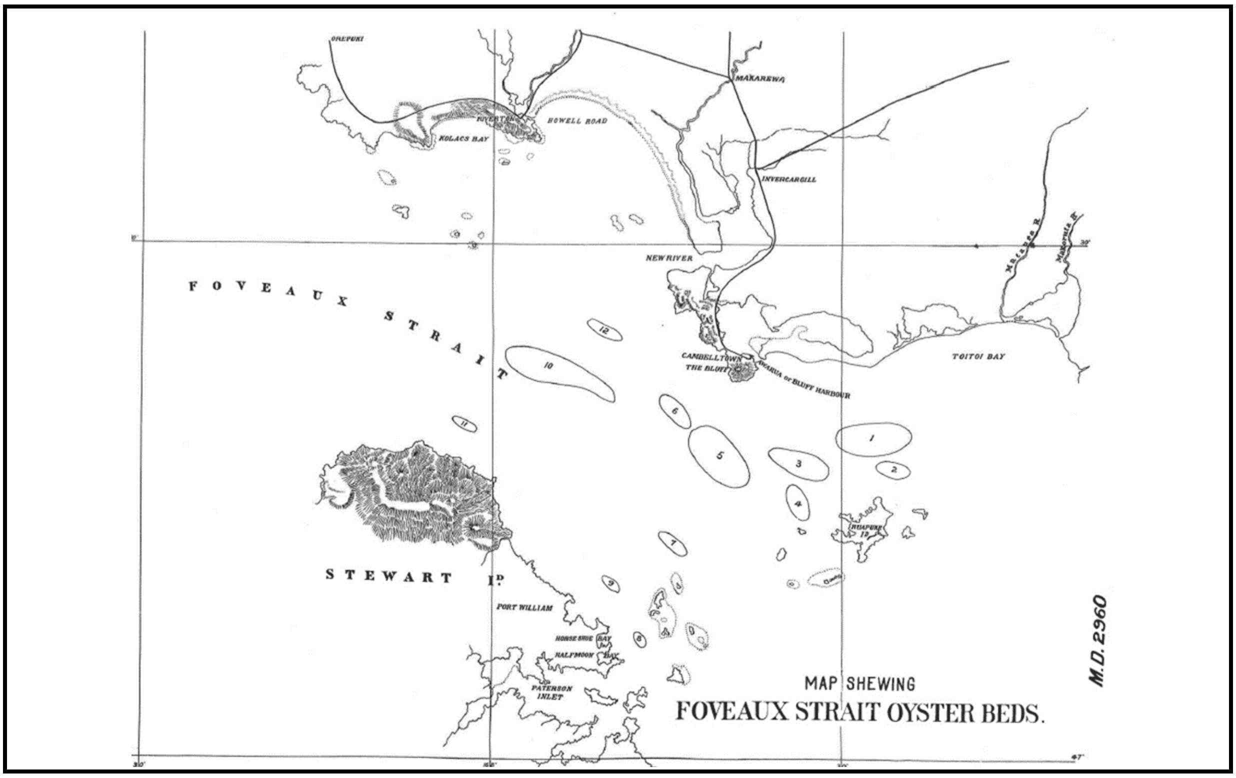


Figure A4.2: Oyster beds identified in Hunter's 1906 survey of the Foveaux Strait oyster beds (Sorenson 1968).

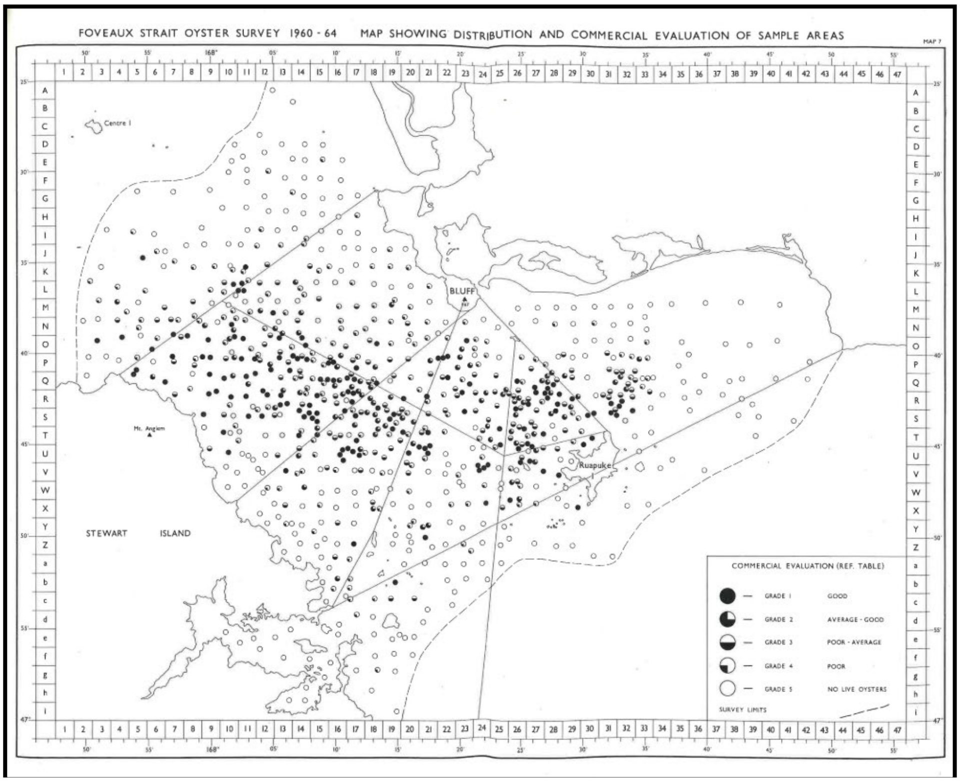


Figure A4.3: Map 7 of Stead (1971b), The distribution and commercial evaluation of oyster beds from dredge surveys in 1960–64.

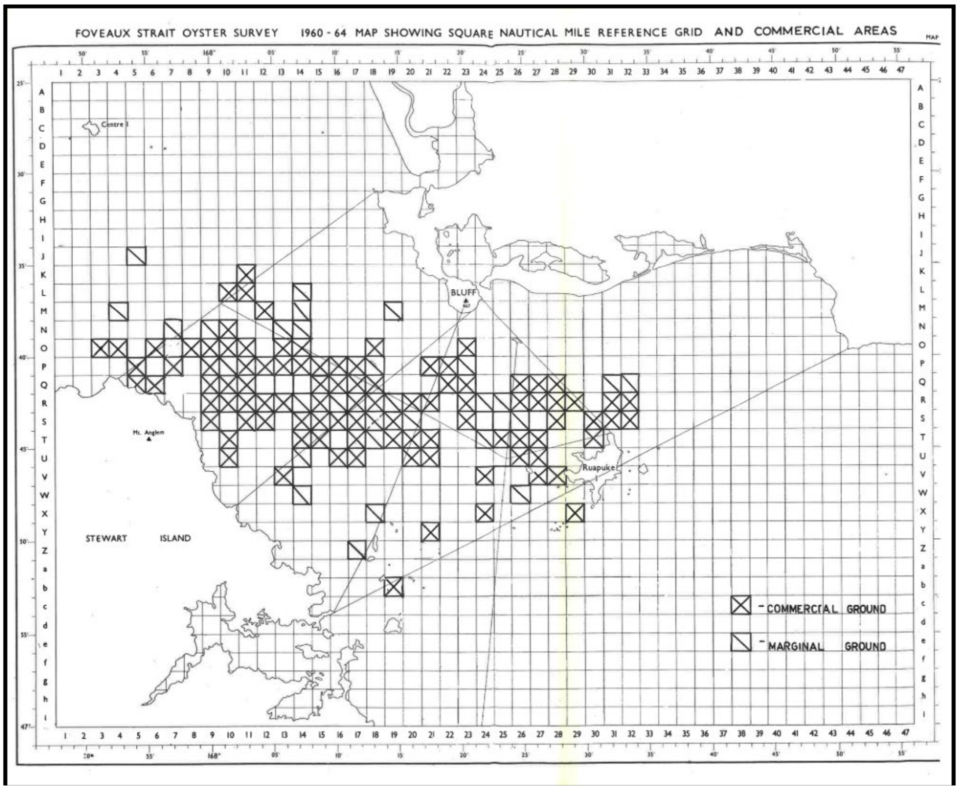


Figure A4.4: Map 8 of Stead (1971b), The distribution of commercial fishery areas by square nautical mile reference grid from dredge surveys in 1960–64.

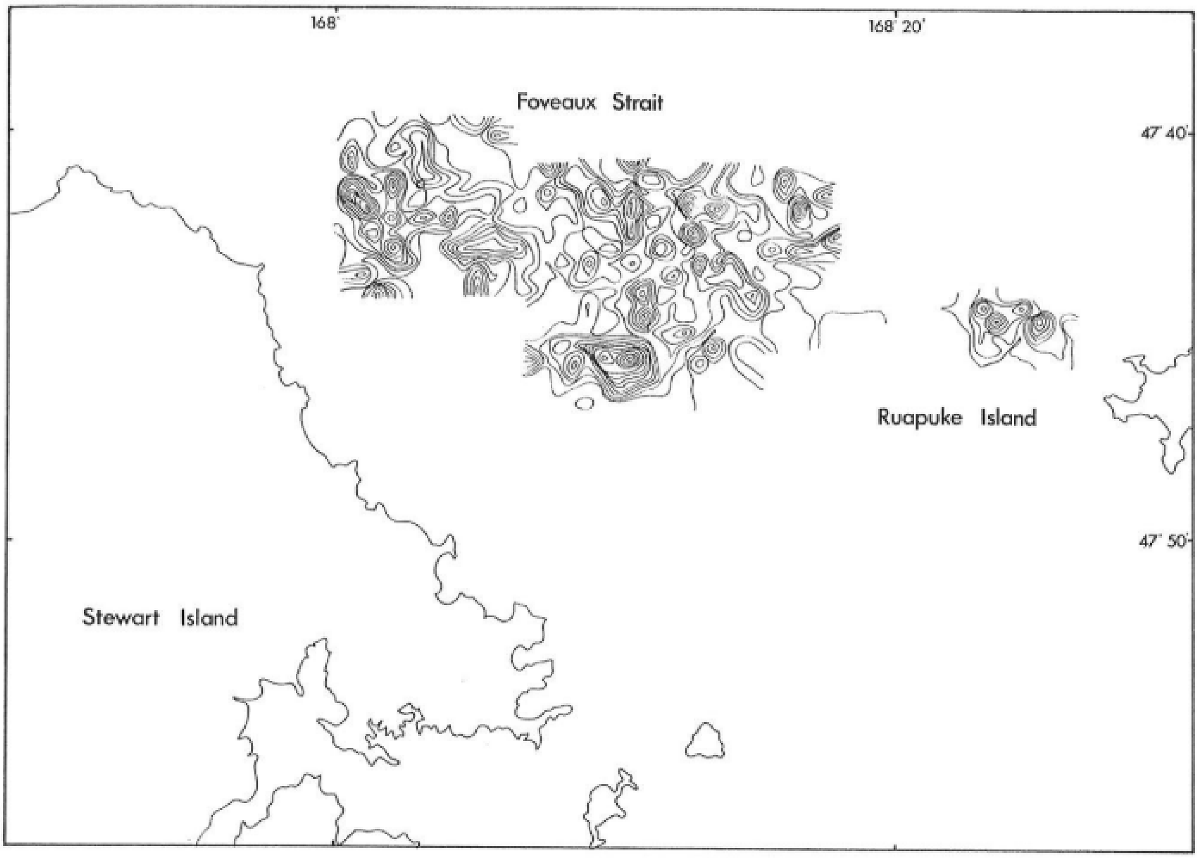


Figure A4.5: The distribution of oysters from Cranfield's 1975 surveys. Sampling estimated oysters from a 5-minute tow over a 1/3 nm grid a with a 1.2 m wide dredge. Oyster beds were separated by bare ground (Allen & Cranfield 1979).

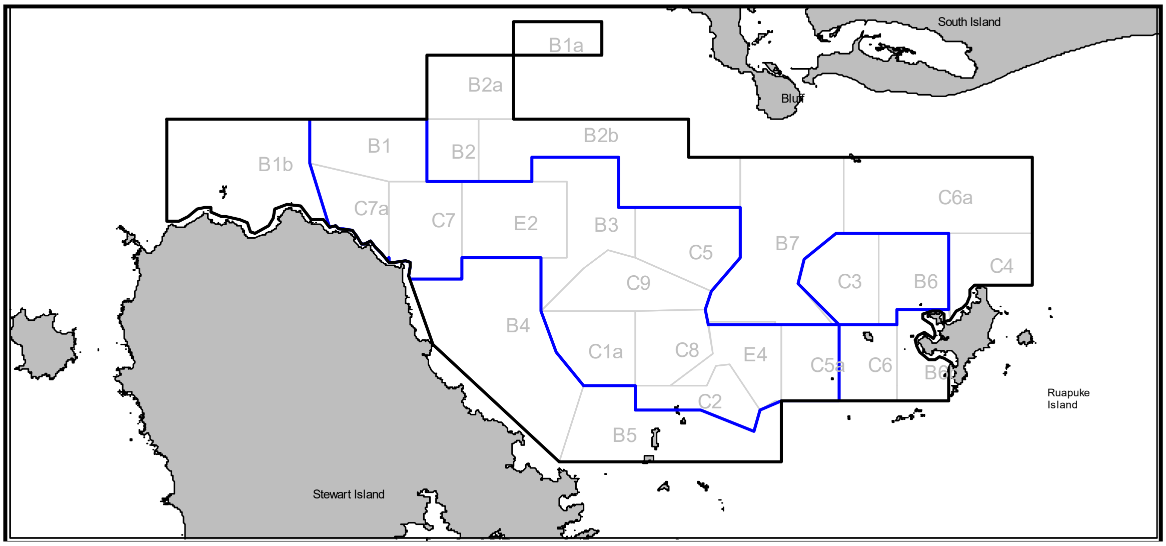


Figure A4.6: The 2007 stock assessment survey area (heavy, black outer line), and the Bonamia survey area (blue line) that covered the commercial fishery area in 2017 (Michael et al. 2019a).

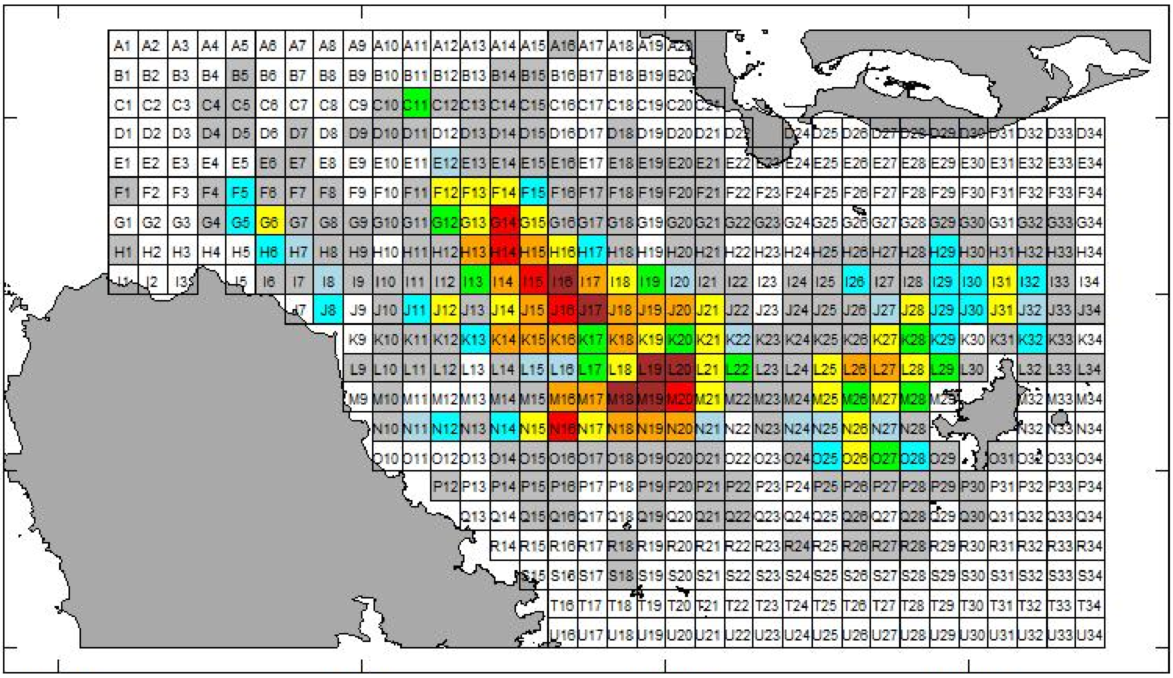


Figure A4.7: The percentage of all tows per cell combined for the 2006–19 oyster seasons. Cells shaded brown ≥ than 3.0% of tows, red < 3.0% & ≥ 2.0 %, orange < 2.0% ≥1.0%, yellow < 1.0% & ≥ 0.5%, green < 0.5 & ≥ 0.3%, blue < 0.3 & ≥0.2%, cyan < 0.2 & ≥ 0.1%, and grey < 0.1 & > 0.

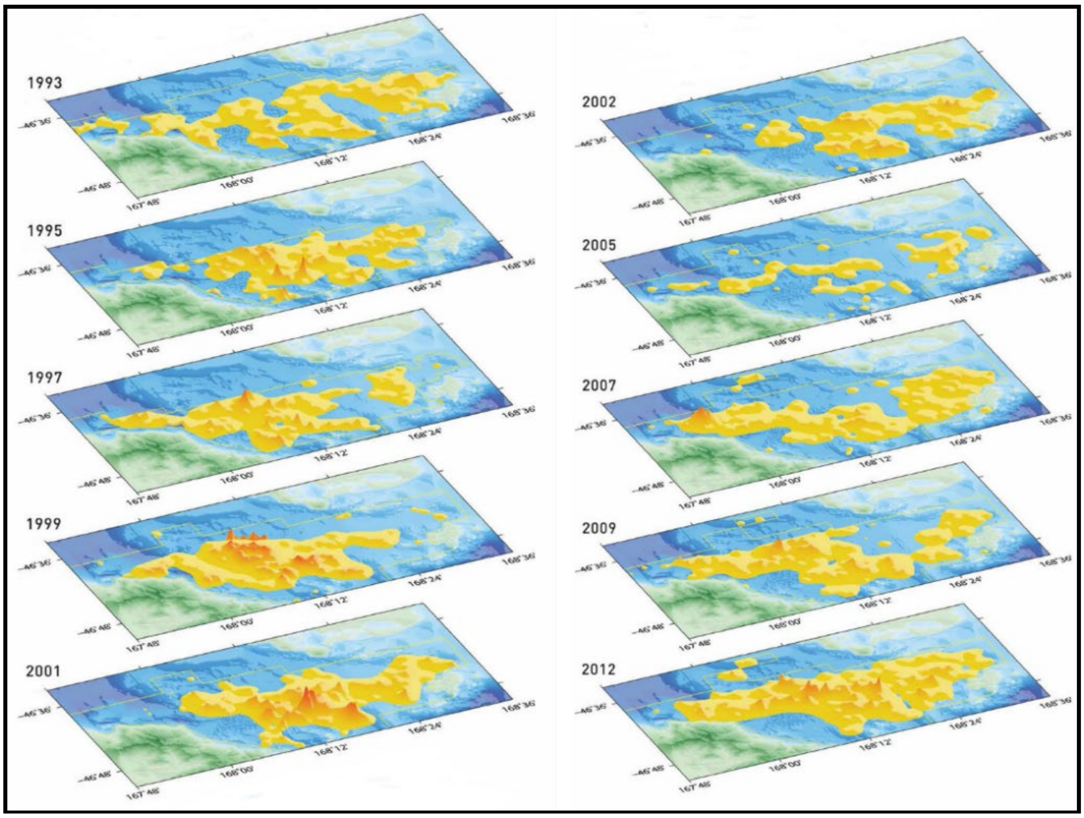


Figure A4.8: The distribution of oysters in Foveaux Strait from dredge surveys 1993–2012. The demographics and biology of oysters suggest the fishery comprises localised populations that have persisted in the same locations after high disease mortality from *Bonamia exitiosa* and periodic high levels of fishing. Image by Erika Mackay (NIWA).

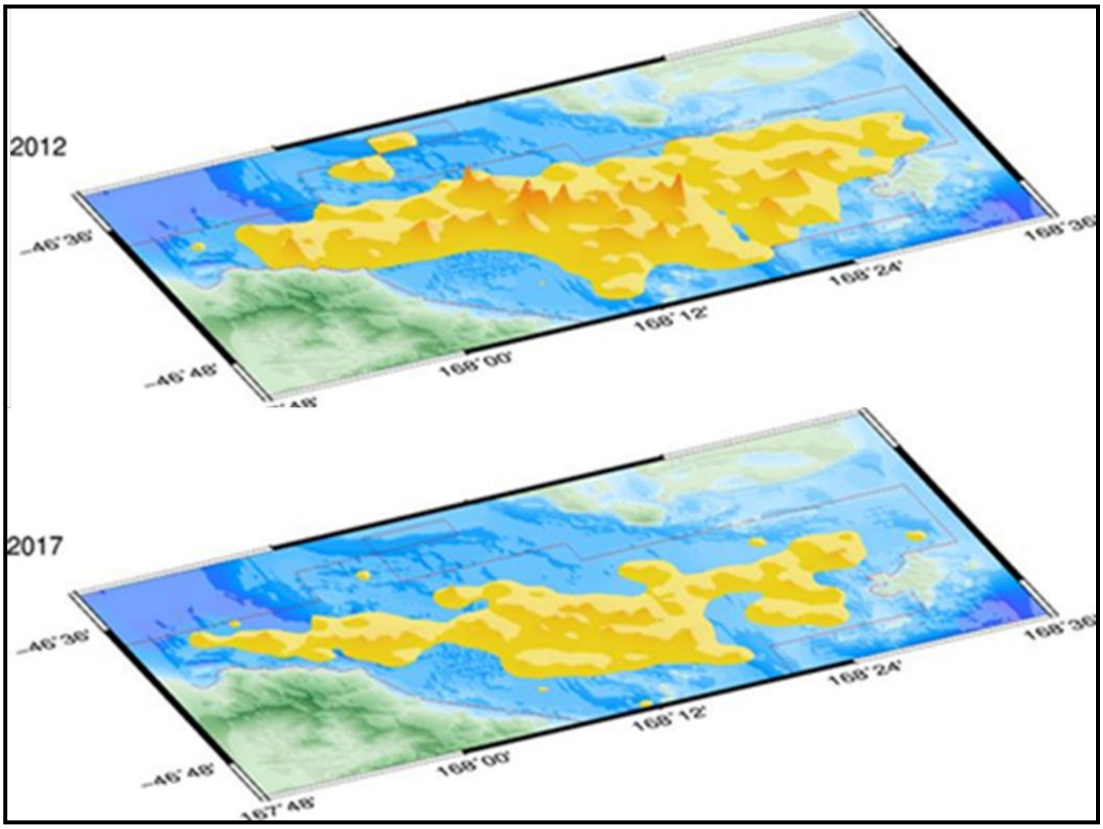


Figure A4.9: The distribution of oyster densities in Foveaux Strait from stock assessment dredge surveys in 2012 and 2017. High oyster densities reduced by *Bonamia exitiosa* mortality. Image by Andy McKenzie (NIWA).

APPENDIX 5: Foveaux Strait oyster surveys

Table A5.1: A summary of Foveaux Strait dredge oyster survey data 1906–2021 (numbers of live, new clocks, and old clocks in millions), whether sampling was undertaken to test for *Bonamia exitiosa* (*B. exitiosa*), and whether size frequencies were sampled, values give sample size . '–' indicates unknown. Data updated from (Dunn 2007) and (Large et al. 2021).

Date	Design[1]	Area (km^2)	Stations	Type[2]	Category	Live	CV	New clocks	Old clocks	*Bonamia exitiosa.*	Lengths	Reference
Jan 1906	Unknown	*ca.* 1 200	–	A		–	–	–	–	–	–	(Hunter 1906)
Mar–Aug 1926[3]	CD	*ca.* 400	–	B		–	–	–	–	–	19 272	(Sorensen 1968)
Jan 1927[3]	Unknown	–	–	B		–	–	–	–	–	4 135	(Sorensen 1968)
1945[4]	CD	*ca.* 400		B		–	–	–	–	–	–	(Sorensen 1968)
1960–64	Grid	*ca.* 1 800	542	E	*Recruit*	~1 000	–	–	–	–	11 576[5]	(Stead 1971b)
		1 055	310	E*	*Recruit*	3 059	0.21	–	–	–	–	Re-analysed estimate
1962	Specific	–	36	Dive	*Recruit*	–	–	–	–	–	–	(Stead 1971b)
1965–1971	Specific	374	6	C	–	–	–	–	–	–	–	(Street & Crowther 1973)
1973	Grid	–	150	F	*Recruit*	–	–	–	–	–	–	(Allen & Cranfield 1979)
Apr–Aug 1974	MR	374	–	C	*Recruit*	~1 800	0.20	–	–	–	–	(Cranfield & Allen 1979)
Apr–Aug 1975	MR	374	–	C	*Recruit*	~1 500	0.11	–	–	–	–	(Cranfield & Allen 1979)
1975–76	Grid	374	929	F	*Recruit*	1 140	0.15	–	–	–	–	(Allen & Cranfield 1979)
Sep 1986	Specific	–	27	F	*Recruit*	–	–	–	–	Yes	–	(Dinamani et al. 1987)
Jan 1987	Specific	–	67	F	*Recruit*	–	–	–	–	Yes	–	(Dinamani et al. 1987)
Jul 1990	Grid	1 116	293	D*	*Recruit*	771	0.14*	–	–	Yes	–	(Doonan et al. 1992)
		1 055	293	D*	*Recruit*	707	0.11	41	574	–	–	Re-analysed estimate
Oct 1990	SR	646	83	Dive	*Recruit*	–	–	–	–	–	412[5]	(Cranfield et al. 1991)
		646	83	Dive	*Pre-recruit*	–	–	–	–	–	420[5]	(Cranfield et al. 1991)
		646	83	Dive	*Small*	–	–	–	–	–	1 280[5]	(Cranfield et al. 1991)
Oct 1990	SR	646	116	F	*Recruit*	607	0.11	–	–	Yes	–	(Cranfield et al. 1991)
		1 055	116	F*	*Recruit*	623	0.12	35	–	–	–	Re-analysed estimate
Mar 1992	Grid	1 229	370	D*	*Recruit*	319	0.18	–	–	Yes	–	(Doonan & Cranfield 1992)
		1 055	293	D*	*Recruit*	285	0.12	2	285	–	–	Re-analysed estimate
Nov\Dec1992	Specific		128	C								Stead, D.H. (1994),
Oct 1993	Grid	875	177	D*	*Recruit*	372	0.21	–	–	–	–	(Cranfield et al. 1993)
		1 055	177	D*	*Recruit*	397	0.10	1	292	–	–	Re-analysed estimate
		1 055	177	D*	*Pre-recruit*	383	0.11	2	173	–	–	Re-analysed estimate
		1 055	177	D*	*Small*	1 004	0.10	–	–	–	–	Re-analysed estimate
Nov 1993	Specific		65	C								Stead, D.H. (1994
		1 055	49	D*	*Small*	402	0.25	–	–	–	–	Re-analysed estimate

Table A5.1: Continued.

Date	Design[1]	Area (km^2)	Stations	Type[2]	Category	Live	CV	New clocks	Old clocks	***Bonamia exitiosa.***	Lengths	Reference
Mar 1995	SR	680	50	D*	*Recruit*	543	0.30	–	–	Yes	–	(Cranfield et al. 1995)
		680	50	D*	*Pre-recruit*	–	–	–	–	Yes	–	(Cranfield et al. 1995)
		1 055	49	D*	*Recruit*	576	0.25	6	48	–	–	Re-analysed estimate
		1 055	49	D*	*Pre-recruit*	401	0.28	15	40	–	–	Re-analysed estimate
Oct 1995	SR	680	154	D*	*Recruit*	639	0.19	–	–	–	–	(Cranfield et al. 1996)
		1 055	154	D*	*Recruit*	782	0.11	1	44	–	–	Re-analysed estimate
		1 055	154	D*	*Pre-recruit*	380	0.10	~0	22	–	–	Re-analysed estimate
Oct 1997	SR	693	107	D*	*Recruit*	630	0.21	–	–	–	–	(Cranfield et al. 1998)
		1 055	107	D*	*Recruit*	660	0.14	~0	74	–	–	Re-analysed estimate
		1 055	107	D*	*Pre-recruit*	727	0.14	~0	111	–	–	Re-analysed estimate
		1 055	107	D*	*Small*	918	0.14	–	–	–	–	Re-analysed estimate
Jan 1998	Specific	–	–	D*	*Recruit*	–	–	–	–	Yes	–	(Cranfield 1998)
		–	–	D*	*Pre-recruit*	–	–	–	–	–	–	(Cranfield 1998)
Oct 1999	SR	1 055	199	D*	*Recruit*	1 461	0.16	–	–	–	–	(Michael et al. 2001)
		1 055	199	D*	*Recruit*	1 453	0.16	~0	176	–	16 054	Re-analysed estimate
		1 055	199	D*	*Pre-recruit*	896	0.12	0	97	–	8 424	Re-analysed estimate
		1 055	199	D*	*Small*	1 364	0.11	–	–	–	16 085	Re-analysed estimate
Mar 2000	Specific	–	35	D*	*Recruit*	–	–	–	–	Yes	–	(Dunn et al. 2000)
Oct 2001	SR	1 055	192	G*	*Recruit*	995	0.11	10	466	Yes	4 227	(Michael et al. 2004b)
		1 055	192	G*	*Pre-recruit*	872	0.12	3	111	Yes	3 460	(Michael et al. 2004b)
		1 055	192	G*	*Small*	1 410	0.12	–	–	Yes	7 475	(Michael et al. 2004b)
Jan 2002	Specific	–	35	G*	*Recruit*	–	–	–	–	Yes	–	(Dunn et al. 2002b)
Mar 2002	Specific	–	35	G*	*Recruit*	–	–	–	–	Yes	–	(Dunn et al. 2002a)
Oct 2002	SR	1 055	155	G*	*Recruit*	502	0.14	68	587	Yes	–	(Michael et al. 2004a)
		1 055	155	G*	*Pre-recruit*	520	0.11	11	94	Yes	–	(Michael et al. 2004a)
		1 055	155	G*	*Small*	1 243	0.10	–	–	–	–	(Michael et al. 2004a)
Feb 2003	Specific	–	16	G*	*Recruit*	–	–	–	–	Yes	–	(Dunn et al. 2003)
Jan 2004	Specific	–	40	G*	*Recruit*	–	–	–	–	Yes	–	(Michael et al. 2005)
Jan 2005	SR	1 055	80	G*	*Recruit*	408	0.13	3	287	Yes	–	(Michael et al. 2006)
		1 055	80	G*	*Pre-recruit*	415	0.15	4	152	Yes	–	(Michael et al. 2006)
		1 055	80	G*	*Small*	1 345	0.12	–	–	Yes	–	(Michael et al. 2006)
Feb 2006	Specific	407	44	G*	*Recruit*	242	0.14	13	148	Yes	–	(Michael et al. 2008a)
		407	44	G*	*Pre-recruit*	257	0.17	9	72	Yes	–	(Michael et al. 2008a)
		407	44	G*	*Small*	622	0.13	–	–	Yes	–	(Michael et al. 2008a)
Feb 2007[6]	SR	1 070	103	G*	*Recruit*	624	0.10	11	222	Yes	–	(Michael et al. 2008b)
		1 070	103	G*	*Pre-recruit*	464	0.11	4	72	Yes	–	(Michael et al. 2008b)
		1 070	103	G*	*Small*	848	0.09	–	–	Yes	–	(Michael et al. 2008b)
		1 055	101	G*	*Recruit[7]*	622	0.10	11	222	Yes	–	Re-analysed estimate

Table A5.1: Continued.

Date	Design[1]	Area (km^2)	Stations	Type[2]	Category	Live	CV	New clocks	Old clocks	*Bonamia exitiosa.*	Lengths	Reference
Feb 2007[6]		1 055	101	G*	*Pre-recruit*[7]	463	0.11	4	72	Yes	–	Re-analysed estimate
		1 055	101	G*	*Small*[7]	842	0.09	–	–	Yes	–	Re-analysed estimate
Feb 2008	Specific	671	40	G*	*Recruit*	694	0.11	18	136	Yes	–	(Michael et al. 2009a)
		671	40	G*	*Pre-recruit*	269	0.10	5	42	Yes	–	(Michael et al. 2009a)
		671	40	G*	*Small*	702	0.13	–	–	Yes	–	(Michael et al. 2009a)
Feb 2009[8]	SR	1 070	105	G*	*Recruit*	725	0.08	17	170	Yes	–	(Michael et al. 2009b)
		1 070	105	G*	*Pre-recruit*	358	0.10	4	68	Yes	–	(Michael et al. 2009b)
		1 070	105	G*	*Small*	910	0.10	–	–	Yes	–	(Michael et al. 2009b)
		1 055	101	G*	*Recruit*[7]	720	0.08	16	166	Yes	–	Re-analysed estimate
		1 055	101	G*	*Pre-recruit*[7]	354	0.10	4	67	Yes	–	Re-analysed estimate
		1 055	101	G*	*Small*[7]	889	0.10	–	–	Yes	–	Re-analysed estimate
Feb 2010	Specific			G*	*Recruit*	809	0.12	602	–	Yes	–	(Michael et al. 2011)
				G*	*Pre-recruit*	367	0.10	–	–	Yes	–	(Michael et al. 2011)
				G*	*Small*	939	0.09	–	–	Yes	–	(Michael et al. 2011)
Feb 2011	Specific			G*	*Recruit*	596	0.11	23	–	Yes	–	(Michael et al. 2012b)
				G*	*Pre-recruit*	278	0.11	–	–	Yes	–	(Michael et al. 2012b)
				G*	*Small*	516	0.12	–	–	Yes	–	(Michael et al. 2012b)
Feb 2012[8]	SR	1 070	146	G*	*Recruit*	918	0.08	30	–	Yes	–	(K.P. Michael, unpublished)
		1 070	146	G*	*Pre-recruit*	414	0.10	12	–	Yes	–	(K.P. Michael, unpublished)
		1 070	146	G*	*Small*	612	0.14	–	–	Yes	–	(K.P. Michael, unpublished)
		1 055	143	G*	*Recruit*[7]	913	0.08	29	–	Yes	–	Re-analysed estimate
		1 055	143	G*	*Pre-recruit*[7]	410	0.10	12	–	Yes	–	Re-analysed estimate
		1 055	143	G*	*Small*[7]	607	0.14	–	–	Yes	–	Re-analysed estimate
Feb 2014[9]	SR	1 070	60	G*	*Recruit*	1021	0.12	84.1	–	Yes	–	(Michael et al. 2015a)
		1 070	60	G*	*Pre-recruit*	226	0.14	5.3	–	Yes	–	(Michael et al. 2015a)
		1 070	60	G*	*Small*	303	0.11	–	–	Yes	–	(Michael et al. 2015a)
	SR	578	55	G*	*Recruit*	538	0.11	39.4	–	Yes	–	(Michael et al. 2015a)
		578	55	G*	*Pre-recruit*	148	0.12	3.6	–	Yes	–	(Michael et al. 2015a)
		578	55	G*	*Small*	156	0.10	–	–	Yes	–	(Michael et al. 2015b)
Feb 2015[9]	SR	1 070	60	G*	*Recruit*	510	0.09	23.7	–	Yes	–	(Michael et al. 2015b)
		1 070	60	G*	*Pre-recruit*	122	0.11	4.5	–	Yes	–	(Michael et al. 2015b)
		1 070	60	G*	*Small*	249	0.20	–	–	Yes	–	(Michael et al. 2015b)
	SR	578	55	G*	*Recruit*	351	0.08		–	Yes	–	(Michael et al. 2015b)
		578	55	G*	*Pre-recruit*	89	0.14		–	Yes	–	(Michael et al. 2015b)
		578	55	G*	*Small*	303	0.11	–	–	Yes	–	(Michael et al. 2015b)

Table A5.1: Continued.

Date	Design[1]	Area (km^2)	Stations	Type[2]	Category	Live	CV	New clocks	Old clocks	***Bonamia exitiosa.***	Lengths	Reference
Feb 2016[9]	SR	1 070	60	G*	*Recruit*	561	0.13	3.6	–	Yes	–	(Michael et al. 2016)
		1 070	60	G*	*Pre-recruit*	191	0.17	0.8	–	Yes	–	(Michael et al. 2016)
		1 070	60	G*	*Small*	364	0.15	–	–	Yes	–	(Michael et al. 2016)
	SR	578	55	G*	*Recruit*	385	0.09	1.4	–	Yes	–	(Michael et al. 2016)
		578	55	G*	*Pre-recruit*	121	0.03	0.2	–	Yes	–	(Michael et al. 2016)
		578	55	G*	*Small*	256	0.07	–	–	Yes	–	(Michael et al. 2016)
Feb 2017[9]	SR	1 070	60	G*	*Recruit*	527	0.09	7.8	–	Yes	–	(Michael et al. 2019a)
		1 070	60	G*	*Pre-recruit*	168	0.10	1.3	–	Yes	–	(Michael et al. 2019a)
		1 070	60	G*	*Small*	361	0.09	–	–	Yes	–	(Michael et al. 2019a)
	SR	578	55	G*	*Recruit*	364	0.11	5.3	–	Yes	–	(Michael et al. 2019a)
		578	55	G*	*Pre-recruit*	123	0.12	0.9	–	Yes	–	(Michael et al. 2019a)
		578	55	G*	*Small*	262	0.10	–	–	Yes	–	(Michael et al. 2019a)
Feb 2018[9]	SR	1 070	60	G*	*Recruit*	883	0.27	3.4	–	Yes	–	(Michael et al. 2019b)
		1 070	60	G*	*Pre-recruit*	225	0.15	0.4	–	Yes	–	(Michael et al. 2019b)
		1 070	60	G*	*Small*	552	0.18	–	–	Yes	–	(Michael et al. 2019b)
	SR	578	55	G*	*Recruit*	494	0.11	2.9	–	Yes	–	(Michael et al. 2019b)
		578	55	G*	*Pre-recruit*	178	0.11	0.4	–	Yes	–	(Michael et al. 2019b)
		578	55	G*	*Small*	402	0.13	–	–	Yes	–	(Michael et al. 2019b)
Feb 2019[9]	SR	1 070	60	G*	*Recruit*	868	0.17	9.2	–	Yes	–	(Michael et al. 2020)
		1 070	60	G*	*Pre-recruit*	310	0.15	1.0	–	Yes	–	(Michael et al. 2020)
		1 070	60	G*	*Small*	868	0.11	–	–	Yes	–	(Michael et al. 2020)
	SR	578	55	G*	*Recruit*	543	0.13	4.1	–	Yes	–	(Michael et al. 2020)
		578	55	G*	*Pre-recruit*	217	0.15	1.0	–	Yes	–	(Michael et al. 2020)
		578	55	G*	*Small*	596	0.10	–	–	Yes	–	(Michael et al. 2020)
Feb 2019[9]	SR	1 070	60	G*	*Recruit*	868	0.17	9.2	–	Yes	–	(Michael et al. 2020)
Feb 2020[9]	SR	1 070	60	G*	*Recruit*	879	0.13	8.5	–	Yes	–	(Michael et al. 2021)
		1 070	60	G*	*Pre-recruit*	436	0.11	5.0	–	Yes	–	(Michael et al. 2021)
		1 070	60	G*	*Small*	1 357	0.11	–	–	Yes	–	(Michael et al. 2021)
	SR	578	55	G*	*Recruit*	530	0.12	3.5	–	Yes	–	(Michael et al. 2021)
		578	55	G*	*Pre-recruit*	265	0.11	0.5	–	Yes	–	(Michael et al. 2021)
		578	55	G*	*Small*	1 052	0.14	–	–	Yes	–	(Michael et al. 2021)
Feb 2021[9]	SR	1 070	60	G*	*Recruit*	868.1	0.06	5.5	–	Yes	–	(Michael et al. 2021a)
		1 070	60	G*	*Pre-recruit*	522.3	0.08	2.0	–	Yes	–	(Michael et al. 2021a)
		1 070	60	G*	*Small*	1 202	0.07	–	–	Yes	–	(Michael et al. 2021a)
	SR	578	55	G*	*Recruit*	801	0.06	5.5	–	Yes	–	(Michael et al. 2021a)
		578	55	G*	*Pre-recruit*	487	0.08	2.6	–	Yes	–	(Michael et al. 2021a)
		578	55	G*	*Small*	1 091	0.07	–	–	Yes	–	(Michael et al. 2021a)

Table A5.1: Continued.

Date	Design[1]	Area (km^2)	Stations	Type[2]	Category	Live	CV	New clocks	Old clocks	*Bonamia exitiosa.*	Lengths	Reference
Feb 2022[9]	SR	1 070	60	G*	*Recruit*	824	0.20	10.3	–	Yes	–	(Michael et al. 2023a)
		1 070	60	G*	*Pre-recruit*	522	0.20	3.1	–	Yes	–	(Michael et al. 2023a)
		1 070	60	G*	*Small*	2 177	0.80	–	–	Yes	–	(Michael et al. 2023a)
	SR	578	55	G*	*Recruit*	558	0.09	7.4	–	Yes	–	(Michael et al. 2023a)
		578	55	G*	*Pre-recruit*	370	0.09	2.6	–	Yes	–	(Michael et al. 2023a)
		578	55	G*	*Small*	1 117	0.10	–	–	Yes	–	(Michael et al. 2023a)

1. Survey designs either circumscribed the known oyster beds (CD), sampled specific stations non-randomly (specific), followed a grid pattern (grid), were stratified random (SR), or were mark-recapture surveys (MR).
2. * Indicates a calibrated estimate. A–F indicate the type of dredge, while ‘Dive’ indicates a dive survey. The dredges are: (A) Light, hand-hauled commercial dredge about 1 m-wide, used up to 1913; (B) Commercial dredge, about 3.35-m wide with single-bit and single ring bag, weighing ~150 kg and used up to 1968; (C) Commercial dredge, about 3.35-m wide, introduced in 1968 with double-bit and double ring bag and weighing about 400 kg; (D) The 1968 commercial dredge, about 3.35-m wide, modified in 1984 increasing weight to about 530 kg; (E) 0.91-m wide light survey dredge with a rigid mesh catch bag; (F) 1.25-m wide survey dredge, designed to be a smaller version of 1968 commercial dredge with double-bit and double flexible ring bag; (G) Survey dredge 3.32-m wide commercial dredge similar to the 3.35-m wide dredge introduced in 1968 with double-bit and double ring bag, and weighing 400 kg.
3. The 1945 survey data are suspected of being destroyed in a fire in the 1950s.
4. The original reports detailing the Mar–Aug 1926 and Jan 1927 surveys have been lost; these summaries are reproduced from Sorensen (1968).
5. Data recorded as height, not length. In the October 1990 dive survey, height frequencies were grouped by size class according to the height measurement, and not their ability to pass through a 50 mm or 58 mm diameter ring.
6. The February 2007 included an additional stratum in north Foveaux Strait. Re-analysed estimates ignore this stratum, and hence are estimates of abundance over an area comparable with earlier surveys.
7. Two errors in the length of tows resulted in a revised estimate of the number of recruits and small oysters for the February 2007 survey. Model runs presented below used values of 661 recruits and 877 smalls for the February 2007 abundance indices, instead of the corrected values of 663 and 879 respectively.
8. The February 2007 included an additional stratum in north Foveaux Strait. Re-analyzed estimates ignore this stratum, and hence are estimates of abundance over an area comparable to earlier surveys.
9. Population estimates from Bonamia surveys, 12 of the 26 stock assessment survey strata combined into a single stratum and sampling intensity is low (n=5).