Fisheries New Zealand

Tini a Tangaroa

A review of the Foveaux Strait oyster (OYU 5) stock assessment model and recommendations for future development

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EXECUTIVE SUMMARY

The Foveaux Strait oyster (*Ostrea chilensis*) fishery (OYU 5) is a single population that comprises many spatially stable, localised areas with relatively high densities of oysters ('oyster beds'). Oyster beds wax and wane, in cycles driven by disease mortality from the oyster pathogen *Bonamia exitiosa* (Bonamia), and by recruitment to the oyster population and the fishery. The highest recruitment to the population has occurred at times of low disease mortality and at low oyster densities. In the absence of disease mortality, the oyster population has rebuilt quickly in fishery areas that have been fished for many years. Management of OYU 5 is based on the relative levels of future stock size under different catch scenarios from stock model projections to virgin spawning stock reference points. However, catch accounts for < 3% of the stock, and the abundance of oysters is mainly determined by the levels of disease mortality and, to a lesser extent, levels of recruitment which vary markedly. Management of OYU 5 also recognises that at the current harvest levels (Total Allowable Commercial Catches), any effects of fishing on either oyster production, or on exacerbating Bonamia mortality, are not detectable. This research programme sought to review the most recent ('current') assessment model and develop a plan for future development of this model, or alternative models, to better inform effective management and fishing strategies.

The current model uses historical abundance data series as observations of the trajectory of the population and balances unaccounted for losses or increases to the stock between surveys by estimating disease mortality and recruitment within the model. The model cannot predict future disease rates. If a disease sub-model could be developed to provide projections of future disease mortality, projections of future stock status could be greatly improved. A better understanding of the disease process is required to do this. In the short-term, the current model could also be improved through better information on disease mortality at oyster size. The use of empirical data on disease and recruitment would further improve the model, along with better estimates of numbers at length (year class strengths) from improved selectivity ogives. This report provides a summary of key knowledge gaps and future research to address them.

Conceptual models of climatic, environmental, habitat, disease, and biological drivers of oyster production were developed from the primary and grey literature, using data from the fishery and expert opinion. These models highlighted a number of key knowledge gaps in the relationships between putative drivers. A concurrent study (OYS2020-03) found climatic indices, e.g., Southern Oscillation Index and its effects on temperature, primary production, storm frequency, and sediment movement, appear to drive 'year' effects on oyster condition and energy levels that have flow-on effects onto reproduction, growth, and disease. Years with high oyster energy levels were associated with high disease mortality, high growth, but, counter-intuitively, low recruitment to the oyster population. These findings raised important questions about disease processes in Foveaux Strait oysters.

Research to inform the development of a predictive disease model is suggested as the highest priority. We believe it will provide the greatest gains in information available to fishery stakeholders for effective management and fishing. Key to the development of such a model is the understanding of trigger points for heightened disease mortality and/or predictable temporal cycles. In the short- to medium-term, suggestions to improve the current OYU 5 stock assessment model are also summarised. The revision of the OYU 5 strategic research plan, to prioritise and schedule research suggestions in this report, is strongly recommended.

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1. INTRODUCTION

The Foveaux Strait oyster (*Ostrea chilensis*) fishery (OYU 5) is one of New Zealand's oldest and most important fisheries for its social and economic values. OYU 5 is part of the Group 1 stocks in the draft National Fisheries Plan for Inshore Shellfish (Ministry of Fisheries 2011) and is also subject to an approved collaborative fisheries plan (Ministry of Fisheries 2009). This plan is underpinned by a strategic research plan (e.g., Michael 2010) which is regularly reviewed and updated by a Foveaux Strait oyster management group that comprises Fisheries New Zealand, tangata whenua (Ngāi Tahu), the oyster industry (fishers and processors), and recreational fishers. A key objective of the fisheries plan is to mitigate the effects of *Bonamia exitiosa* (hereafter Bonamia; Berthe & Hine 2003) on the fishery, and the highest priority objective of the strategic research plan is to develop the capability to predict where and when Bonamia mortality will occur.

OYU 5 is considered a single population (genetic stock); however, different regions of the fishery appear to have different productivities. The 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. Recurrent mortality from Bonamia since 1985 (Doonan et al. 1994, Cranfield et al. 2005, Michael et al. 2021) has caused substantial declines in oyster densities in these localised populations. Oyster beds waxed and waned, in cycles driven by Bonamia mortality and by recruitment to the oyster population and the fishery. Cycles of mortality have prevented oyster densities and stock sizes rebuilding to pre-Bonamia levels, with upper limits approximately 65% of 1965 to 1985 levels. At relatively high oyster densities, Bonamia mortality increases and substantially reduces oyster densities and population sizes to low levels (60%–90% reductions in abundance over 3–5 years). The effects of Bonamia mortality are disproportionately high in 'beds' with high oyster densities. In contrast, oyster removals through fishing have been estimated to account for less than 3% of the stock. Perhaps counter-intuitively, the highest recruitment to the population has occurred at times of low Bonamia mortality and at low oyster densities. In the absence of Bonamia, the oyster population has rebuilt quickly in fishery areas that have been fished for many years.

Management of OYU 5 is based on spawning stock reference points (Mace 2012). For oysters in Foveaux Strait, it is widely accepted that management based on these reference points alone is ineffective because the relationship between recruits and spawners is weak (Michael & Shima 2018). Current management of the fishery recognises that recruit-sized stock abundance and future benefits from the fishery (harvest levels) are mainly determined by the levels of mortality from Bonamia and the levels of recruitment, which both vary markedly and (it seems) unpredictably. The management also recognises that the current harvest levels (Total Allowable Commercial Catch, TACC) and any effects of fishing on either oyster production, or on exacerbating Bonamia mortality, are not detectable (Michael et al. 2015). Currently, stock assessments cannot predict future disease mortality or recruitment and therefore lack the ability to predict future stock status. Additionally, the oyster industry applies annual, pre-, and mid-season TACC shelving adjustments based on annual science updates from a broad range of research initiatives, and implements some fleet agreed spatial fishing strategies. Opportunities to develop alternative stock assessment models could provide better predictions of future stock size to inform management, and to assess fishing strategies that could improve catch rates and quality whilst also ensuring sustainability of localised densities of oysters ('oyster beds').

Stock assessments have recently been undertaken every five years and were more frequent before 2012. In years between stock assessments, annual surveys are undertaken (Michael et al. 2015). The stock assessment models (Dunn 2005, Fu et al. 2016) predict future oyster abundances based on future annual commercial catches of 7.5, 15, 20, or 30 million oysters and assume future disease mortality rates at 0 y^{-1}, 0.10 y^{-1}, and 0.20 y^{-1}. The last stock assessment was in 2017 (Large et al. 2021).

Whilst disease (Bonamia mortality) is the main driver of oyster population abundance, we have not yet built a model that captures the dynamics of Bonamia, allowing for stock projections to be made with more accuracy. In the 2017 stock assessment, the estimates of disease mortality were the unaccounted-for (residual) decline in abundance after removing the effects of recruitment and natural and fishing

mortality. Our main concern with the current model is its inability to separately account for the effects of disease and recruitment, and thereby to predict disease mortality.

Ostrea chilensis is a hermaphrodite, produces relatively few, large maternally provisioned ova (Cranfield 1979) and broods for the full term of larval development (Michael 2019). Because of the high energy investment in large, lecithotrophic larvae, it is not known whether individual oysters spawn every year. Skipped spawning events might help to explain highly variable larval production and recruitment to the oyster population. Additional to the removal of predominantly female oysters by Bonamia mortality, there may also be non-lethal effects of several pathogens and parasites (e.g., *Alcicornis longicornutus*, previously *Bucephalus longicornutus*) on reproductive success, with flow-on effects on recruitment and size structure.

This Fisheries Assessment Report (FAR) documents a review of the current OYU 5 stock assessment model under research contract OYS2020-02. This research, alongside research on the drivers of oyster productivity (OYS2020-03; Michael 2023), aims to present Fisheries New Zealand with a foundation to further develop the current stock assessment model or to develop alternative stock assessment models for OYU 5 that include the ability to potentially predict disease and other key drivers of future variation in oyster density and population size. To fulfil the specific objectives, we needed to develop alternative conceptual models that better incorporated the putative drivers of oyster population abundance (strongly linked to Fisheries New Zealand research programme OYS2020-03, see Michael 2023) such as disease and its effects on recruitment, and other important biological processes. Available data were collated, and their potential utility was investigated.

This report documents progress on first five of the six key objectives for OYS2020-02:

1. To review the 2017 OYU 5 stock assessment model and new data available for assessments.
2. Describe models of the oyster population.
3. Draft a plan to develop models.
4. Consult with the Foveaux Strait Oyster Management Group.
5. Discuss appropriate platforms for modelling.
6. Present an OYU 5 stock assessment model development plan to a Fisheries New Zealand Working Group (not included in this FAR).

The review is divided into four sections. Section 3.1 was written by Keith Michael and Henry Lane and describes models of the oyster population (Objective 2). Section 3.2 was written by Samik Datta; this section summarises an approach towards developing a disease model, because disease mortality is accepted as the main drive of future stock abundance (Objective 3). Section 3.3 was written by Ian Doonan, the stock assessment modelling expert who reviewed the OYU 5 model and together with Keith Michael reviewed available data (Objectives 1 and 3). Section 4 was written by Keith Michael, Ian Doonan, and Samik Datta and documents information towards a model development plan and strategic research (Objective 6), briefly discusses platforms for modelling (Objective 5), and summarises how this review addresses issues raised by a stakeholder workshop (Objective 4).

These activities were intended to enable a medium-term plan to develop, and test, alternative stock assessment models with increasing accuracy representing oyster stock dynamics, at finer spatial resolutions. Our recommendations include monitoring programmes to provide the data to run candidate models, which overlaps with the monitoring programmes to be developed for Objective 3 of OYS2020-03 (see Michael 2023).

1.1 Describe several conceptual models of the oyster population

Management of OYU 5 is based on spawning stock reference points. This management approach relies on a stock-recruit relationship (Beverton & Holt 1957, Ricker 1975) and is fundamentally based on limiting removals by fishing to maintain or rebuild stock size. For OYU 5, as it is for most shellfisheries, fishing mortality alone is not the main driver of population dynamics (Fu et al. 2016, Fisheries New Zealand 2018). The management of other shellfisheries based on stock-recruit relationships alone has been ineffective (MacKenzie 1997, Lenihan & Peterson 1998, Hobday et al. 2000, Karpov et al. 2000, Anderson et al. 2011, Beck et al. 2011, King et al. 2015, Szuwalski et al. 2015).

Mortality caused by Bonamia can remove up to 90% of the recruit-sized oyster population independent of fishing (Doonan et al. 1994), substantially higher than fishing mortality (<3%). Fisheries New Zealand recognises that oyster abundance in OYU 5 is primarily driven by mortality from Bonamia and that management of the stock through catch limits does not reflect the main drivers of the variation in future oyster abundance (Fu et al. 2016, Fisheries New Zealand 2018).

Although disease mortality and recruitment are key drivers of the variation in oyster abundance, the OYU 5 stock assessment model currently does not use estimates of disease mortality from surveys or estimates of recruitment from spat monitoring and catch sampling. Additionally, the current model gives no consideration to the potential effects and any interactions between *B. exitiosa,* and other oyster pathogens present in the fishery on disease mortality, oyster growth, and recruitment. The interactions among pathogens and with climatic and host factors are likely to have a significant effect on the variation in future stock size (after Snieszko 1974, Bernardo-Cravo et al. 2020, Lane et al. 2020); however, these effects currently remain undescribed and unaccounted for.

1.2 Development of a disease model

Powell & Hofmann (2015) reviewed information on marine molluscan disease models and concluded that disease effects were important drivers of population dynamics, yet disease models remain underused in managing molluscan diseases and their effects on fisheries. The integration of disease into population models was the approach proposed by Powell & Hofmann (2015) to capture the effects of pathogens on host mortality (and we suggest presumably recruitment) and its subsequent influence on population dynamics.

The use of such models may greatly improve management of OYU 5. The effects of pathogens, climatic, and host factors on oyster population dynamics, however, remain substantial and important knowledge gaps to parameterising such models.

1.3 Review of the 2017 OYU 5 stock assessment model and data for assessments

The existing OYU 5 stock assessment comprises two models, a *Basic* model and a *Revised* model. These model structures are described by Dunn (2007) and Fu et al. (2016) and were last used in the 2017 assessment (Large et al. 2021) with data from 1907 to 2017. The next assessment is scheduled for 2023 to allow for any recommendations from this research to be implemented.

These models partition the population into length groups and represent changes in the Foveaux Strait oyster population as numbers at length. Oysters enter the partition following recruitment to the population (R), grow in length, and are removed by natural mortality (M), disease mortality (D), and fishing mortality (F). Movement between length classes is determined by a growth curve, which models growth increments for each length partition. Parameter estimation in all assessments was Bayesian, sampling posterior distributions using Markov chain Monte Carlo (MCMC).

The *Basic model* assumes the following.

- A single homogenous stock model. This is a known weakness, as benthic habitats, environmental factors, and size attributes of the oyster population vary markedly across four or more distinct regions within the stock area.
- A single sex maturity ogive that determines both spawning and disease selectivity. *Ostrea chilensis* is a protandrous hermaphrodite, and in the model:
  a. The maturity ogive is derived from the proportions of sexually mature female oysters, defined as the proportion of oysters with female ova and assumes fertilisation success is correlated with egg production. The ogive represents both sexes in the model.
  b. Maturity is constant from 1900, i.e., there is no time-varying aspect.
- Two time steps, which adequately describe the biological and fishery processes, i.e., spring-summer followed by autumn-winter.
- Disease rates are estimated by the model and are annual and independent of each other, i.e., no temporal connectivity. Further:
  a. disease selectivity is equal to maturation, and
  b. disease mortality occurs in the spring-summer time step.
- Recruitment deviates (Year Class Strengths, YCS) are estimated using a log-normal prior with mean =1.0 and CV of 20%. Further:
  a. the stock-recruitment assumes a Beverton & Holt relationship with a 'steepness' of 0.9,
  b. disease has no effect on recruitment (apart from killing breeding oysters),
  c. new recruits enter at age 1 with a normal length distribution.
- Natural mortality is assumed to be constant across all sizes and assumed to be 0.1 y^{-1}.
- Growth is based on a modified von Bertalanffy growth curve (Dunn et al. 1998).
- Productivity remains constant from 1900 because average recruitment, natural mortality, and growth parameters are constant.
- Dredge surveys have a known catchability from field trials, i.e., they are assumed to be absolute biomass estimates; however, standardisation for dredge widths and survey areas are assumed to be unbiased.
- Unstandardised CPUE provides an index of fishable abundance, fitted in the model with a lognormal likelihood and assumed CV of 0.25 (Dunn 2005).
- Projections have been based on:
  a. Three fixed rates of future disease mortality rate (*D*): 0 y^{-1} (no mortality), 0.10 y^{-1} (moderate mortality), and 0.20 y^{-1} (high mortality). However, future disease is not known and no information to predict future disease is available from the stock assessment.
  b. Future recruitment is log-normally distributed with mean =1.0 and s.d. equal to the s.d. of log of recruitment between 1985 and 2002. This was a CASAL (Bull et al. 2012) option and standard practice when the model was developed in early 2000. Recruitment was estimated by the model when there were no recruitment data available, i.e., prior to 1993.
- Disease mortality and recruitment need to fit the survey estimates of stock size. There are no surveys in some years, and in some survey years disease mortality is 'turned off', so there is no penalty. The model can use recruitment (year class strength) or disease rate in any one year to fit to the survey estimate of stock size. Disease and recruitment are estimated as separate parameters; however, these are likely to be correlated.

The data fitted by the Base model were dredge survey abundance series and commercial CPUE, length compositions, and maturity data (Tables 1 & 2). Maturity data (Jeffs & Hickman 2000) for the maturity ogive were needed to estimate spawning stock abundance (SSA) in millions of oysters, which is used to monitor the population status against the management reference points. The length compositions were used to estimate selectivity for fishing and for the various surveys. These were needed to select the correct fraction for the numbers-at-length so that it was compared correctly with the abundance estimates, and also to subtract the number of oysters caught by fishing (annual landings). Unstandardised CPUE indices were used, and Dunn (2005) found standardised and unstandardised indices showed very similar trends. CPUE and survey abundances were used to indicate how the population was changing. The model fit was strongly influenced by the disease, growth, and recruitment parameters.

The *Revised* model assumptions were largely the same as the *Basic* model above, but it:

1. Estimated growth increments within the model from tag-recapture data.
2. Had a likelihood penalty function to smooth disease mortality between years.
3. Decoupled the maturity and disease selectivity ogive.
4. Assumed that the Diggles (2004) data represent disease selectivity during epizootics. Excluded the 1975–76 survey data from the model runs.
5. Assumed that the prior on survey catchability was log-normal with a 10% CV, i.e., the relative catchability for the abundance surveys was log-normally distributed. The 10% CV made this a highly informed prior.

Biological inputs, priors, and assumptions are given by Dunn (2007) and summarised in Table 3. Only the prior for survey catchability (q) was informed; priors for all other parameters not shown in Table 3 were uniform (with the exception of B_0 which was uniform-log).

The OYU 5 stock assessment models were evaluated in this project, and model input files and outputs were inspected to review the model structures and to find the main drivers of the assessment. Whether all data had a sound statistical foundation to be included in the assessment was also evaluated. A careful, full inspection of files and the model and an evaluation of the assessment against 'best practice' were made by a fisheries stock assessment expert (Ian Doonan).

Table 1: **Abundance series for the *Basic* model using 4 CPUE series by oyster size group (Category, vulnerable is recruit-sized (≥ 58 mm in length), pre-recruit (≥ 50 mm to <58 mm in length) and small oysters (<50 mm in length)). The numbers of samples are given as 'N'. The '1976 Survey' and 'Mark recapture surveys' have an informed prior on q, but very few data points, and so they contribute very little to the model apart from estimating their qs. Surveys and commercial data used different dredges, but these differences are accounted for in the catchabilities (q). Differences in survey areas are accounted for by scaling the original estimates.**

Series	Category	Type	Time step	Years	Comments	q assumption
CPUE-A	Vulnerable	Relative	Step 2	1948–1968	N=21	CPUE-A q (estimated)
CPUE-B	Vulnerable	Relative	Step 2	1969–1984	N = 16	CPUE-B q (estimated)
CPUE-C	Vulnerable	Relative	Step 2	1985–2010	N = 16 or 32 between 1985 and 2016; split into 2 series in one version	CPUE-C q (estimated)
CPUE -D	Vulnerable	Relative		2011–2022	N = 12	CPUE-D q (estimated)
1976 Survey	Vulnerable	Relative	Step 2	1976	N = 1	Survey 1976 q Informed prior (mu = 0.6, CV=0.3)
Mark recapture surveys	Vulnerable	Relative	Step 2	1974–75	N = 2	MR survey q Informed prior (mu = 0.6, CV=0.3)
October surveys	Vulnerable	Absolute	Step 2	1962–2002	N = 8; most in the 1990s	Dredge survey q Set to 1
	Pre-recruits	Absolute		1993–2002	N = 6	
	Smalls	Absolute		1993–2002	N = 6	
July surveys	Vulnerable	Absolute	Step 2	1990		Dredge survey q
March surveys	Vulnerable	Absolute	Step 2	1992–2017	N = 10. Actually, January to March, but assigned to March	Dredge survey q
	Pre-recruits	Absolute		1995–2017	N = 9	
	Smalls	Absolute		1995–2017	N = 9	

Table 2: Length composition data series for the *Basic* model using 3 CPUE series version and other data.

Series	Category	Years	Comments
Commercial LF	Vulnerable	2002–2016 (now 2022)	N = 13
October survey LF	Vulnerable Pre-recruits Smalls	1990, 2001	N = 2
October dive survey LF	All	1990	N = 1. Pop estimate used to estimate Dredge survey q
Proportions mature	All	1970	N = 1; maturity ogive

Table 3: The priors assumed for key parameters. The parameters are mean and CV for lognormal (in natural space), and mean and s.d. for normal, from Dunn (2007).

Parameter	Distribution	Parameters Mean	CV or s.d.	Bounds	
CPUE q	Uniform-log	–	–	1×10^{-8}	0.1
Survey q (*Revised* Model only)	Log-normal	1.0	0.2	0.10	4.0
1976 survey q	Log-normal	0.5	0.3	0.15	0.95
Mark-recapture survey q	Log-normal	0.5	0.3	0.10	0.90
YCS	Log-normal	1.0	0.2	0.01	100.0
Disease mortality	Normal	-0.2	0.2	0.00	0.80

2. METHODS

2.1 Describe several conceptual models of the oyster population

A conceptual model of oyster population dynamics was developed based on Foveaux Strait oyster research data, the shellfish and shellfish disease literature, and hypotheses developed from exploration of available OYU 5 data to highlight likely relationships between climatic and environmental variables, oyster pathogens and parasites, oyster host factors, and population attributes. These relationships are illustrated with simplified schematics.

2.2 Develop new disease model

Substantial knowledge gaps of disease processes and data limitations currently constrain the development of a disease model. Expert opinion (Samik Datta) was used to develop an approach to disease modelling, and strategic research documented below will assist in the provision of data for future developments. In the meantime, available data of pre-survey mortality, and non-fatal, and fatal infection by *Bonamia exitiosa* will be fully explored to investigate triggers for epizootics (heighted disease mortality).

2.3 Review of OYU 5 stock assessment model

The behaviour of the models was investigated using maximum posterior density (MPD) estimates with the *Basic* model, except where explicitly stated. Investigations included the following.

1. Disease rate (*D*) estimation and the fits of 'disease selectivity' to the data on *Bonamia exitiosa* intensity score by oyster size of Diggles (2004) using other parameterisations (*Revised* model).
2. The relative influence of the survey data to that of CPUE data by removing each data set and re-running the assessment. The survey abundances were treated as relative (i.e., uninformed priors on the qs).
3. How one cohort progresses through the length bins. This was calculated by adding a row to the partition (numbers-at-age matrix) that captured just one recruitment event. This cohort then progressed as normal but was subjected to different mortalities: (i) only natural mortality *M*, (ii) natural and disease mortalities *M+D*, and (iii) natural, disease, and fishing mortalities *M+D+F*.

2.4 Future research and consultation

Draft a plan to develop models

A summary of improvements to the *Basic* and *Revised* stock assessment models was determined by expert opinion (Ian Doonan). Future investigations that may help refine a development plan included the following.

- Sensitivity runs to investigate the sub-setting and removal of some datasets.
- Truncation of time series data.
- The introduction of new data.
- Trend analysis of data towards developing predictions of disease mortality.

Consult with the Foveaux Strait Oyster Management Group

A workshop was held with OYU 5 fishery stakeholders on 25th February 2021 at McCulloch & Partners, 20 Don Street, Invercargill. The aim was to discuss the review of the OYU 5 stock assessment, specifically to: examine what drives the Foveaux Strait oyster fishery, discuss the management needs, review the data available, and define what type of stock assessment should be developed and which level of complexity would be expected based on all these points.

Discuss appropriate platforms for modelling

Considerations for the choice of modelling platform should include: a readily accessible platform that can be run by several modellers to ensure capability and consistency in stock assessments, e.g., CASAL2 (Doonan et al. 2016, CASAL2 Development Team 2022[2]). A bespoke model could be written (e.g., in Stan code), but this would require time to write and to also thoroughly test that it delivers an accurate assessment. In practice, a bespoke model could be hard to maintain, especially if the developer moves on. CASAL2 was already written and tested and two fisheries assessments using it have been accepted (age-based). CASAL2 has a pool of researchers that maintain and continue to develop it.

The platform should allow the integration of available disease mortality data (i.e., from new clocks and category 3+ infections collected each fishing year) to estimate mortality rates from disease within the model. The abundance of clocks, the articulated shells of recently dead oysters with the ligament attaching the two valves intact, was estimated from dredge surveys. New clocks are defined as those with clean inner valves that had retained their lustre but may have had some minor speckling from fouling organisms. New clocks were only those oysters that had died since the beginning of summer mortality from Bonamia. Projected short-term (generally within two weeks) disease mortality was estimated from the proportion of oysters with categories three and higher (fatal) Bonamia infections, as determined by histology (see Diggles et al. 2003). If it were not possible to estimate the mortality rates within the modelling platform, an alternative would be to calculate them independently and then to input them into the model as fixed parameters of mortality, in addition to fishing and natural mortality.

Within the CASAL2 development in 2022, the 2017 oyster model in CASAL was replicated in CASAL2, as a potential test model for testing the length-based functionality of CASAL2. To estimate disease mortality from observed data in CASAL2, a new observation class would need to be written to take the new clock and category 3+ infection data from dredge surveys. This is not an onerous task. Using CASAL is not a feasible option because this software is no longer being maintained.

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[2] https://casal2.github.io/

3. RESULTS

A workshop was held on the 25th of February 2021 with OYU 5 fishery stakeholders including participants from: Fisheries New Zealand (Allen Frazer, Marine Pomarède, Ian Tuck, Jean Davis), Bluff Oyster Management Company Ltd (BOMC; David Skeggs and Graeme Wright), Ngāi Tahu (Rodney Tribe), and NIWA (Keith Michael, Ian Doonan, and Samik Datta).

Four key issues were discussed.

1. The Fisheries Act 1996 requires that OYU 5 is managed to provide for the utilisation of fisheries resources while ensuring sustainability.
2. The Harvest Strategy Standard (Ministry of Fisheries 2008) is a policy document that provides a technical interpretation of various sections of the Fisheries Act (1996), particularly section 13(2). It requires a target that is compatible with B_{MSY}, soft and hard biomass limits, and an overfishing threshold against which to evaluate stock status. A modelling approach is preferred by Fisheries New Zealand because it uses a range of available data and has some predictive capability.
3. Further development of the OYU 5 stock assessment model should focus on the ability to predict disease mortality.

3.1 Conceptual models of the oyster population

Factors that may influence the drivers of oyster population dynamics have been identified from the literature and unpublished data. Putative interactions are highlighted in the conceptual model. The conceptual model of the Foveaux Strait oyster fishery presented in this section assumes that oysters (post settlement) are immobile, i.e., that they are not moved and reaggregated by storms. A conceptual model of oyster population dynamics (see Figures 1–7) assumes the recruit-sized population numbers are primarily driven up by recruitment and driven down by disease mortality. Variations in growth and mortality, other than that from disease, are assumed secondary to these two drivers. Several factors are likely to have positive and negative effects on recruitment and disease mortality. The conceptual model describes the relationship and strength of interactions between recruitment and disease mortality, and several other key factors. Each factor may vary spatially and temporally across the fishery, i.e., there are at least 4 different regions with different habitats and environmental factors.

Heightened mortality from disease has the greatest effect on oyster population size in OYU 5. Mortality primarily caused by *B. exitiosa* reduced the recruit-sized population by 91% in one disease cycle (epizootic) in 1985 (Doonan et al. 1994). Variation in recruitment is dependent on successful spawning and fertilisation, brooding, and larval settlement. The percentages of brooding-sized oysters that are actually brooding are low (<2%, BOMC data). Relatively high larval settlement events translate into high oyster cohort strengths. High variation in growth influences the speed at which small oysters grow to pre-recruit and recruit sizes. Oysters are commercially harvested (>65 mm in length), larger than recruit size (≥58 mm in length), i.e., above minimum legal size. Oysters between 58 mm and ~65 mm are mostly returned to sea (as high-graded catches), and therefore there is a lag between increases in the recruited stock and an increase in the commercial population.

The energy available (energy budget) and how energy is partitioned amongst biological processes (i.e., growth and reproduction) and disease processes is fundamental to oyster abundance. Factors driving energy availability for these processes are summarised first (Figures 1 & 2), followed by information on the partitioning of energy for biological and disease processes (Figure 4), and how these factors may affect key model parameters of oyster abundance (Figure 7).
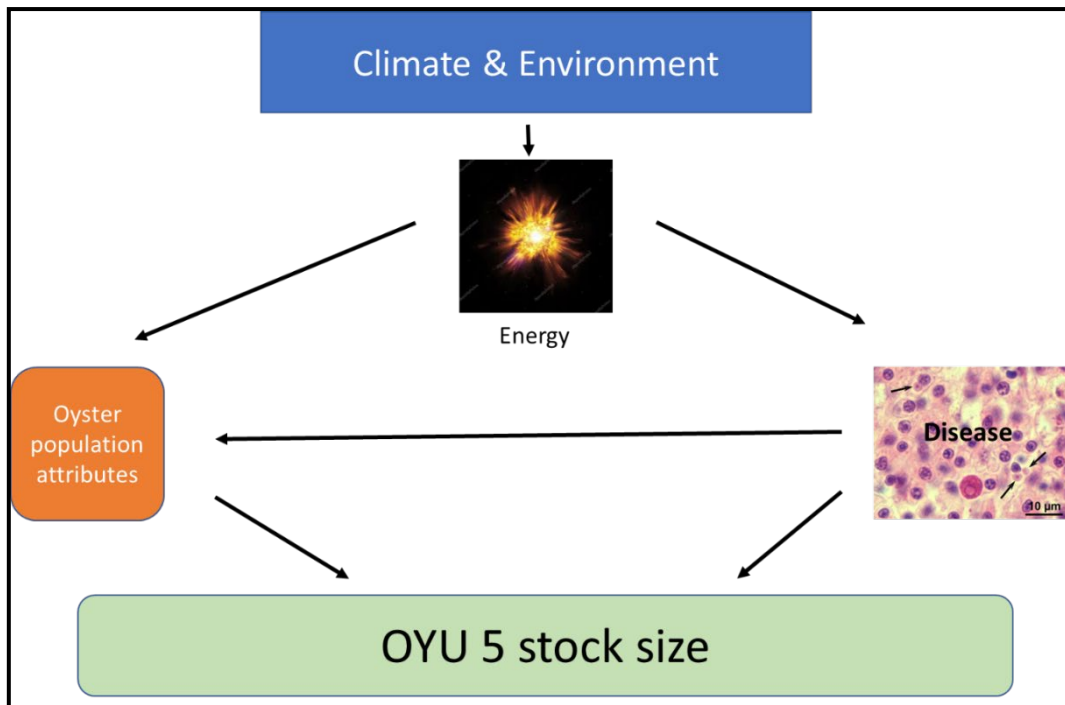
3.1.1 Climate

An overview of high-level conceptual model components for drivers of oyster population dynamics in the Foveaux Strait oyster fishery is shown in Figure 1. Climatic factors have a global effect in the OYU 5 fishery area, that determine, in part, energy available for biological and disease processes. Key components and processes are shown in more detail in Figures 2–4.

Although we may not be able to predict climate factors that affect biological and disease processes, an understanding of the magnitude of influence of climate on these processes will help explain the drivers of future stock size and disease status. This understanding may allow reliable predictions of future stock size and disease status under different climate scenarios. Climate variables affect host physiology (Engelsma et al. 2010), recruitment processes (Hjort 1914, Canning 2013, Joyce et al. 2013, Robert et al. 2017), and intensification of disease and mortality (Hine 2002, Arzul et al. 2009, Engelsma et al. 2010, Rowley et al. 2014). Climate is known to drive annual variation in recruitment in the *Ostreidae* family, e.g., *Crassostrea virginica* (Kimmel & Newell 2007, Kimmel et al. 2014). Three-way interactions between climate, recruitment, and disease can be expected.

Of the climate variables, temperature and food rations are likely to have marked effects on gametogenesis and disease. High temperatures may intensify *B. exitiosa* infections (Hine 1991a). An abundance of microalgae can increase gonad condition, enhance spawning success of *O. chilensis* in Chile (Chaparro 1990), increase maternal provisioning (Wilson et al. 1996, Chaparro et al. 2006), and produce larger larvae that have increased rates of settlement and post-settlement survival in *O. edulis* (Robert et al. 2017). A data limited study by Michael (2019) suggests that food availability and the ability of *O. chilensis* to feed were more important to recruitment than temperature. Consistent climate data are available for the years 2002–21.

The high energy system of Foveaux Strait also suggests that storms capable of moving large quantities of sediment and their relatively high frequency are likely to affect feeding and opportunities to utilise high levels of food available in the water column.

"The Southern Oscillation Index (SOI, Figure 2) is correlated with both chlorophyll a concentration (CHL, mg/m3)and sea surface temperature (SST, °C). 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 northern (New Zealand) shows a coefficient of 0.62 (see figure 10 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" (Hurst et al. 2012).

Figure 1: An overview of conceptual model components for drivers of oyster population dynamics in the Foveaux Strait oyster fishery. Climatic factors include global drivers such as the Southern Oscillation Index (SOI) that drives wind directions and speed and has marked effects on sea surface temperatures (SST), levels of upwelling and primary productivity, and there by energy available to biological and disease processes.
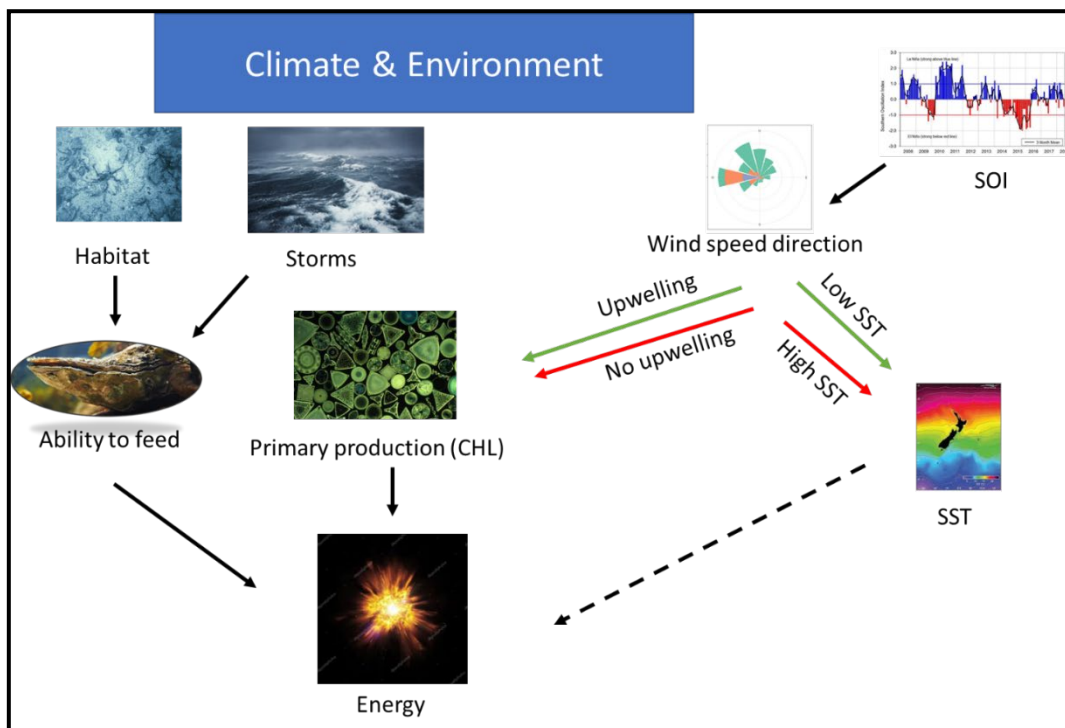
Figure 2: A conceptual model of climatic factors include global drivers such as the Southern Oscillation Index (SOI) that drives wind directions and speed, which have a marked effect on sea surface temperatures (SST), levels of upwelling, and primary productivity, and thereby energy available to biological and disease processes. Wind directions and speed also have an effect on the frequency of storms that mobilise sediments, cover oysters, and thereby reduce feeding.

Upwelling has been found to be related to increased nutrient flux and phytoplankton growth in these areas (Hurst et al. 2012). This primary production is measured as chlorophyll a (CHL, Huot et al. 2007, Figure 2) that is transported into Foveaux Strait, which is known to be a highly productive area (Bradford et al. 1991). The strong tides in Foveaux Strait ensure the water mass is well mixed, both vertically and horizontally (Butler et al. 1992).

During El Niño conditions, periods of enhanced westerlies, with associated cooler air and sea temperatures enhance a west-east precipitation gradient. These conditions increase rain in south-western New Zealand. An increased freshwater input into Foveaux Strait via Fiordland and the Waiau River further increases nutrient input into Foveaux Strait (see Zeldis et al. 2008 for an example).

Storms mobilise and suspend coarse calcareous sediments that cover oysters, greatly reducing their ability to feed (Stead 1971a). Depending on the duration of burial, this may reduce physiological condition and energy, resulting in oysters of poor meat condition and lower commercial value.

The energy available to drive biological and disease processes in OYU 5 is critical to fishery productivity. Oyster meat condition is a good proxy for the energy available (Michael et al. 2022). In any one year, meat condition probably reflects food availability, ability to feed (i.e., the negative effects of storms), and reproductive activity over the previous spring-summer (see meat condition data in Figure 3). Of the climatic variables, storms (the number of days of wind greater than 51 knots per month) was the most important from the analysis of Variable Importance Measures (VIM) using cforest (Hothorn et al. 2006) and was significant in the modelled variables driving high oyster meat quality. SST had a significant negative effect on oyster meat quality. The warmer temperatures may be the results of predominant north and easterly winds, known to reduce upwelling that reduces the food available to oysters in Foveaux Strait.
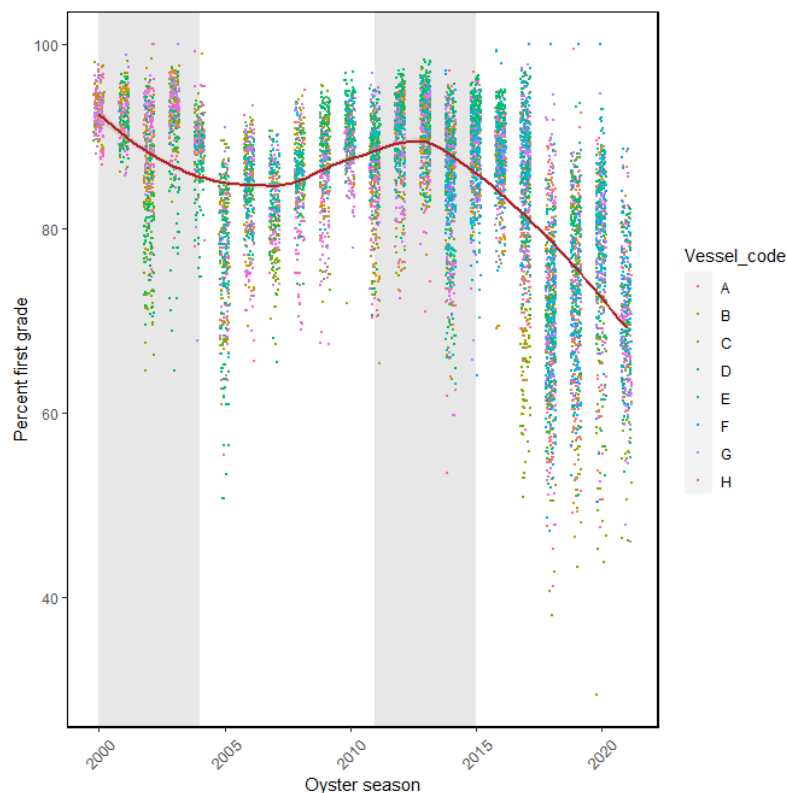
Figure 3: **Scatter plot of the daily percentage of first grade oysters landed each year during 2000–2021 for each vessel. Each vessel (Vessel_code) plotted in a separate colour (see legend). Red line is a loess smoother applied to all data from all vessels each year. Filled grey polygons show the period of heightened oyster mortality caused by Bonamia.**

3.1.2   Habitat

Complex biogenic habitat was hypothesised to be important to oyster recruitment (Cranfield et al. 1999, Cranfield et al. 2004); however, fishery data from oyster and bycatch surveys show oyster larval settlement and survival is mainly on simple habitats with occasionally mobile sediments. Survey data and fishers' logbook data also show that simple sand, gravel, and shell habitats provide good habitat for oysters.

Filter feeding epibenthic taxa are also hypothesised to reduce *B. exitiosa* propagule densities thereby mitigating the spread of infection (Cranfield et al. 2005). These taxa may also provide alternative hosts and reservoirs of infection (Costello et al. 2021). The role of epibenthic taxa in mitigating or providing alternative hosts and reservoirs of *B. exitiosa* infection comprises an important knowledge gap.

3.1.3   Energy for biological processes

The energy available to oysters is determined by an interaction of primary production and the environment. Although phytoplankton levels may be high, oysters may be regularly covered in coarse calcareous sand and gravel inhibiting their ability to feed (Cullen 1962, Cullen 1967, Stead 1971a). Severe storms with strong southerly to westerly winds generate large oceanic swells and high wind-driven currents that result in high orbital velocities capable of resuspending bottom sediments that are then transported by the tides and currents (Cullen 1967, A. Orpin & C. Stevens, NIWA, pers. comm.). These storms generally last 4–5 days (Gorman et al. 2003), creating new bedforms (e.g., sand waves) and changing the seascape morphology (for examples see Carter & Lewis 1995, Stanton et al. 2001, Walters et al. 2001, Hemer 2006). After these large storms, normal wave climate and tidal regimes redistribute sediments to an equilibrium state (A. Orpin & C. Stevens, NIWA, pers. comm.).

The energy available from feeding is partitioned among three biological processes (Huot et al. 2007, Figure 4). Those processes at the individual oyster level most relevant to population dynamics include:

1. growth that includes shell growth (size) and repair, and somatic growth and meat condition,
2. reproductive processes, i.e., gametogenesis, and,
3. energy used by pathogens for replication and/or by the oysters to tolerate pathogens, e.g., haemocyte production.
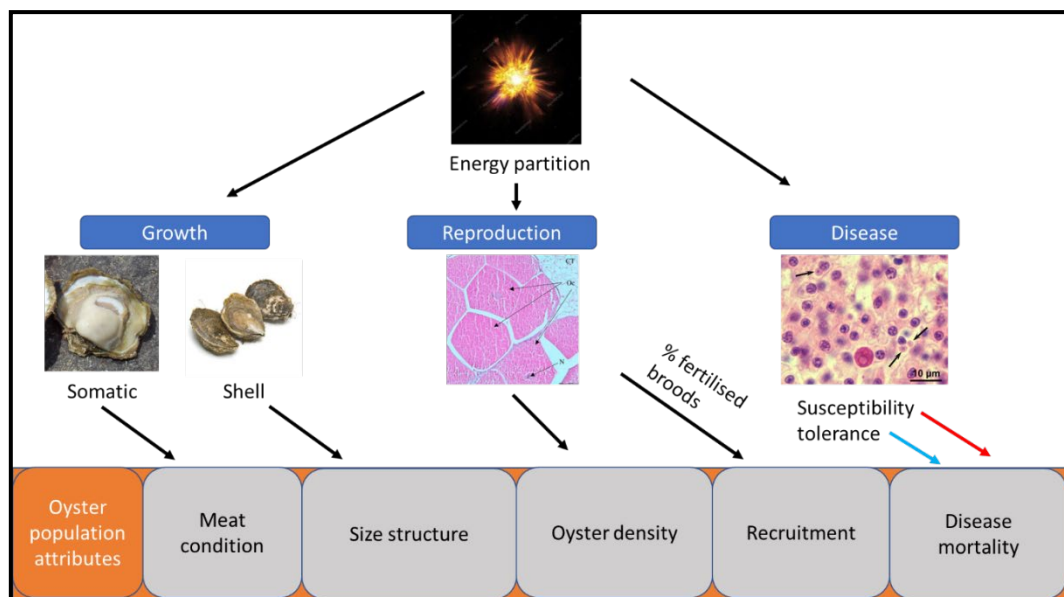

Figure 4:   A conceptual model of energy partition by oysters (*Ostrea chilensis*) in Foveaux Strait. Collectively, these processes contribute to oyster population attributes that drive production and losses in the OYU 5 fishery.

3.1.4 Partitioning of energy

Simple mechanistic descriptions of how individual organisms take up and use energy have led to the theory of dynamic energy budgets (DEB) (Kooijman et al. 2008). A simple illustration of DEB in individuals is shown in Figure 5 (reproduced from figure 1 of Sousa et al. 2010).

The DEB modelling approach has been used to predict variation in biological processes for different oyster species. For instance, a DEB model predicted changes in growth and reproductive activity of the American oyster *Crassostrea virginica* under different river conditions and climate (Lavaud et al. 2021). A trade-off between growth and reproduction was observed in Olympia oysters *O. lurida*, with the fastest growing individuals exhibiting delayed and reduced reproductive activity (Silliman et al. 2018).
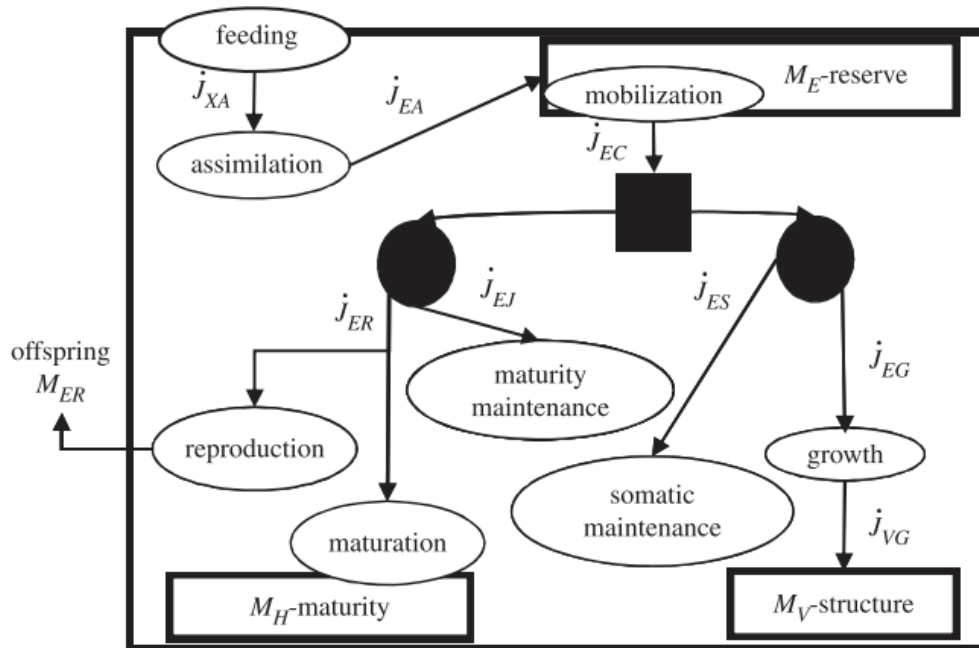
Figure 5: **An example of a simple dynamic energy budget for animals, excluding disease processes from Sousa et al. (2010). Circles are processes and rectangles are state variables. Arrows show the flows of energy and partitioning between biological processes. See Sousa et al. (2010) for more details.**

3.1.5 Growth

Several factors may regulate the partitioning of energy available to shell and somatic growth (Figure 5), reproductive and disease processes, and how switching occurs from one to the other. These factors may include food availability and temperature (Pritchard et al. 2015, Fuentes-Santos et al. 2019), and possibly other environmental variables and disease status.

Shell growth and repair

Growth is also dependent on energy partitioning and the disturbance of the shell deposition process. Shell repair, primarily from severe *Cliona* spp. infestation (Carroll et al. 2015), may reduce or cease normal shell growth. The effects of environmental factors such as temperature on post settlement oyster growth have not been studied in Foveaux Strait. Higher temperatures increase growth and maximum size in *O. lurida* (Pritchard et al. 2015), produce good growth in shell and somatic growth in mussels (*Mytilus galloprovincialis*) (Fuentes-Santos et al. 2019), but decrease growth and size in *C. virginica* where increase in temperature increases feeding but reduces allocation to shell and somatic growth (Hofmann et al. 1994).

Large shell growth increments are more likely to occur when meat volume and condition are high. Shell growth in oysters is 'plastic' and proportional growth increments may vary across three dimensions (length, height, and depth). Length is measured as the maximum distance along the anterior-posterior axis, height along dorsal-ventral axis, and depth the maximum distance between the left and right valves (Figure 6).

Two-dimensional estimates of growth such as length, height, or diameter may not be the best measures of individual growth. For small oysters, these measures may vary considerably interannually, seasonally, and across different fishery areas. For large oysters, these measures may overestimate reproductive maturity and commercial size. Growth is likely to be better represented by three-dimensional measures where growth continues in depth ('cupping') after length and height growth curves approach their asymptote. Increments in weight are also likely to be good estimates of growth; however, they are more time consuming to measure, especially when epifauna and fouling organisms need to be removed.

Growth in Foveaux Strait *O. chilensis* was last estimated in the 1970s (Dunn et al. 1998). Oysters from four sites across the fishery area were on-grown at a single eastern site. Growth was strongly seasonal; all growth occurred in the summer and storm damage in the winter produced negative growth increments in some oysters. Meat condition recorded by processors may provide an index of good growing years the following summer (see Figure 3).

Richardson et al. (1993) estimated age and growth rate of *O. edulis* using shell sections. Using the same methods for *O. chilensis,* continuous growth rings from the umbo (origin) to the outer shell margin could not be discerned to provide age and size-at-age data for stock assessment (Michael et al. 2000). The OYU 5 stock assessment model is a length-based model that partitions the oyster population by length classes (Fu et al. 2016). Accurate progression of length classes is dependent on good estimates of growth and levels of variation in growth rates.
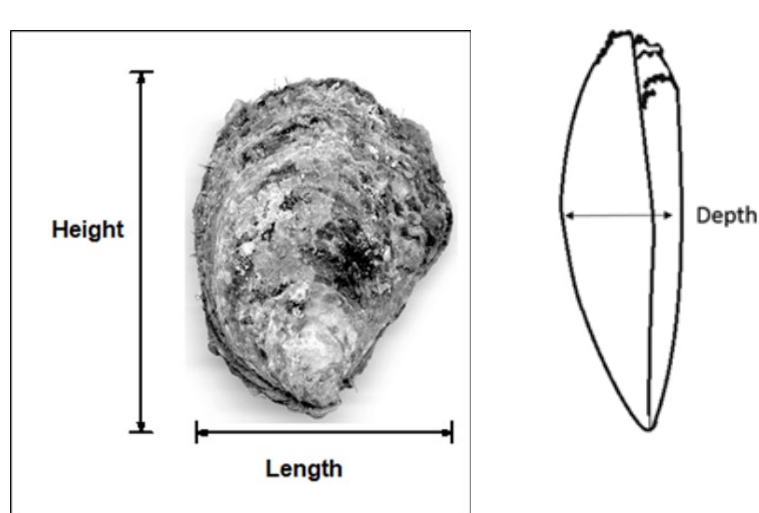
Figure 6: **Size dimensions of oysters: length (anterior-posterior axis) and height (dorsal-ventral axis) shown in left panel and depth (maximum distance between left and right valves) shown in right panel.**

Somatic growth

Increases in meat (tissue) volume and condition (meat condition) are likely to reflect overall energy surplus after reproduction, shell growth and repair (depending on energy partitioning processes), and disease processes. Some processors of oysters from OYU 5 record the percentages of first and second grade oysters based on subjective meat quality attributes such as size, plumpness, and colour from individual catches. The three qualitative visual meat quality categories developed for the oyster industry show good coherence with quantitative measures of oyster meat quality: a meat quality index, a

condition index, and meat dry weight (Michael et al. 2022). The large volume of data from commercial processing may provide indices of growth in oysters.

3.1.6 Reproduction

Recruitment to the population

Recruitment to the oyster population is the key driver of rebuilding the oyster stock. *Ostrea chilensis* produces large, maternally provisioned ova that require high levels of energy. Limitations in energy available for reproductive processes may limit the production of ova and to a lesser extent sperm, and thereby levels of spawning and brooding success. Post settlement survival is greatly enhanced by maternal provisioning.

Gametogenesis

Temperature and food availability have marked effects on gametogenesis (Westerskov 1980, Buroker et al. 1983, Joyce et al. 2015). At high water temperatures (≥ 20 ºC) the gonad cycle may advance rapidly and asynchronously to phagocytosis, thereby reducing fertilisation and brooding (Jeffs & Hickman 2000).

Gametogenesis requires high levels of energy, so reproductive success is likely to be determined by the total energy available, how it is partitioned, and temperature cues to initiate gametogenesis and gonadal development. *Ostrea chilensis* conditioned for spawning in Chile with high levels of food produced larger ova, larger pediveliger, better settlement and survival of larvae, and higher growth of spat (Wilson et al. 1996).

In Foveaux Strait, temperatures drop to winter minima for a relatively short time in July–August. Temperatures below 12 °C may play an important role in conditioning, stimulating gametogenesis, and synchronising female spawning (Jeffs 1998a). However, these low temperatures may increase variability amongst individuals (Jeffs 1998a, Jeffs 1998b, Jeffs & Hickman 2000, Joyce et al. 2015). Temperature minima initiate switches in energy utilisation from somatic and shell growth to glycogen stores and maternal provisioning in a closely related species, *O. edulis* (Joyce et al. 2013).

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), and an apicomplexan has been shown to disrupt reproduction and cause substantial mortality and population decline in the Iceland scallop *Chlamys islandica* (Kristmundsson et al. 2011).

We propose the hypothesis that pathogens compete with the host and other pathogens for the host's energy. Concurrent, non-fatal infections may cause a reduction in, or complete cessation of gametogenesis, through energy limitations. While no mechanism of how Bonamia may disrupt gametogenesis has been identified, the energy drain associated with replacement of haemocytes lost during the intensification of infection, and the timing of the increase in dense and necrotic bi-nucleate cells in July and August (Hine 1991b), coincides with the beginning of gametogenesis in *O. chilensis* in Foveaux Strait.

Any diversion of energy to tolerate non-fatal *B. exitiosa* infections (and other pathogens) may also result in the reabsorption of ova that increases the intensity of infections and subsequent oyster mortality (Hine 1991a). If the host is not killed by the intensification of infection, *B. exitiosa* may compete with the host and other pathogens (e.g., an undescribed apicomplexan referred to as APX) for energy made available through the reabsorption of ova. There may be legacy effects for survivors, one of which may be reduced energy budget that compromises reproduction in the following reproductive cycle. Similar effects have been observed in *C. virginica*, where oysters infected with *Perkensis marinus* produce fewer eggs than uninfected oysters (Kennedy et al. 1995). *Crassostrea virginica* colonised by *Cliona celata*, also present

in *O. chilensis* in Foveaux Strait, diverted significant energy from growth (and presumably reproductive processes) to shell maintenance and repair (Carroll et al. 2015).

Pathogens most likely complicate the partition of available host energy amongst biological processes. Apart from the allocation of energy for growth and reproduction, the host allocates energy for the suppression of disease, usually through mounting an immune response. Diseased shellfish typically appear emaciated or 'watery', exhibiting a decrease in condition index indicating that the development of disease affects the energy budget of the host (Egerton et al. 2020). There are two principal opposing hypotheses, high energy reserves either increase or decrease individual disease susceptibility:

> Hypothesis 1: high food availability, good physiological condition, and associated high energy reserves of hosts lower their susceptibility to disease through an increased immune response.

> Hypothesis 2: Conversely, limited food availability and poor host physiological condition limit resources available to pathogens. When energy levels are high, energy obtained by pathogens from hosts intensify infections to fatal levels (e.g., Pernet et al. 2019); i.e., there is a trade-off between oyster growth 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 herpes virus (OsHV-1) in Pacific oysters *C. gigas* under laboratory challenge conditions (Pernet et al. 2019).

Energy partitioning in oysters can locally adapt in response to pathogens. European flat oysters *O. edulis* grown in areas in Ireland where *B. ostreae* is enzootic grow more slowly with lower reproductive activity than oysters from areas without *B. ostreae* (Egerton et al. 2020). Oysters are typical r-strategists (small in size with fast development and high fecundity), and the transition to oysters with S-strategy life traits demonstrated by Egerton et al. (2020) suggests greater energy allocation and investment into enhanced immune function to combat pathogens. 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 comprise an important knowledge gap.

3.1.7   Recruitment

Recruitment to the population

Recruitment to the oyster population is the key driver of rebuilding, and the flow-through effects of year class strength substantially contribute to the annual variation in oysters available to the fishery. Success in four concurrent processes is required for successful recruitment.

1.   Gametogenesis, see above,
2.   Synchrony in the release of male and female gametes,
3.   Brooding and larval development, and
4.   Larval settlement and survival of spat.

Synchrony in the release of male and female gametes

Seasonal patterns of *O. chilensis* gametogenesis are similar in populations throughout New Zealand; males tend to trickle-spawn throughout the year and females spawn predominantly in spring (September-October) (Jeffs & Hickman 2000). Synchrony in the release of spermatozoa (after disassociation of spermatozeugmata) into the water and oocytes (viable ova) released in the inhalant chamber in the mantle of female and hermaphrodite oysters for fertilisation is critical for successful spawning. The asynchronous gonadal development of males and females in *O. chilensis* reduces fertilisation success within populations (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 of 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. Unfertilised ova are typically white in colour. Sperm from neighbouring oysters is drawn through the inhalant chamber for fertilisation of the brood.

Self-fertilisation is possible (Jeffs 1998b) but reportedly is prevented by the structure of spermatozeugmata (Hassan et al. 2016). Asynchronous development and release of gametes may lead to poor fertilisation and brooding percentages.

The durations of spermatozeugmata dissociation and sperm viability in *O. angasi* were longer in males than in hermaphrodites. The unique structure and capability for spermatozeugmata to maintain the functional integrity after spawning have adaptive significance for fertilisation. In Foveaux Strait, years of poor recruitment to the population may reduce the number of males and limit fertilisation success. Moreover, the close proximity of attached, small epibiont males in clusters of *O. puelchana* facilitate sperm transfer and successful fertilisation (Pascual et al. 1989) and may be important to maintain fertilisation success in Foveaux Strait *O chilensis*, especially where oyster densities are low.

Brooding and larval development

Ostrea chilensis in Foveaux Strait have the longest brooding periods of Ostreinae (flat oysters); larvae fully develop in broods until fully competent and can settle within minutes to hours of release (Cranfield 1979, Westerskov 1980). Larvae can feed during development to boost the energy available for metamorphosis and settlement. Some larvae are released early and continue to develop to full competency (Hickman 2000). Whether significant percentages of broods, fertilised and unfertilised in the mantle, are released early is not known. Larvae can disperse throughout the fishery and can be advected out of the fishery area by the strong tidal currents. The relative abundance of competent larvae available for settlement are monitored annually by a BOMC spat monitoring programme.

Stages of development are indicated by larval colour changes, with three stages progressing from the white unfertilised ova, to grey and black during development, and finally to a golden colour from the prodissoconch (shell) of larvae that are ready to settle. Broods are from a single spawning and are all one colour, and colour stages represent consistent size groups and stages of larval development (Victoria Pearsey, Bluff Oyster Enhancement Company, pers. comm.). Brooding occurs throughout the year and consistently peaks in November-December in Foveaux Strait (Hollis 1962, Stead 1971b, Cranfield 1979, Westerskov 1980, Jeffs & Hickman 2000). Peak spawning should occur about a month or more before peak brooding and is consistent with the period of a rapid rise in temperature. Temperature also affects brooding period (Chaparro 1990, Toro & Morande 1998) and the stage of development when larvae are released (Joyce et al. 2015). Larval size at release affects settlement success (Cranfield & Michael 1989, Chaparro 1990, Utting et al. 1991).

Broods were sampled from the commercial catch during an extended season (September to October) for the 2011 Rugby World Cup. A low proportion of the brooding-sized population (1–2%) was brooding over the sample period. Only 4.8% of the brooding oysters sampled over 54 days (*N*=7243) were fertilised and developing, and this proportion remained consistent over the September-October period (Michael et al. 2014). The very low percentages of fertilised broods suggest female and hermaphrodite oysters of brooding size may not produce fully developed ova ready for fertilisation every year, and/or sperm limitation may greatly reduce fertilisation success. Potential causes of sperm limitation include low larval settlement and spat survival over the previous three years leading to low numbers of predominantly small, male oysters. Alternatively, energy available for reproduction could be mostly diverted to the production of ova rather than sperm in hermaphrodite oysters.

Several other factors may determine brooding success and the subsequent spatfall. Environmental and climatic variables affect recruitment processes (Hjort 1914, Canning 2013, Joyce et al. 2013, Robert et al. 2017), as do pathogens (Hine 2002, Egerton et al. 2020) and spawner density; however, little is known about their interactions and how they affect recruitment in *O. chilensis*.

Larval settlement and survival of spat

Recruitment to the oyster population in Foveaux Strait differs to other commercial oyster fisheries in that larval settlement of *O. chilensis* is not substratum limited. Bycatch compositions of survey and commercial dredge tows show settlement of larvae and survival of spat on live oysters, oyster shell, and

the shells of several bivalves and gastropods. No oyster spat have been observed on bryozoans. The substantially higher survival of oyster spat on live oysters relative to other settlement surfaces provides a different context for a stock-recruit relationship, where recruitment to the population is primarily determined by the numbers of competent larvae; however, their survival is dependent on, but not limited to, the numbers of live oysters. This constitutes a type of feedback loop for recruitment.

Spawning success indicated by levels of larval settlement and survival on artificial collectors drives annual variation in recruitment to the population. Temporal patterns of spat settlement were similar across the commercial fishery area (Michael & Shima 2018). Larval availability was not related to spawner densities (Michael & Shima 2018). Survey data showed high spatfall translates to large year class cohorts and, eventually, high recruitment to the commercial oyster fishery.

3.1.8   Size structure and oyster density

Increases in size are determined by growth rates that can vary greatly between years, and seasonally (Dunn et al. 1998). Several year classes may be represented for any given range of lengths. Additionally, the maximum size of oysters varies over the fishery area, and it is likely to be influenced by sediment composition and environmental factors associated with the habitat.

3.1.9   Disease mortality

During epizootics, *B. exitiosa* is the main source of mortality in Foveaux Strait *O. chilensis* (Hine 2002). The role played by levels of host energy in disease mortality is not known for *O. chilensis* in Foveaux Strait. There are two opposing hypotheses of drivers of disease mortality:

1.   Limited food availability leading to low energy reserves and poor physiological condition of the hosts increases their susceptibility to disease.
2.   Limited food availability and poor host physiological condition limit resources available to pathogens and thereby decreases oyster susceptibility to disease.

Data from the OYU 5 fishery suggest hypothesis 2 is more likely, 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, conversely, years with low meat condition and hence low energy levels coincide with low prevalence of infection and low oyster mortality. Effective oyster to oyster transmission of *B. exitiosa* requires high propagule pressure, a result of high oyster mortality. Additionally, Hine (1991a) suggested a link between an increase in energy available to pathogens resulting from an increase in lipids from the reabsorption of host 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).

3.1.10   Simple model of the OYU 5 fishery

A simple model of the Foveaux Strait oyster population is shown in Figure 7. Several 'oyster population attributes' influence the drivers of stock increases and decreases: population size structure, oyster density, oyster meat condition and reproductive state, and infections by oyster pathogens and parasites. Mortality, primarily from disease, is the largest driver of decreases in stock size and recruitment to the population is the greatest driver of increases.
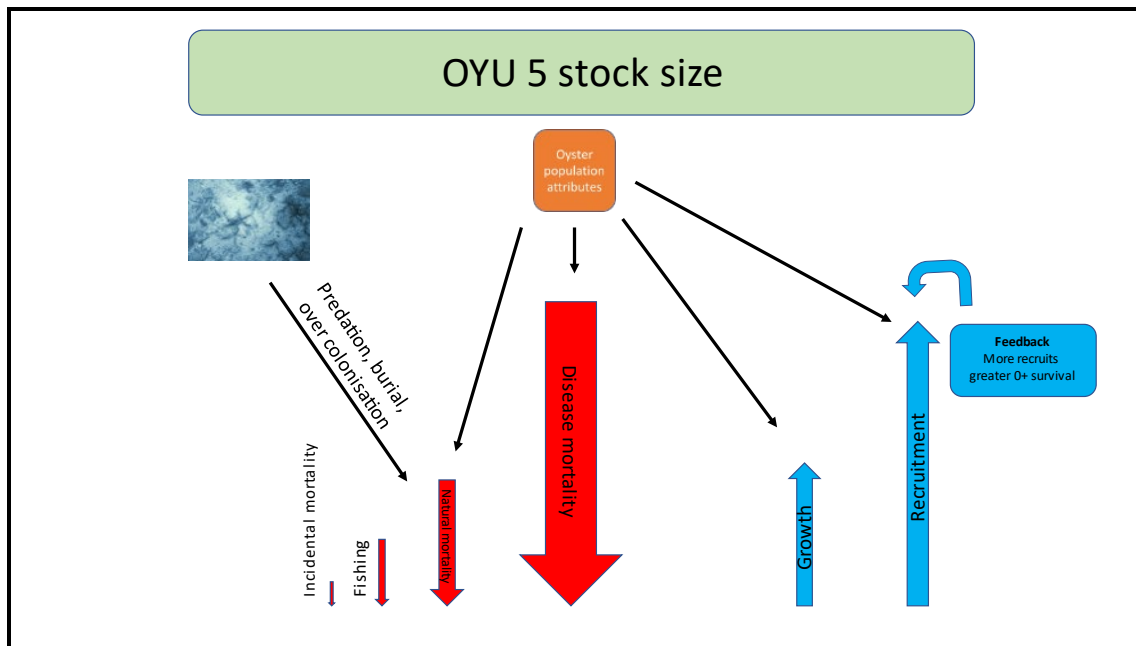
Figure 7: **A simple model of the Foveaux Strait oyster population. Several 'oyster population attributes' influence the drivers of stock increases and decreases. The colour and direction of arrows that represent these drivers of oyster population size show removals as red arrows and additions as blue arrows. Arrow size represents subjective scaling to show magnitude of effect. Mortality, mostly from disease, is the largest driver of decreases in stock size and recruitment to the population the greatest driver of increases.**

Mortality

Oyster mortality is the most significant driver of oyster population dynamics in Foveaux Strait. Mortality is size dependent. Mortality of recently settled spat and juvenile oysters is putatively high, as it is for most marine invertebrates. During epizootics (i.e., disease mortality events), oysters are assumed to have a 'U' shaped mortality curve, 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.

1. Disease mortality,
2. Fishery removals,
3. Natural mortality, and
4. Incidental fishing mortality.

Disease mortality

Disease mortality accounts for almost all the mortality of oysters in OYU 5 during epizootics. *Bonamia exitiosa* is the primary cause of disease mortality in Foveaux Strait oysters; however, other known 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, and oyster densities 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 longicornutus* (Howell 1967). *Bonamia exitiosa* was not described until the first epizootic in 1985, where it spread rapidly through the oyster population, indicative of a naïve host population, despite its earlier presence in the fishery (Doonan et al. 1994, Cranfield et al. 2005). The relatively high oyster densities (best

estimated above a threshold of 1.26 recruit-sized oysters per square metre) (Doonan et al. 1999) were critical for the effective spread of *B. exitiosa* in 1985. Oyster mortalities in areas of high host densities produced large-scale shedding of pathogens, causing high propagule pressure in the environment. The downstream dispersal of pathogens was high enough to cause a wave of mortality (Doonan et al. 1999). The closely related pathogen *B. ostreae* can remain viable in seawater for up to a week under optimal conditions (Arzul et al. 2009); therefore, it is conceivable that the environmental tolerance of *B. exitiosa* will be similar. Consequently, in that time, *B. exitiosa* could disperse throughout Foveaux Strait. Heightened mortality from *B. exitiosa* in 2000–05 and 2013–16 presented different patterns of infection across the Foveaux Strait, which is indicative of an endemic pathogen (Dunn et al. 2003, Michael et al. 2008, Michael et al. 2019).

Infection by several different pathogens in addition to *B. exitiosa* is common in *O. chilensis* in Foveaux Strait and these include *A. longicornutus* (Hine & Jones 1994), APX (Hine 2002, Lane et al. 2016, Suong et al. 2017), *Microsporidium rapuae*, Rickettsia-like organisms (RLOs), and Endozoicomonas-like organisms (ELOs) (H. Lane pers. obs.), and other putative viruses (Dinamani et al. 1987, Diggles 2004). Oysters are commonly infected by more than one pathogen (Michael et al. 2022); however, the effects of co-infections on host energy and oyster population dynamics are a substantial knowledge gap. Co-infections of APX, *A. longicornutus*, and others may be additive, increasing the severity of disease; for instance, an analysis of over 6000 oysters over five years found a statistically significant association between the presence of APX and the intensity of *B. exitiosa* (Hine 2002). Yet, co-infections could be antagonistic, especially when they are competing for the same resource within the host or limiting access to a resource. Branching sporocysts of *A. longicornutus* castrate the host, conceivably limiting the putative energy source used by *B. exitiosa* to rapidly proliferate

The occurrence of shellfish disease is determined by a three-way interaction between the host, pathogen, and environment (Figures 8 & 9) (Snieszko 1974, Bernardo-Cravo et al. 2020, Lane et al. 2020). What impact climate change will have on the incidence of marine disease is uncertain and requires empirical data to forecast future disease trends. All organisms have an environmental range where they physiologically perform at their best. When the environment becomes less favourable for an organism, it moves the organism beyond its ability to adjust, known as stress. The occurrence of stress can leave oysters more susceptible to infection. Temperature is the most well-studied driver of disease (de Kantzow et al. 2016). Often an increase in temperature can cause a direct effect on disease and mortality. Yet, the relationship is not linear, because some pathogens physiologically perform better at cooler temperatures. *Bonamia ostreae* and presumably *B. exitiosa* survive better at cooler more saline conditions (Arzul et al. 2009); therefore, it is conceivable that any increase in water temperature may not greatly impact disease in Foveaux Strait oysters. The oceanic high energy environment of Foveaux Strait mixes the water column greatly, potentially acting as buffer against variations in temperature.

Two additional factors in the occurrence of disease are the role of the host microbiome and the parasite microbiome (Figure 8); these factors are only now starting to be understood with our understanding of their influence on disease in its infancy (Dheilly et al. 2019). Each oyster hosts a myriad of microorganisms and variations within these microscopic communities are linked to outbreaks of disease (Bass et al. 2019). These communities, coined pathobiomes, challenge the one pathogen-one disease paradigm yet remain to be fully tested. Hine (2002) showed APX may increase the susceptibility of oysters to *B. exitiosa*. Changes in the microorganism communities of other aquatic ectotherms such as corals have been demonstrated to cause disease (Harvell & Lamb 2020).
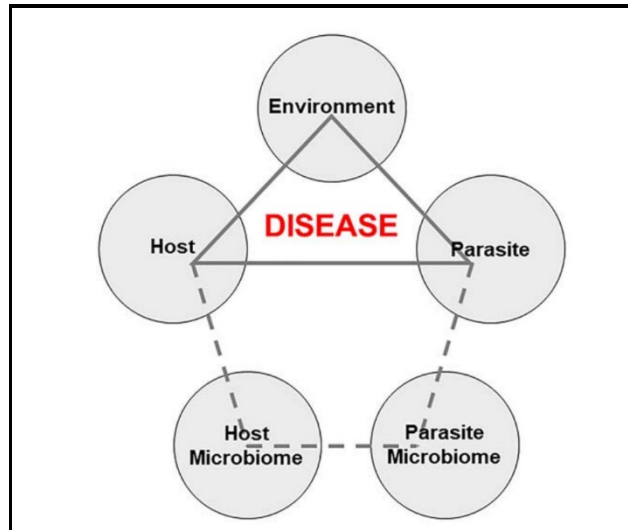
Figure 8: The epidemiological triangle demonstrating the three interacting factors that govern the outbreak of disease, including the prospective epidemiological pentagon (dotted lines) with two proposed additional factors of host microbiome and parasite microbiome (reproduced from Lane et al. 2020).
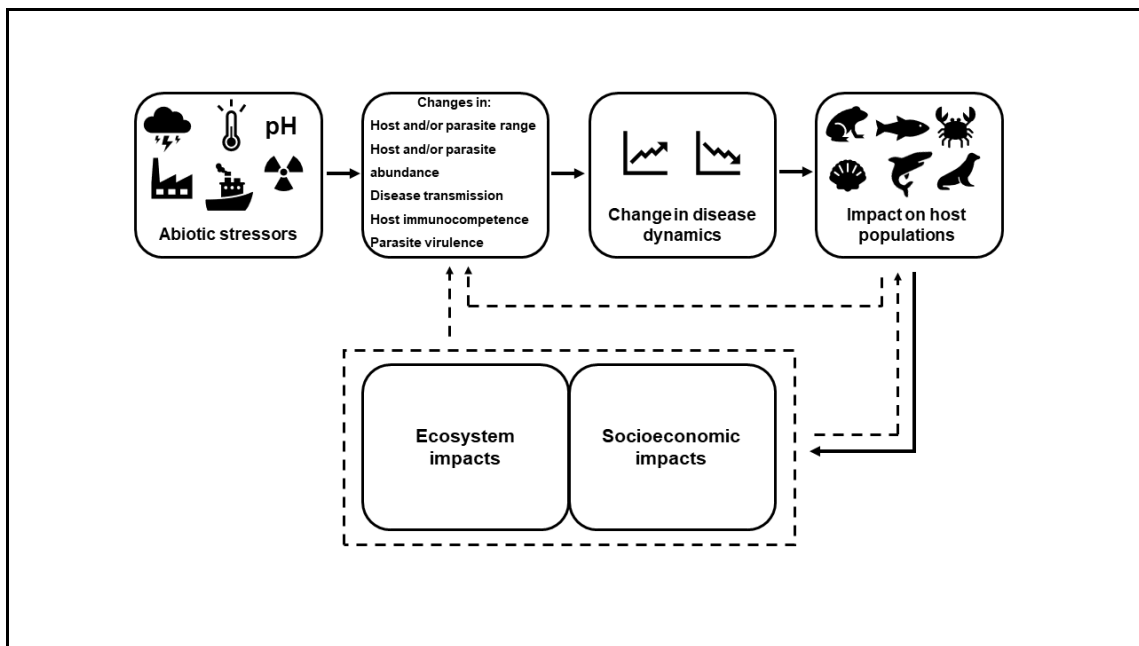
Figure 9: Schematic of how abiotic stressors can cascade through a system resulting in ecosystem and/or socioeconomic impacts. Dashed lines represent feedback interactions (reproduced from Lane et al. 2020).

Host reproduction and disease

The intensification of *B. exitiosa* infection is linked to the reproductive state of the oyster (Hine 1991a). Reabsorption of host ova increases the lipid content within the haemolymph (oyster blood), increasing energy available to fuel the proliferation and intensification of *B. exitiosa* leading to greater risk of mortality in the population (Hine 1991a). Oyster reproductive state is determined by oyster size as a proxy for age and somatic condition. *Ostrea chilensis* is a protandrous hermaphrodite (Cranfield 1979), maturing first as male then simultaneously possessing male and female gonads at ≥ 50 mm in length (Jeffs & Hickman 2000), from year class 3+ (Cranfield 1979). Brooding-sized oysters are ≥ 60 mm in length and possess predominantly female gonad (Jeffs & Hickman 2000).

A study of *O. edulis* and its response to *B. ostreae* in Ireland (Egerton et al. 2020) showed that oysters are locally adapting to disease through a change in energy investment from reproduction and growth to enhanced immune function, i.e., disease changes the partitioning of host energy through local adaptation to combat disease. Changes in energy partitioning may, in part, explain changes in reproductive success in *O. chilensis* before and after the 1985 *B. exitiosa* epizootic. Before 1985 (1960s and 1970s) between 7% and 18% of brooding-sized individuals brooded in any year (Hollis 1963, Stead 1971b, Cranfield 1979, Jeffs & Hickman 2000). Brooding percentages declined markedly to 1–2% post-1985 (Bluff Oyster Enhancement Company unpublished data).

The low brooding rates suggest either oysters do not fully develop ova and transfer brood into the mantle cavity (breed as females) every year, with a high level of reabsorption of ova each year, or oysters may have a variable strategy of brooding and an early release of larvae. Years with high levels of reabsorption drive high annual mortality from *B. exitiosa* (Hine 1991a) and potentially other pathogens.

Effects of pathogens on oyster population size and oyster beds

In Foveaux Strait, fisheries-independent variation in oyster densities is driven by periodic disease mortality (Doonan et al. 1994, Cranfield et al. 2005, Fu et al. 2016) caused by *B. exitiosa*. Epizootics of *B. exitiosa* appear to be a recurrent feature of the Foveaux Strait oyster population, having caused epizootics in 1985, 2000, and 2013. Reports of heightened mortality date back to 1906 (Hunter 1906).

Substantial declines (ca. 90%) in the recruit-sized oyster population from *B. exitiosa* mortality were recorded from 1985 to 1992, and in 2000 (Doonan et al. 1994, Cranfield et al. 2005, Fu et al. 2016) and to a lesser extent in 2013 (Michael et al. 2019). While recruited population size is important to the management of OYU 5 (Fisheries New Zealand 2021), the numbers of localised areas of high oyster densities, 'oyster beds', are the most important to the oyster fishery. High oyster densities provide high catch rates and maintain the economics of fishing. Recruit-sized oyster densities fell from 7 oysters m^{-2} in the 1960s (Stead 1971a) to 0.3 oysters m^{-2} in 1992 after the 1985 epizootic. Oyster density is likely to have been higher in the early 1980s. In 1999, there was some recovery with an increase to 13 oysters m^{-2} (Michael et al. 2001); however, these numbers have not increased further because of recurrent disease mortality. Oyster mortality appears to be density dependent and disproportionately reduces the numbers of oysters in high-density patches. The reduction in the numbers of 'oyster beds' has a significant effect on the catch rates and the distribution of fishing.

Pathogens are reliant on high oyster densities for effective spread. Michael (2019) suggests that effective spread of infection and disruption to recruitment may occur at 0.5 oysters m^{-2}. The 1985 *B. exitiosa* epizootic spread rapidly through the fishery in a wave of infection and mortality (Cranfield et al. 2005). Doonan et al. (1999) estimated a threshold density of 1.26 recruit-sized oysters m^{-2} triggered the 1985 epizootic and subsequent wave of mortality. Since then, patterns of infection and mortality have varied spatially and temporally throughout the fishery. *Bonamia exitiosa* is directly transmitted from oyster to oyster and is density dependent. Oysters dying from *B. exitiosa* release some ~10^6 infective particles that can survive >48 hours in the environment at normal Foveaux Strait summer water temperatures (Diggles & Hine 2002) to spread and infect nearby oysters. High mortality (~20% of recruit-sized oysters per year) produces high infection pressure caused by the release of substantial numbers of infective particles dispersed by rapid tidal flows. High prevalence of infection may persist in oyster patches for 2–3 years (Cranfield et al. 2005), suggesting that infections may take some time to intensify to fatal infections. These non-fatal infections probably affect spawning and recruitment.

Effects of environmental factors on disease

Environmental variables affect host physiology (Engelsma et al. 2010) that can influence the intensification of disease and subsequent host mortality (Hine et al. 2002, Arzul et al. 2009, Engelsma et al. 2010, Rowley et al. 2014). There have been several studies on different environmental factors on disease dynamics of *Bonamia* parasites, with seawater temperature and salinity studied most frequently. Temperature modulates host physiology by altering the velocity of chemical and enzymatic reactions, rates of diffusion, membrane fluidity, and protein structure (Hochachka & Somero 2002, Pernet et al.

2007). Laboratory trials carried out in New Zealand on *B. exitiosa* and *O. chilensis* found significant differences in prevalence, intensity, and mortality between treatments representing mechanical disturbance, cold (7 °C) and warmer (26 °C) seawater, hyper-salinity (39–40 ‰), and exposure to air than in experimental controls (Hine et al. 2002). Similar results were found by Audemard et al. (2008), who reported higher mortality of *C. ariakensis* associated with *B. exitiosa* when exposed to warm water (>26 °C) and high salinity (30‰, parts per thousand) conditions. Interestingly, recent outbreaks of *B. exitiosa* (1985, 2000, and 2013) occurred during strong El Nino events, suggesting a possible link between disease and cooler temperatures and more gales.

The relationships between environmental factors and *B. ostreae* are well studied, mainly because of the historical importance of this parasite to the health of European and North American oyster populations. Mortality from *B. ostreae* was lower in the North American autumn and winter at temperatures <20 °C (Carnegie et al. 2008), with higher prevalence observed following warmer autumns and winters (Engelsma et al. 2010). Cold winters (<5 °C) were associated with lower prevalence and intensity of *B. ostreae* in *O. edulis* from Denmark. Further, during 'ice-winters' where intertidal and near shore areas ice over, *B. ostreae* was at undetectable levels (Madsen et al. 2013). Free *B. ostreae* within the water column had lower survival at higher seawater temperatures and lower salinities (Arzul et al. 2009) and it is likely that similar results will be found for *B. exitiosa*.

Inundation by sediments during storm events and fishing effects (van Banning 1991, Cranfield et al. 1999, Cranfield et al. 2005) may play critical roles in physiological stress and therefore disease susceptibility. Inundation and storm events may limit food availability. Engelsma et al. (2010) found that *O. edulis* was more susceptible to *B. ostreae* after years of low food availability and lower salinity, probably as a result of isolation, where the oyster remains closed and ceases feeding for long periods of time to isolate it from an unfavourable external environment. Understanding and quantifying the relationship between climatic and environmental factors on disease and including them in the OYU 5 stock assessment model could incorporate the effects of climate and environmental variability on the frequency and severity of disease events (after Rowley et al. 2014).

3.1.11 Fishing mortality

Fishing mortality is the removal of recruit-sized oysters from the population by fishing, i.e., the catch. The patterns of fishing vary within and between years, and between regions within OYU 5. Patterns of fishing are primarily driven by distance from port, sea conditions, and tides, and, importantly, oyster size, meat quality, and catch rates. Patterns of fishing and catch are recorded in fishers' logbook data (during 2006–21). Survey, bycatch, and logbook data show four distinct regions within the 2007 stock assessment survey boundary that comprise different habitats, environmental factors, and oyster characteristics such as size, meat quality, and the numbers of spat (0+ and 1+ year old oysters) attached. After the ability to predict disease, spatially explicit stock assessments which partition the stock area into these regions may better represent the fishery.

The distribution of relatively high density oyster patches is primarily driven by the spatio-temporal patterns of disease mortality from *B. exitiosa*. A putative link between fishing and disease has been suggested as a reason for the recurrent disease mortalities since 1985. Stress caused by dredging may exacerbate disease (van Banning 1991). *Ostrea edulis* infected by *B. ostreae* had higher levels of prevalence from stressed beds; however, sources of stress included fishing and outlaying (handling) and environmental stress, and their effects were determined by host condition and female reproductive maturity (van Banning 1991). Cranfield et al. (2005) suggested that dredging for *O. chilensis* in Foveaux Strait causes a high level of mechanical disturbance that could make oysters more susceptible to infection and mortality from *B. exitiosa.* A laboratory trial investigating the effects of disturbance on *B. exitiosa* infection and mortality in *O. chilensis* found significant differences in prevalence, intensity, and mortality between treatments than in controls (Hine et al. 2002). However, these data were not consistent with the analysis of *B. exitiosa* infection and mortality data from surveys and fishing effort from fishers' logbooks shown in Figure 10. At the spatial scale of one nautical mile squares, there is no relationship between the fishing intensity (dredge tows per logbook grid cell per year) during the

autumn-winter oyster season and fatal and non-fatal *B. exitiosa* infections the following summer (Michael 2023).
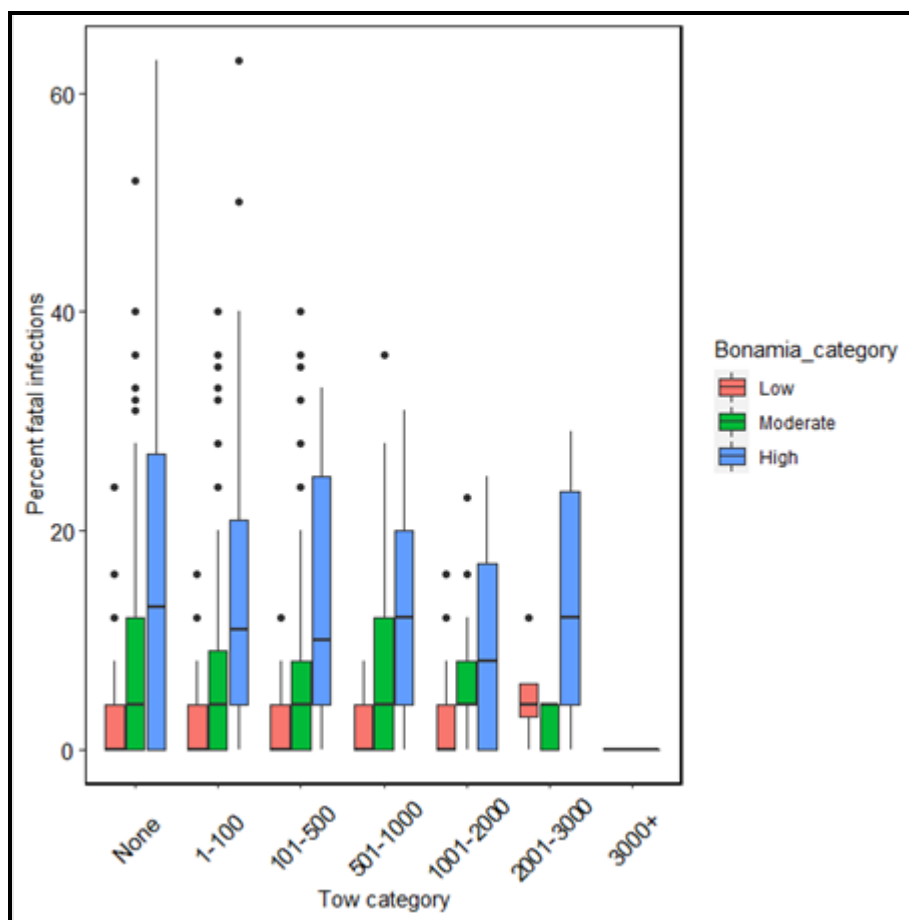
Figure 10: **Boxplots of the percentage of fatal Bonamia infections of recruit-sized oysters by categories of the numbers of commercial dredge tows in each of the fishers' logbook grid cells each year. Each category of dredge tows is further stratified by low (0.1–4.9%), moderate (5.0–9.9%), and high (greater than 10%) categories of percentage of annual Bonamia mortality. 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 reproduced from Michael (2023).**

Incidental fishing mortality

Incidental mortality of oysters from dredging with light (320 kg) and standard (450 kg) dredges was compared experimentally in March 1997 (Cranfield et al. 1997). Oysters in the experiment had only a single encounter with the dredge. Both the damage and mortality of oysters left behind on the dredge track were inversely related to size. Spat (0+, ≤10 mm in length) attached to recruit-sized oysters were the most vulnerable to damage. The mortality of 0+ spat was higher using a standard dredge (19%) than for the light dredge (11%). Damage and mortality in both juvenile and recruit-sized oysters left on the dredge track did not differ significantly between standard and light dredges. Juvenile (10–57 mm) oyster mortality (7%) was notably greater than that for recruit-sized (≥58 mm in length) oysters (2%).

The mean mortality of 0+ spat passing through the dredge ringbags during washing was 25% and did not differ between dredges. More of the spat that were retained in the standard dredge were killed (36%) compared with the light dredge (23%). Juvenile oysters passing through the dredge ringbags during washing suffered notably higher rates of heavy damage than those remaining in the dredges; 11% of oysters washed through the ringbags were heavily damaged compared with 5% in the dredge. Mortality of juvenile oysters was also greater in those passing through the ringbag (10%) than in those retained

within the dredge (4%). The levels of damage and mortality of oysters during washing of the light and standard dredges did not differ notably (Cranfield et al. 1997).

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 recruitment to the fishery.

Natural mortality

Natural mortality (other than disease mortality) is not well estimated (Dunn et al. 2000) but considered low for recruit-sized oysters. Natural mortality is size dependent, is generally low for 0+ spat (< 6%, Cranfield 1968a, 1968b), however can be high (R. Hickman from Cranfield 1979), and generally low for 1+ age cohort and older oysters. Sources of natural mortality include predation, over-colonisation, poor condition, and old age, and the occasional effects of large storms that may move and bury large numbers of oysters. Mortality from intense infestations from the boring sponge *Cliona* spp. may be occasionally significant in some areas of the fishery (Stead 1971b, Cranfield 1975), as it is for *C. virginica* (Carroll et al. 2015).

Mortality of recently settled spat and 0+ oysters can be high. Storms that mobilise sediments cause significant mortality through the dislocation of spat from light settlement substrata (shell) (Figure 11) that are tumbled by tidal currents, and burial of spat on those settlement substrata by moving sediments. Survival of 0+ spat is greatest on live oysters and large gastropods, e.g., *Astrea heliotropium* (Michael 2019). A shell return experiment that showed enhanced settlement of oyster spat and a range of benthic taxa was obliterated by storms between October 2007 and December 2007 (Michael 2011) (Figures 12 & 13).

Figure 11: Recently settled spat (blue arrows) on two different bivalve shells: *O. chilensis* on the left and *Oxyperas elongatum* right.
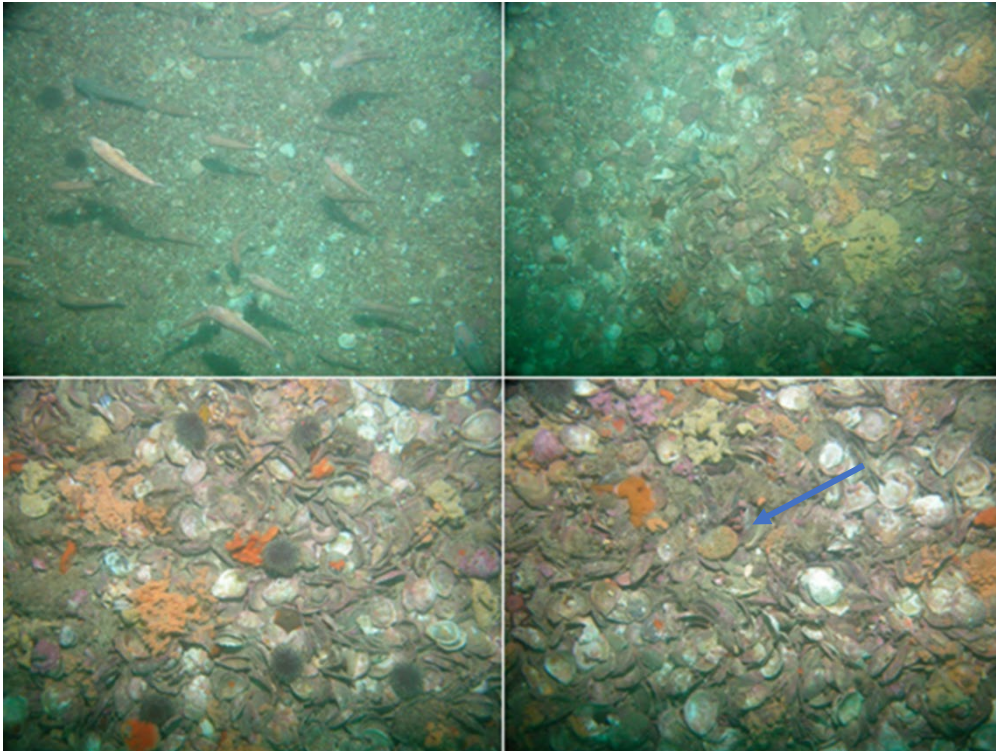
Figure 12: **A shell return experiment to enhance habitat and quantify increased settlement and survival of oyster spat. Top left panel shows the seabed around the heaps of oyster shell;and the top right panel shows the edge of the returned shell. The bottom two panels show a range of benthic taxa, including *Cinctipora elegans* (shown by blue arrow, bottom right panel), that rapidly colonised the shell heaps.**

Figure 13: Shell return experiment buried in sediment after storms.

Predators of 0+ spat and juveniles are thought to include: the Ophiuroid *Ophiopsammus maculata*; asteroid starfish *Coscinasterias muricata*, *Allostichaster insignis*, and *Sclerasterias mollis*; cushion starfish *Patiriella regularis*, *Pentagonaster pulchellus*, and *Asterodon miliaris*; crustaceans *Metacarcinus novaezealandie*, *Pagurus novizealandiae*, *Eurynolambrus australis*, *Nectocarcinus* sp.; and gastropods *Astraea heliotropium*, *Modelia granosa*, *Xymene pusillus*, *Charonia* sp., *Cabestana spengleri*, *Argobuccinum pustulosum tumidum*, *Maoricolpus roseus*, *Calliostoma tigris*, and *Maurea punctulate* (previously recorded in bycatch as *Calliostoma punctulatum*) (Stead 1971b, Michael 2023). *Astraea heliotropium* and *Ophiopsammus maculata* are abundant and ubiquitous throughout the commercial fishery area. Starfish predation can be high for experimental oysters held on and just above the seabed (K. Michael, NIWA, pers. obs.).

Over-colonisation may be an important and unquantified source of oyster mortality. Succession and over-colonisation may drive changes in epibenthic communities in Foveaux Strait and the spatial temporal patterns of colonisation and over-colonisation are likely to be highly variable within the oyster fishery regions. Cranfield et al. (2004) give a conceptual model of macrofaunal assemblage succession and habitat regeneration on the seafloor of Foveaux Strait. Live oysters provide stable, clean substratum for the settlement of other taxa. The over-colonisation of oysters depends on sources of larvae or body fragments and delivery mechanisms (Caddy & Defeo 2003). Colonisers likely to cause mortality of oysters include the ascidian *Botryloides leachi* and the sponges *Chondropsis topsentii*, *Crella incrustans*, and *Dactyllia palmata*. The growth of colonisers can be rapid, such as the colonial ascidian *Botryloides leachi* that can quickly over-colonise extensive areas of epibenthic fauna.

The large swells and high tidal currents generated by the high-energy environment of Foveaux Strait determine the distribution and stability of sediments and the composition and distribution of benthic communities (see Bricheno et al. 2015, Joshi et al. 2017). Western Foveaux Strait is more exposed and subjected to greater sediment mobility during storms than eastern areas; however, normal tidal current flows are higher in the eastern strait. Commercial densities of oysters occur on shell, sand, and gravel substrates with little or no other epibenthic taxa, and typically on substrates that can be mobile during storms. Oysters can be covered by coarse calcareous sediments and survive well. The layer of sediment probably offers protection from predation and over-colonisation. However, prolonged burial will cause a loss in condition and potentially death. Conversely, oysters on complex epibenthic habitats are more likely to be exposed to higher predation and over-colonisation.

3.2   Towards a new disease model

Currently disease is included in the assessment model as an additional mortality term. The parameterisation has an independent rate for each year, and these are free parameters to enable the model to fit to the abundance data from surveys (Large et al. 2021).

Ideally, infection and disease mortality would be included as a functional form (i.e., dependent upon parameters which can be fitted to observational data), which would mean there is a mechanistic relationship to explain increases and decreases in population abundance and reduce the number of independent parameters to be estimated within the model. A mechanistic understanding and disease model would potentially bring greater confidence in model projections.

Epidemiological models refer to individuals or populations occupying one of several states. The most common model is the SIR model (Susceptible – Infected – Recovered, or Susceptible – Infected – Removed) (Kermack & McKendrick 1927), whereby individuals are either susceptible (i.e., able to be infected), infected (able to transmit infection to other susceptible) or recovered/removed (post-infection and no longer able to be infected or transmit infection). The dynamics of the Foveaux Strait oyster population suggest that a more appropriate model would be SIDM (Susceptible – Infected – Diseased – Mortality), to distinguish those individuals which are clinically infected but not exhibiting visible signs of disease, and those considered diseased, and which have a higher probability of future mortality from disease.

Furthermore, what is clear from the data is that being infected or diseased is not sufficient to cause periods of high mortality. At least one additional factor is necessary to explain these periods of increased mortality: factors include, but are not limited to, density-dependent disease mortality, environmental factors, host factors, and co-infections. Determining which factors influence the process of disease mortality is key to incorporating a mechanistic disease component into the model. Identifying appropriate datasets to inform the disease model will be an important component; examples include the infection prevalence data collected since 2000 and data on new clocks indicating recent disease mortality. The outputs of such a disease model, parameterised on the data, could feed into the mortality estimates used in the current CASAL model, rather than being used to tune the model to the abundance data from surveys.

Shown in Figure 14 is an example of how such a disease component of the model could be implemented into the current assessment, given sufficient data to inform the disease mortality rate. In brief, the model is an ordinary differential equation (ODE) model with four compartments for individuals (SIDM, as described above), with two life stages (juveniles and adults). New susceptible juveniles are fed into the model at rate a annually (hence the spiked shape of the juvenile curve), oysters are infected at rate b, become diseased at rate c, and die at rate m. We set recruitment at $a = 100$, $b = 4 \times 10^{-4}$, $c = 3 \times 10^{-1}$ and $m = 5 \times 10^{-2}$ (values chosen for illustration, not specifically for *Bonamia*). Then we simulate for 100 years (enough time to run the system to steady state) with periods of high mortality (increasing m to 3×10^{-1} in every 3 years for one year) to observe the effects on the population size.

The simulation in Figure 14 is at steady state with most adults in the diseased state. The increase in mortality causes a drop in diseased individuals, which then rise as more individuals become infected. This simple representation assumes constant recruitment; linking recruitment to spawning population abundance would make dynamics more complex.

We note the simplistic nature of the simulation used. This was a purposeful decision, to highlight the basic dynamics at play with respect to infection, disease, and disease mortality. We use the example only to highlight the potential uses of a disease sub-model (i.e., to inform the disease mortality parameter fed into the model).
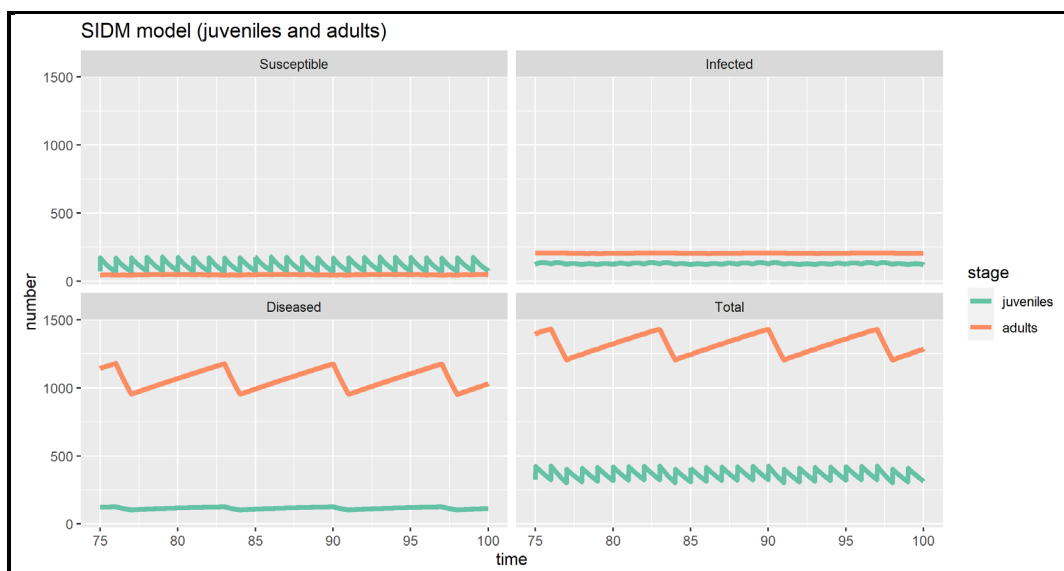
Figure 14: Example output from the ODE model produced to simulate the infection and disease prevalence in juvenile and adult oysters (shown in green and orange respectively). Plots are, from left to right, and then top to bottom: (top left) number of susceptible; (top right) number of infected; (bottom left) number of diseased; (bottom right) number in total.

More complex models could use spatial data if the resolution of the data was sufficient. This would lead to spatially explicit models, such as that of Datta et al. (2013), although the data available in that paper were of much higher resolution than available for the Foveaux Strait, due to the aforementioned study having a smaller area, concerted effort, and terrestrial data collection having fewer complications. It is unlikely such data will be able to inform the modelling approach used for Foveaux Strait oysters.

3.3 Review of the OYU 5 stock assessment models

Early abundance surveys may have biased B_0 to be high due to the adjustment when standardising across surveys. As an example, the 1962 survey (providing the first absolute abundance estimate) produced impossibly high catch sizes once scaling was performed. Hence, since the introduction of the oyster pathogen *Bonamia exitiosa* (Berthe & Hine 2003) in the mid-1980s, productivity in the fishery has been higher than expected at low population sizes (Large et al. 2021). However, recurrent disease mortality prevents spawning stock abundance (SSA) rebuilding to pre-disease levels.

There are no data on early recruitment (*R*) (pre-1993) and disease mortality (*D*) incorporated into the current model. From 1993, surveys estimated the abundance of the small size group (<50 mm length) which can inform recruitment strength. The *Basic* and *Revised* models are structured so that recruitment and disease mortality parameters are estimated within the models to account for the variations in vulnerable abundance that cannot be explained by fishing (*F*) or natural mortality (*M*) alone. As a consequence, recruitment and disease estimates are considered to be overfitted given the data limitations. Outputs from the two models were similar.

The dominating influence on future SSA is disease mortality from *B. exitiosa*. To make predictions of future stock size, predictions of disease mortality are required. These predictions require either information on some regularity in the disease occurrence, or the conditions that signal a new outbreak (heightened levels of *D*).

3.3.1 Model behaviour

Model abundance estimates and the overfitting of disease rates, year class strengths, recruitment, and survey abundance estimates highlight the need to better understand how the datasets (along with data weightings) and the priors behaved within the model.

Disease estimates and selectivity

Since the mid-1980s Bonamia epizootic, disease has clearly been the main driver of oyster population abundance (Figure 15). Consequently, a disease dynamic sub-model that could project over multiple years is the most useful potential development. Issues in estimating disease mortality using the *Basic* and *Revised* models, and the potential ways to remedy these issues, are outlined below.

The current models estimate annual disease rates independently from each other. Disease mortality has an independent rate for each year, and in some years is subjectively 'turned off', i.e., set to zero. The models estimate disease for years when it is turned on: 1949–51, 1960–66, 1985–95, 2000–17. However, over these four periods, 2000–17 contained two heightened periods of *D* with a lower rate of 0.08–0.12 in the years between them. The *Revised* model attempted to mitigate the independent rates of *D* by using a smoother (Figure 16). Annual disease rates are overfitting the data (i.e., spurious disease estimates), thereby limiting any opportunity to model disease within the stock assessment model.

The restrictive prior biases the estimates of disease mortality, which means that a *D* of 0.4 is unlikely, 0.5 not at all likely, but the model estimates values of 0.4 in 6 of the model years, i.e., the model suppressed high mortality. The maximum disease rate allowed was 0.8 (equivalent to 45% of the population in one year because the disease rate is instantaneous). The estimated disease rates were heavily weighted towards zero, see Appendix 1, Table A1.1. No smoothing penalties were used for disease in the *Basic* model, so they were independent of each other, whereas the *Revised* model introduced a smoothing function to allow more consistent disease rates through time (Figure 16).
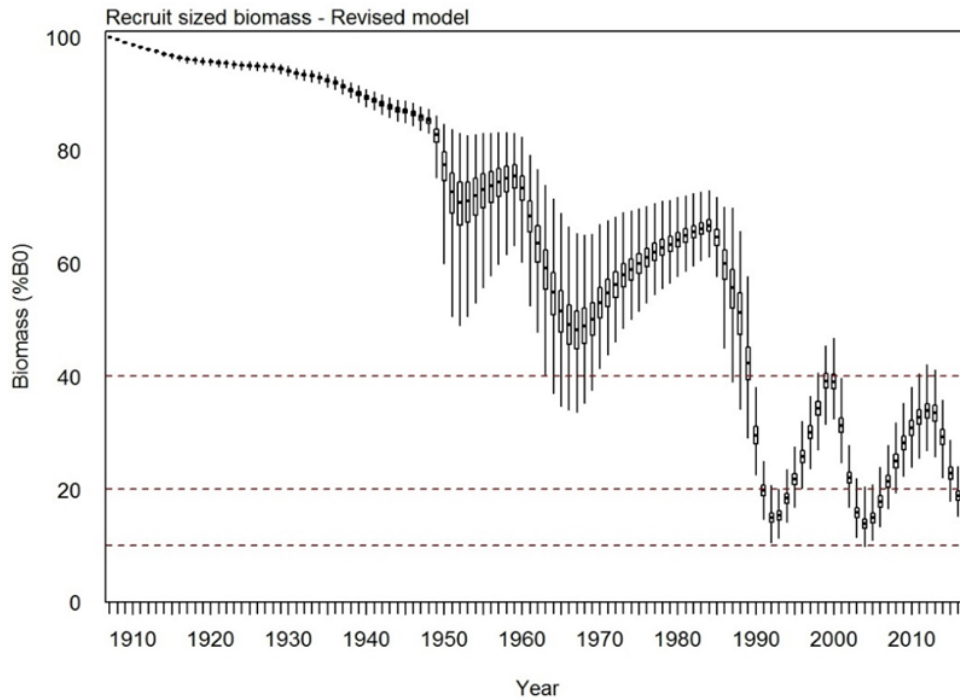
Figure 15: Recruit-sized (legal-sized oyster) population size as a percentage of B_0 (the population before fishing began) from the last (2017) Foveaux Strait oyster stock assessment. Horizontal dashed lines show 40%, 20%, and 10% B_0. The rapid declines of population size from three Bonamia epizootics can be clearly seen from 1985, 2000, and 2013. For earlier declines, 1948–1952 is an unidentified heightened mortality event, and 1958–1964 was initially attributed to *A. longicornutus* (Howell 1967), but later attributed to Bonamia (Cranfield et al. 2005). Figure reproduced from (Large et al. 2021).
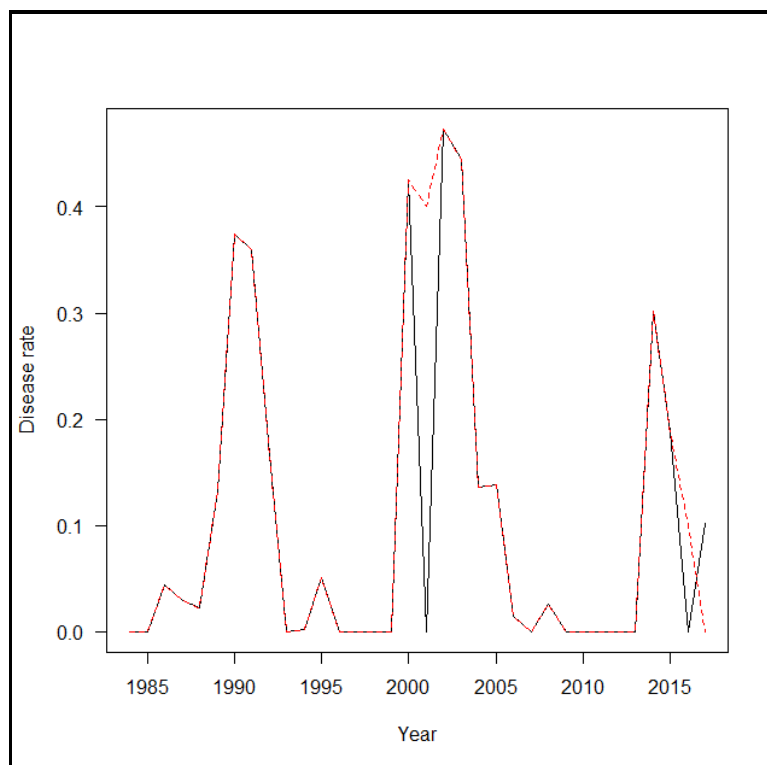
Figure 16: MPD estimated disease rates. Black line is from the *Basic* model (2 of the 4 CPUE series), and the red dotted line is from the *Revised* model.

Without estimates of disease mortalities, the models use the abundance series as way points for the trajectory of the population given the losses due to fishing and natural mortality, and additions from recruitment into the population. The abundance before fishing (B_0), and hence mean productivity, can be estimated from losses attributed by the model to fishing and natural mortality. Disease mortality and recruitment are used by the model to account for unexplained variations in absolute abundance estimates.

When disease mortality was estimated, the prior used only the right-hand tail of a normal distribution, this means using a mean -0.2, standard deviation 0.2, and bounds ((0.0, 0.8) is used, see figure 6 of Dunn 2007). The derivation of this prior is not described, and it appears to be a subjective proposal by Dunn (2005) to enable the assessment to proceed. The disease selectivity ogive was assumed to be the same as the maturity ogive, i.e., that disease causes oyster mortality, for each length class, at a rate equal to the maturity selectivity multiplied by the estimated yearly rate.

The *Revised* model used the Diggles (2004) data on oyster infection rate by oyster size to fit a logistic selectivity ogive for disease, but this produced a very poor fit to the data (Figure 17). The estimated selectivity ogive was similar to the maturity ogive that the *Basic* model used for the disease mortality ogive.

We explored the Diggles (2004) dataset with another parameterisation:

$$D_{L,y} = D_y/Z_{L,y} (1-\exp(-Z_{L,y})) N_{L,y}$$

where

$$Z_{L,y} = M + D_y*D\text{sel}(L)+F_{L,y}$$

where $D_{L,y}$ is the disease mortality rate at length L in year y,

D_y is the disease mortality rate in year y,

$Z_{L,y}$ is the total mortality at length L in year y,

$N_{L,y}$ is the number of oysters at length L in year y,

M is the natural mortality rate (assumed to be 0.1)

$D\text{sel}(L)$ is the 'disease selectivity' at length L, and

$F_{L,y}$ is the fishing mortality at length L in year y.

The models estimate oyster mortality at size by oyster size (length) bins as:

Mortality for the jth length bin is $D*\text{logistic}(j)/Z(j)*(1-\exp(-Z(j))*N(j)$.

The Diggles (2004) dataset contained only one oyster in the largest length bin that had a fatal infection (i.e., 100% mortality, Figure 17), which looks like a logistic curve; however, these data show an asymptote for the proportions of infected oysters at about 0.55 (Figure 17). To make this data into a selectivity, the Diggles (2004) data were divided by 0.55, and any data point over 1 was truncated to 1 (Figure 18).

We refitted the latter data (Figure 18) in the *Revised* model, but the fits were poor, and the estimated selectivity curve was close to the maturity curve. Substantially upweighting the transformed data did get a better fit (green dashed line, Figure 18). Excluding the disease selectivity data (i.e., no disease selectivity data but still fitting the disease ogive) gave an entirely different curve that selected the larger recruited sizes. Clearly, the selectivity data were outweighed by other data in the model, and this resulted in a very poor fit (dashed red line, Figure 18).

Whilst completing this part of the analysis, we detected an error in the CASAL code, where *D* was applied in both time steps rather than just to the summer time step, so the estimated *D* was half the value that would be estimated if it was applied in time step 1 only. A version of this assessment was converted into a CASAL2 model as a test for length-based modelling and this showed that the above error has very little effect on the assessment.

The disease selectivity ogive was estimated from data recorded in 2004, when the 2000–04 epizootic was near its end and so the selectivity ogive may not represent mortality at length during periods of peak mortality. Additionally, figure 9 of Dunn (2007) gives selectivity of Bonamia infections (prevalence) based on infection categories 1–5 of Diggles et al. (2003) and the Diggles (2004) infection data. However, these data (n = 500) represent both non-fatal infections (categories 1–2, n = 93) and fatal infections (categories 3–5, n = 145).

Dunn (2007) used the oyster maturity data for females as a disease selectivity in the *Basic* model and used the Stead (1971a) mortality data to justify the use of the maturity data as a proxy for disease selectivity. Dunn (2007) interpreted dead oysters recorded by Stead (1971) during the 1962–64 surveys as new clocks (Stead does not specify new clocks and the counts were probably new and old clocks). Dunn (2007) used the maturity curve as a disease selectivity curve because his new clock ratios (1962–64) lengths fitted reasonably well to the maturity ogive. This implies that mortality from disease for the largest individuals was nearly 100%. The figures 2–11 of Stead (1971) show 'dead' oysters to be less than 60% over most of the size range and 100% for the largest oysters.
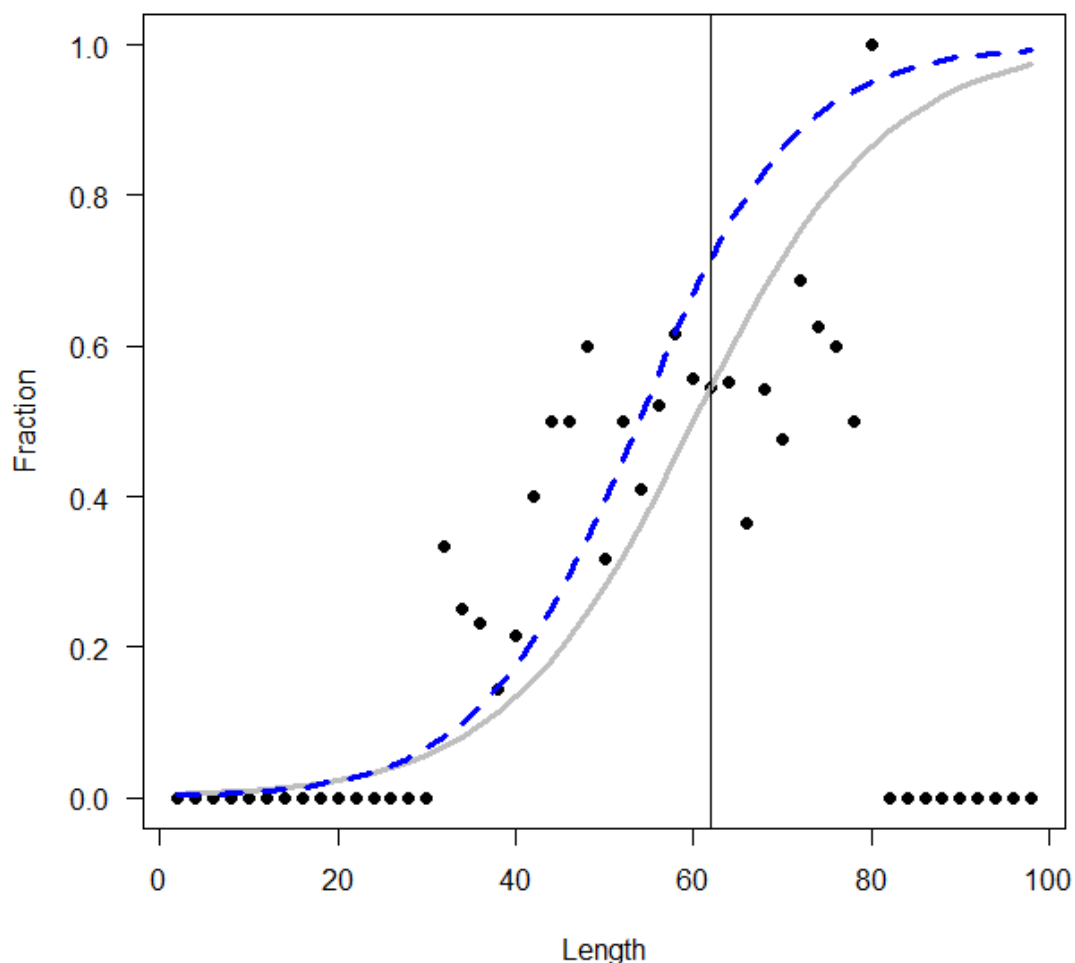
Figure 17: Proportions of oysters (solid dots) with *B. exitiosa* infection of level 1+ from *B. exitiosa* histological sampling from the January 2004 surveys by length (mm) (B.K. Diggles, NIWA, unpublished data). Solid grey line is the fit from the revised model; the dashed blue line is the ogive used for the *Basic* model (maturity ogive).
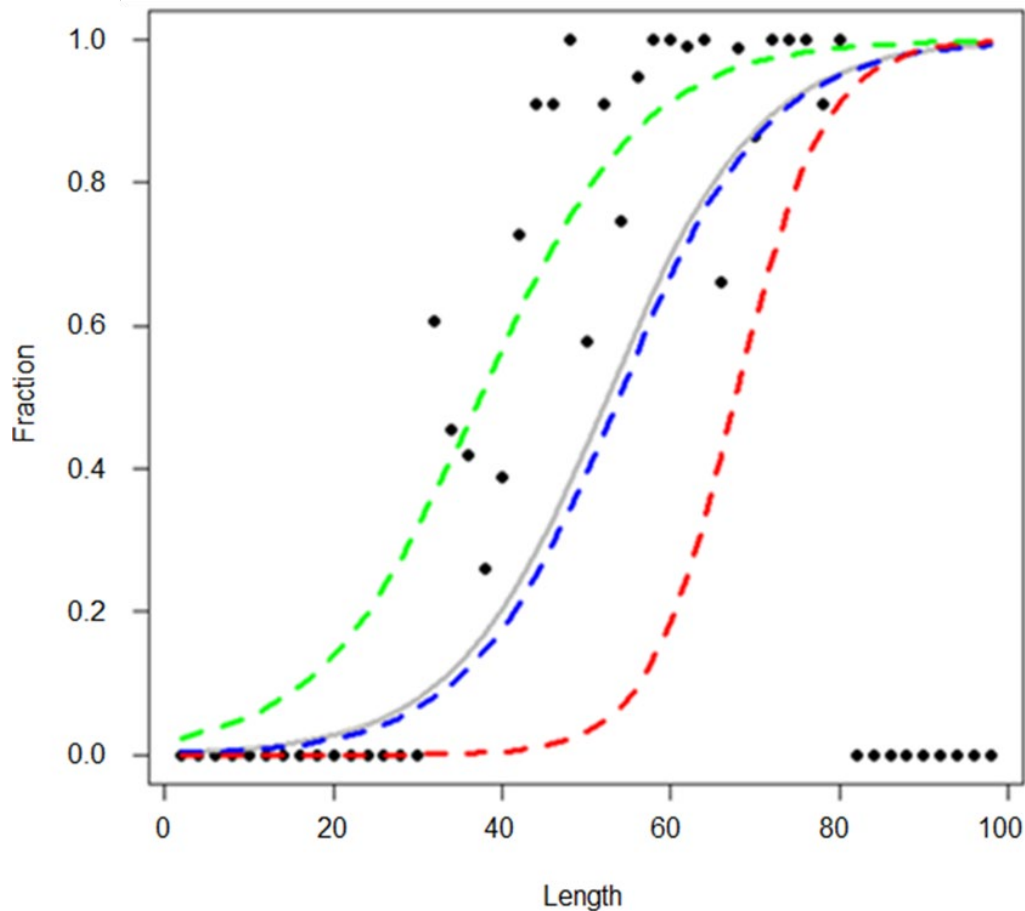
Figure 18: **Transform proportions of oysters (solid dots) with a *B. exitiosa* infection of level 1+ from *B. exitiosa* histological sampling from the January 2004 surveys by length (mm) (B.K. Diggles, NIWA, unpublished data) into selectivity values by dividing by 0.55 (the flattish bit) and setting values over 1 to 1. Solid grey line is the fit from the *Revised* model; the dashed blue line is the maturity ogive used for the *Basic* model. The green dashed line is the fit using increased weight by 2000 times. The red line is excluding the selectivity data.**

Potential methods to predict future disease mortality

Heightened disease mortality events occur over three or more consecutive years and have been cyclic in nature since 1992 (Figure 15). If an ability to reliably predict annual levels of D for the OYU 5 fishery can be established, the number of independent parameters to be estimated to account for lower-than-expected stock sizes from survey abundance (i.e., D) can be reduced. Population estimates of new and old clocks could be used to estimate recruit-sized and pre-recruit mortality 1–3 years prior. Additionally, the progress of non-fatal to fatal infections could predict levels of future mortality if a time-lag relationship could be established.

The two most recent mortality events have corresponded to similar total oyster abundances (~40% B_0) at the top of the cycle (Figure 15). Two possible explanations for the cyclic nature of the declines include oyster density thresholds and temporal factors associated with disease mortality.

The current models are unable to project the course of disease mortality effects. Using independent estimates of disease mortality in the model and/or using a disease dynamic sub-model to model the temporal dynamics of disease mortality would greatly improve model performance and projections.

Estimated percentage disease mortality and its partial autocorrelation

The disease rate by year (annual percent disease mortality) shows three periods corresponding to the three disease events, i.e., disease events are multi-year phenomena and the rates do not appear to be random and independent within each event (Figure 19). The disease rates are similar between models, but the *Basic* model's estimates contain zeros in two internal sequences (2001 and 2016) that the *Revised* model does not.

Taking data from 1984, the disease rates from the *Basic* model had no autocorrelation, but the *Revised* model did (0.66 at a lag of one year). The time series is short so it would be hard to estimate autocorrelation, which is why the 95% CI for zero autocorrelation in the *Revised* model is ± 35% (Figure 19). Because annual disease mortality rates are assumed independent, predictions of future mortality cannot be made. The current model therefore assumes rates, i.e., the three scenarios at 'low', 'medium', and 'high' rates of future disease mortality, which has marked effects on projections of future stock status. The single largest improvement in the current models would be an accurate disease dynamic model to estimate future mortality.

The future level of fishing is unknown; however, it is unlikely to be twice the current TACC (14.95 million oysters; this represents between 1% and 3% of the recruited population).
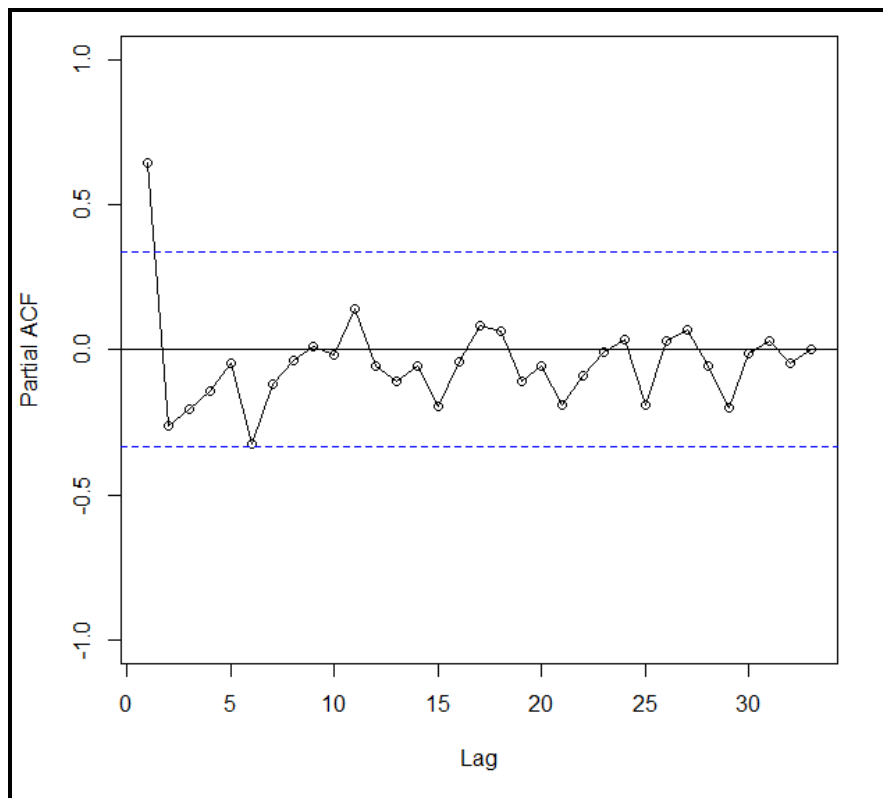
Figure 19: **Partial autocorrelation estimates for disease from the *Revised* model. Dotted blue lines are the 95% CI for zero correlation. Lag 1, the correlation between disease mortality that is one year apart, is significant and has a value of 0.66.**

3.3.2 The relative influence of the survey data to that of CPUE data

Stock assessment rely mostly on data series of abundance estimates. These comprise a mixture of dredge and dive surveys, commercial CPUE, and abundance estimates from mark recapture experiments (1974 and 1975); see Dunn (2007) for details. Many of the abundance estimates have been adjusted to standardise oyster density estimates and survey areas; however, it is likely that many of these abundance estimates, especially pre-1990, are not adequately comparable. Comparable dredge surveys began in

1992. CPUE indices from 1948 bridge a data gap; however, recent CPUE indices have little influence on model fits.

Most abundance datasets were well fitted by the models (Appendix 1, Table A1.2). The two early CPUE series (A & B) were poorly fitted in all models. Absolute abundance estimates (1962–2017) were scaled by dredge efficiency estimated from two trials: however, only the estimate of Doonan & Cranfield (1992) is used so the error in dredge efficiency is correlated with the abundance fits in the model, i.e., the error is actually a bias and not a random error. The revised model uses a tight prior for the dredge abundance estimates (CV of 10%).

The second series of abundance estimates are unstandardised CPUE data from 1948 (Dunn 2007). CPUE has lower weight than the survey estimates of abundance. Models run with CPUE alone gave a different stock status and higher B_0 than those with the absolute survey abundances included. Except for CPUE series A (1948–68), which is a period for which there are no dredge survey data, CPUE contributes very little to model fits, i.e., the dredge surveys determine the stock status. CPUE series C (1985–present) has been split into C and D from 2010, when changes in fisher behaviour (high-grading for oyster meat quality) and industry limits (fishing to demand resulted in daily bag limits imposed by processors) occurred. The 'smooth' shaped length frequency distribution from commercial catch sampling with one mode has changed to one of four well defined modes which cannot be fitted by the models. There are also differences in maximum size and potentially growth. These differences may be accounted for by the introduction of 3–4 fishery regions within the models.

The predicted commercial length frequencies (LF) from 2012 do not fit the observed multi-peak structure that has developed since the targeting of oysters with good meat quality, which is indicative of a change in regional behaviour of the fleet. The right-hand side of the model size distribution does not fit the 1990 dive survey LF.

For the *Basic* model structure, the March survey LFs for smalls and pre-recruits had poor fits in the model. Instead of using the maturity ogive as a proxy for disease selectivity used by the *Basic* model, the *Revised* model fitted 3+ disease proportions to LFs that produced a better disease selectivity curve, and thereby better fits.

Since the 1985 Bonamia epizootic, there has been a regime shift in oyster stock size. Recurring disease mortality has limited rebuilding of the oyster population size. The differences in inferred abundance from available data pre- and post-1985 have a marked influence on estimates of B_0 and thereby stock status relative to SSA reference points.

3.3.3 Recruitment

To model changes in future oyster abundance, understanding recruitment to the population and the speed at which cohorts transition into the commercial fishery is important for reliable projections. Whilst improved estimates of disease mortality will provide the greatest improvement to the current OYU 5 stock assessment model, especially during epizootics, any improvement in recruitment estimates will likely have relatively small overall benefit. In periods of low or no disease mortality, improved estimates of recruitment and cohort progress will allow for stock projections to be made with more accuracy.

Ignoring mortality processes, projections of new oysters into the adult stock is based on the estimated mean recruitment adjusted by the estimated year class strength six years ago. It is estimated by the models as a variation in year class strength so future recruitment into the first length partition at year 1+ can be predicted. Age one oysters take six years on average to become vulnerable to fishing (recruit-sized), so in five yearly stock assessments recruitment is now a very important part for adult population predictions.

Since about 2000, surveys have reported the abundance of 'small' and 'pre-recruit' sized oysters. Recruitment to the population is tied to survey abundance estimates of small oysters, that represent 2–4-year classes that are already present and growing in the population. Hence, smalls represent an average of early year class strengths (YCS) from the three years prior to the survey. The model already has the information to project adult population size because it can estimate what is going to be recruited into adult sizes in the coming years.

If survey estimates of abundance are higher than expected in an assessment year, the model may increase recruitment six–nine years before to account for the increase in the vulnerable abundance. For assessments, oysters entered the partition of the population size structure at mean 15.5 mm and CV of 0.4, truncated at 2 mm. Year class strengths are spread over several length bins and so following cohorts overlap in the partition, making identifications of a specific cohort 'fuzzy'. Year class strength in near terminal years can fit to other effects (e.g., changes in growth or disease rates) because there are no future YCS data available to the model to constrain YCS. Data on the relative abundance of recruits to the population (0+ age class) are available from Bluff Oyster Management Company Ltd (BOMC) spat monitoring programme and from spat on oysters landed as part of the annual catch (0+ and 1+ age classes). The estimates of small size group oysters from surveys could also be used as an index of recruitment. There has been significant variation in growth of the small size group, as evidenced by recent surveys between 2014 and 2017, where the high abundance of small oysters did not transition to recruit-size (vulnerable abundance) due to low growth. Few observed population length frequencies are available. Dunn (2007) constructed a length frequency from a graph of height frequencies from 1960 to 1962 (Stead 1971a), one converted from a 1990 dive survey height frequency, and three length frequencies from dredge surveys in October 1999 and 2001, and February 2017. Regular length frequencies from annual surveys could better track both recruitment and early growth.

Growth is highly seasonal, with all growth occurring over the summer (step 1 in the OYU 5 model). Marked differences in growth are apparent from the observations of summer resource surveys (K. Michael, NIWA, pers. obs.). The growth increment data are from 1970 and 1981, from a caged experiment at a single site in the eastern fishery area. Interannual, seasonal, and individual variation was high; however, this variation was not captured by the growth parameters used in the models, and modelled transitions across length partitions may not reflect changes in the oyster population size structure and conflict with the abundance of small oysters. Modelled growth has oysters entering the vulnerable abundance—50% at age 6 and 100% by age 9. Slow growth can be problematic because the proportions of large oysters in the population size structures inform the upper limit to B_0 in MCMC estimation.

3.4 Recommendations for further development of stock and disease models

This investigation has highlighted some key questions on important drivers of oyster population abundance, especially disease, and some of these may in part be answered by the analysis of existing data. The model review also highlighted the lack of key data, such as population length frequencies.

3.4.1 Improvements for current OYU 5 stock assessment model

Improving the handling of disease mortality within the model and ultimately developing a predictive disease model will provide substantial benefits to the model predictions (see Section 5). A summary of suggested improvements to the *Basic* and *Revised* stock assessment models (Dunn 2007, Fu et al. 2016) is given in the following text and Table 4. Knowledge gaps to be filled include the following.

1. Gain a better understanding of disease, including the development of new modelling approaches, novel hypotheses around disease dynamics, and data collection.
   a. Determine what factors initiate heighted disease mortality, e.g., oyster density threshold, co-infections of oyster pathogens, climatic factors, and any interactions*. Important climatic factors to consider include temperature, El Nino effects, and storm effects.
   b. Update disease selectivity. The research of Diggles (2004) needs to be updated to include Bonamia and other pathogens by oyster size and sex, and reproductive state.

    c.   Determine how well new clocks account for disease mortality prior to surveys?

    d.   Determine how well fatal and non-fatal infections predict future mortality?

    e.   Develop a method to predict new outbreaks, i.e., model an outbreak (only the following year of outbreak, with a few parameters to control disease progression).

2. Determine the following: what percentage of female oysters produce broods and what percentage are fertilised each year, and how does this percentage vary annually? Specifically, do female oysters breed each year?

3. Estimate future recruitment with an alternative project by resampling the last ten years of year class strengths.

4. Develop improved estimates of the variation in individual, regional, and interannual growth.

5. Investigate spatial differences of biological parameters across the fishery including more frequent length frequency data.

* Epidemic 'burn out' should be quantified to allow model conditions for 'burn out' to be defined. A burn out of zero infection is highly unlikely given the direct oyster to oyster transmission of Bonamia especially during heightened mortality, and the unexplained persistence of *Bonamia* spp. in the environment for many years.

To further tune the model of Dunn (2007), an assessment of model runs should be carried out incorporating, in order of ease of implementation:

1. Drop combinations of all uncertain data, especially some of the abundance estimates.

2. Investigate starting the model later (i.e., exploited state) that better relates to the current stock's dynamics with *B. exitiosa* endemic in the population and its transformed state of sustainability, i.e., truncate data from 1992, and estimate B_0 as B_{1999}.

3. Incorporate survey estimates of disease mortality.

4. Incorporate estimates of recruitment to the population.

5. Record more population length frequencies from surveys.

6. Test the following in the model: whether recruitment and spat collector data inform on YCS and 'smalls' data inform R with a lag. Estimates of recruitment are available and may be greatly improved, i.e., estimating the numbers of 0+ and 1+ oyster based on their year class lengths from surveys.

Table 4: **Suggested improvements to the *Basic* and *Revised* OYU 5 stock assessment models. (Continued on next page)**

Assumption	Data/treatment	New data required?
Disease operates on its selected population	*Basic* model: Disease selectivity assumed to be maturity ogive. Reportedly matches proportion of clock by length in the 1960–64 surveys when a suspected *Bonamia* event occurred – some data interpretation issues.	Fit to estimates of disease rates by size. Adapt Bonamia surveys to collect over a wider length range in one survey. Investigate proportion of new clocks and infected 3+ oysters by length from the current surveys?
	Revised model: fitted to disease proportion-at-length (1+ infections), but this ogive is similar to maturity and so made little difference. *D* applied to both time steps. Data from 2004 when disease event was at an end and so may not be relevant for peak infection. *Revised* model fits disease proportion-at-length poorly and so it was not useful as applied here. Also, the nature of the data was not really a selectivity in terms of what fishery models use as selectivity.	Update disease selectivity data for 'high' and 'low' Bonamia years. Disease selectivity ogive should be using proportion with 3+ infections. The estimated ogive produces a very poor fit to the data. The data imply a capped logistic at about 55%. Highlights that we really need to know more about the way the disease works.

Table 4: *Continued.*

Assumption	Data/treatment	New data required?
Growth is unchanging	1979 & 1981 caged oyster experiments at one site.	Update growth data using mark recapture programme. Ideal time is post oyster season in spring before summer growth period.
Spawning	Female and hermaphrodite *O. chilensis* in Foveaux Strait have very low brooding percentages and may not spawn (as females) every year.	Investigate reproductive capability and effects of pathogens on brooding and fertilisation.
Maturity is unchanging	Jeffs & Hickman (2000) estimated measures of maturity from the re-analysis of sectioned oyster gonads.	Update post-1985 epizootic to check. Assess data in Heenan et al. (2021) paper on reproduction of *O. chilensis* in Foveaux Strait.
Maturity is a simple process like in fishes	Assumed. Important for the biology, but the model will adapt parameters so that it fits the absolute abundances. The mechanism may be different (not females may spawn each year), but the level of recruits into the model remains the same. It could be important for stock status calculations.	Needs lab experiments. Maybe not important in modelling. Perhaps generating simulated data from various hypotheses to check its impact.
Natural mortality (M) is 0.1	Assumed, but supported by two recovered oysters at liberty for 26 & 29 years. Oysters take about 6 years to reach recruited size. Years as a recruit before being tagged cf. 1% of population is 46 years. Sensitivity runs over a plausible range.	Too hard. Suggest estimating within model, but dangerous. Use other values (29 years at liberty?)
Productivity remains constant	Assumed. There may be regime shifts, but New Zealand modelling does not account for this.	
Steepness is 0.9	Assumed. No reason given.	If new spat require other oysters to settle on and to survive to 1+, then might expect a steepness of 0.5, say.
Recruitment CV is 20% and independent of each other	Assumed. Maybe kept low to get stable performance from the model?	In the longer term, may have enough YCS to estimate this. Current YCS estimates do not look independent and are highly correlated with the preceding cohorts. Pattern is low YCS period, a few very high ones, followed by declining YCS to very low, with indications of increasing YCS in recent years. The low years would be helped by a lower *h* since it is a multiplier in the recruitment level in that year. YCS better behaved; suggest 0.5?
Recruitment behaviour is known	Model version is R_0*YCS*fn(*h*,SSA).	Some evidence of very good recruitment 1998 & 2 years either side, but not repeated since; was a low disease rate period (rates of 0).

3.4.2 Discuss appropriate platforms for modelling

The development of a model to predict disease is suggested as the highest priority. Once a model structure has been developed and the input data made available, the platform may not be so relevant. However, any platform needs to be readily available to provide consistency of delivery and be familiar to Fisheries New Zealand modelers. One possibility is to use CASAL2 for the OYU 5 assessment.

4.   DISCUSSION

The OYU 5 stock assessment model requires future levels of disease mortality (that cannot be currently predicted) and different harvest levels (that can be reliably determined) to project future stock status and spawning population abundance for comparison with reference points for management. When stock assessments occurred every two years, the last stock assessment survey provided the stock size, and levels of disease mortality were estimated from annual Bonamia surveys. Projections of future stock size were corroborated by subsequent surveys of the oyster population (Fu et al. 2016). Although this model is unable to predict disease mortality and future stock size independently, it has been critical in demonstrating to fishery stakeholders that Bonamia mortality has been the principal driver of oyster abundance since 1985 and the subsequent low fishery exploitation rates have had little effect on future stock size.

Fu et al. (2016) suggested the development of a disease model by incorporating critical relationships between the OYU 5 stock and disease established by research, to predict the speed of progression to fatal infection and levels of mortalities in localised populations. The highest priorities in the short term are to address disease mortality and recruitment in the current model. Thereafter, a predictive model for future disease mortality should be developed. This review recommends that a better understanding of the epidemiology of *Bonamia exitiosa* and research to inform a predictive disease model will add the greatest value to stock assessments of OYU 5.

Bonamia infection data and co-infection data, and new and old clock data from surveys, some of which are being analysed as part of Fisheries New Zealand research programme OYS2020-03 may help develop a prior on annual disease mortality.

Almost all the available abundance data (dredge survey estimates and CPUE) are used by the model. The estimates of abundance from dredge surveys are standardised to make them comparable. Michael (2003) suggests that these surveys are not likely to be comparable because of the different dredges, estimates of tow lengths, and methods of position fixing for surveys. Putatively high, early dredge estimates, together with the changes in factors affecting CPUE, may overestimate B_0 and affect spawning stock abundance in relation to reference points.

Spatially explicit regional models could better reflect environmental and habitat characteristics that drive oyster productivity. Such models would require estimates of recruitment, growth, and mortality for each region to provide contrast to the whole of stock assessment model. Gains in information for stock assessment and management at the scale of stock would be relatively small; however, the partition of the fishery into sub-units would provide information for spreading fishing effort and other fishing strategies.

The next stock assessment of OYU 5 is scheduled in 2023. As part of that process, further improvement (agreed to by the Shellfish Working Group) should be considered. These include dropping uncertain data from the assessment, starting the model in 1992, and incorporating independent estimates of disease mortality and recruitment.

5.   POTENTIAL RESEARCH

Based on Section 3.3, and on recommendations given in the report for drivers of long-term change in the OYU 5 fishery (OYS2020-03, Michael 2023), in order of recommended priority:

1. The development of a predictive disease model. Critical to this development is an understanding of:
    a. *Bonamia exitiosa*, its epidemiology in the *Ostrea chilensis* population in Foveaux Strait, and its interaction with other pathogens and climatic factors.
    b. 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 size range of the population.
    c. Determine the triggers for heightened disease mortality. Although critical oyster densities are important to the spread of infections (Cranfield et al. 2005), they may not be triggers for an epizootic. Non-fatal and fatal infections appear to increase similarly in the same year, and non-fatal infections give no warning of future mortality. Determining a predictable cycle of mortality and factors that exacerbate disease mortality are critical knowledge gaps.
    d. Factors that drive successful spawning, and consequences for the reabsorption of ova. Reabsorption of female gametes is known to intensify *B. exitiosa* infection leading to oyster mortality.
    e. Research to better understand if and how disease effects oyster mortality, growth, and recruitment. This may include surveys of *Alcicornis longicornutus*, and its effects on reproductive success, with flow-on effects on recruitment and size structure.

2. Research to improve inputs into the OYU 5 stock assessment model:
    a. Update and improve estimates of growth, specifically from 3–4 regions within the fishery area, with different habitats and environmental factors. Estimate growth using an industry tagging programme and investigate the utility of sequential population size frequency distributions. Ideally robust estimates from the four distinct fishery regions can be obtained for spatial assessments.
    b. Decide on whether to use two-dimensional growth (length and height) or three dimensions (length, height, and depth).
    c. Better delineate year class strengths through regular estimates of population size frequency.
    d. Continue to record recruitment to the oyster population while investigating the utility of spat monitoring, estimates of 0+ from annual dredge sampling, and data from shed sampling of the commercial catch.
    e. Further investigate the utility of new clocks as estimates of mortality. This will require a better estimate of their dredge selectivity, their persistence as new clocks through a better understanding of fouling rates (i.e., the settlement and growth of fouling organisms) and the erosion nacre in the inner shell (i.e., loss of lustre), and their persistence at location on the seabed where they died.

6.   ACKNOWLEDGEMENTS

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8. APPENDIX 1

Table A1.1: Estimated percentage disease mortality from the *Basic* (D_Basic) and *Revised* (D_Revised) models (1944–2017), and survey estimated (D_survey, recruit-sized new clocks, and 3+ infections). '-' denotes years when disease was not turned on (i.e., set to zero), disease turned off 1907–1943 (not shown). NA for no survey estimates of percentage disease mortality, i.e., estimated from recruit-sized new clocks and 3+ infections.

Year	D_Basic	D_Revised	Year	D_Basic	D_Revised	D_surveys
1944	-	-	1981	-	-	NA
1945	-	-	1982	-	-	NA
1946	-	-	1983	-	-	NA
1947	-	-	1984	-	-	NA
1948	-	-	1985	0.0000	0.0000	NA
1949	0.0000	0.0000	1986	0.0443	0.0443	NA
1950	0.0000	0.0000	1987	0.0290	0.0290	NA
1951	0.0003	0.0003	1988	0.0224	0.0224	NA
1952	-	-	1989	0.1331	0.1331	NA
1953	-	-	1990	0.3748	0.3748	NA
1954	-	-	1991	0.3600	0.3600	NA
1955	-	-	1992	0.1668	0.1668	NA
1956	-	-	1993	0.0000	0.0000	NA
1957	-	-	1994	0.0024	0.0024	NA
1958	-	-	1995	0.0507	0.0507	NA
1959	-	-	1996	-	-	NA
1960	0.0095	0.0095	1997	-	-	NA
1961	0.0097	0.0097	1998	-	-	NA
1962	0.0005	0.0005	1999	-	-	NA
1963	0.1923	0.1923	2000	0.4260	0.4260	NA
1964	0.0000	0.0000	2001	0.0000	0.4000	NA
1965	0.0000	0.0000	2002	0.4733	0.4733	NA
1966	0.0001	0.0001	2003	0.4446	0.4446	0.140
1967	-	-	2004	0.1360	0.1360	0.200
1968	-	-	2005	0.1381	0.1381	0.220
1969	-	-	2006	0.0148	0.0148	0.114
1970	-	-	2007	0.0000	0.0000	0.085
1971	-	-	2008	0.0261	0.0261	0.053
1972	-	-	2009	0.0000	0.0000	0.082
1973	-	-	2010	0.0000	0.0000	0.075
1974	-	-	2011	0.0000	0.0000	0.100
1975	-	-	2012	0.0000	0.0000	0.120
1976	-	-	2013	0.0000	0.0000	NA
1977	-	-	2014	0.3022	0.3022	NA
1978	-	-	2015	0.1885	0.1885	0.140
1979	-	-	2016	0.0000	0.1000	0.051
1980	-	-	2017	0.1025	0.0000	0.049

Table A1.2: Fits of datasets used in the 2017 OYU 5 assessment model using the '4cpue' version of the *Basic* model and the *Revised* model. '-', dataset not used. Fits coded 'poor' are highlighted in grey.

Component	*Basic* 4cpue	*Revised* 4cpue
1976 survey	OK, over-fitted	–
1979 recapture data	–	OK
1981 recapture data	–	OK
Bonamia selectivity data	–	?
CPUE-A	Poor	Poor
CPUE-B	Poor	Poor
CPUE-C	Good	Good
CPUE-D	Good	Good
Commercial catch sampling to 2012	Good	Good
Commercial catch sampling post 2013	OK - multi-peak structure not fitted	OK - multi-peak structure not fitted
Jeffs Hickman maturity data	Good	Good
July survey (dive, recruits)	OK, one point	OK, one point
Mark recapture Survey (recruits)	OK	OK
March survey (recruits)	OK	good
March survey (pre-recruits)	Poor	Good
March survey (smalls)	Poor	Good
October survey (recruits)	Good?	Good?
October survey (pre-recruits)	OK	OK
October survey (smalls)	Good	Good
October dive survey length frequency	Poor	Poor
October survey length frequency (recruits)	OK	OK
October survey length frequency (pre-recruits)	Good	Good
October survey length frequency (smalls)	Good	Good