

Four-year decline in *Ostrea chilensis* recruits per spawner in Foveaux Strait, New Zealand suggests a diminishing stock-recruitment relationship

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Summary of significant differences between *O. chilensis* and other oyster species, and their fisheries

O. chilensis is a protandrous hermaphrodite (Cranfield 1979). Spawning occurs in the late austral spring, October–November with one main spawning event. Multiple spawning events are common in *Crassostrea virginica* (Knights & Walters 2010), *O. edulis* (Lapegue et al. 2006) and *O. lurida* (Pritchard et al. 2015). Oysters ≥ 60 mm in length (≥ 3 years old, Cranfield 1979) may brood larvae (Jefferies & Hickman 2000). Broods develop to late stage (with eyespots, Cranfield 1968b, Stead 1971a), competent and ready to settle on release. Most settlement occurs within minutes or hours (Stead 1971a, Brown 2011), and putatively around the natal population (Cranfield 1968a). The short pelagic larval duration (PLD) suggests limited opportunity for larval transport. The modelling of Broekhuizen et al. (2011) suggests mostly limited dispersal and self-recruitment to natal populations. Other commercial oyster species have longer PLDs and potentially greater dispersal and connectivity: e.g., *O. edulis* 8–10 days (Lapegue et al. 2006), *O. lurida* 7 days to eight weeks (Pritchard et al. 2015), *O. puelchana* 17–20 days (Pascual & Zampatti 1995), *Crassostrea virginica* 15–25 days (Narváez et al. 2012, Puckett et al. 2014), and *C. gigas* 3–4 weeks (Robins et al. 2017).

Foveaux Strait is exposed to oceanic swells up to 10 m (Gorman et al. 2003), and has swift tidal currents. *O. chilensis* mostly occurs in depths of 25–50 m on gravel substrates overlaid with coarse, calcareous sand (Cullen 1962, Stead 1971, Michael 2008), and differs markedly from the mainly low energy, shallow (≤ 10 m) estuarine and embayment habitats of other oysters (*O. edulis* Lapegue et al. 2006, *O. lurida* Pritchard et al. 2015, and *C. virginica* Knights & Walters 2010).

O. chilensis may form small clusters of oysters from the successive settlement of many generations of spat (authors' unpublished data), but does not form reefs in the fishery area like *Crassostrea virginica* (e.g., Kirby et al. 2012) and *C. gigas* (e.g., Walles et al. 2015). In Foveaux Strait, *O. chilensis* shell is aggregated by currents and bound by epibenthic taxa to form lenticular structures (biogenic reefs, Cranfield et al. 1999, Cranfield et al. 2001) along the tidal current axis. Shell and shell reefs are important to the recruitment of *C. virginica*, but reefs are not important to the recruitment of *O. chilensis* in Foveaux Strait (authors' unpublished data).

The Foveaux Strait *O. chilensis* fishery is an entirely wild fishery with no enhancement of stock, spat, or shell (settlement surfaces), whereas other fisheries are aquaculture based or enhanced (e.g., Shuttle et al. 2009). High disease mortality from *Bonamia exitiosa* (Doonan et al. 1994, Cranfield et al. 2005) and recruitment determine population abundance (Michael et al. 2015).

Location of fishery-scale sampling sites

Table S1: The locations of the six sites across the fishery where the spatio-temporal variation in recruitment was sampled.

| Site | Latitude | | | Longitude | | |
|------------|----------|---------|---|-----------|---------|---|
| East-high | 46 | 42.9000 | S | 168 | 25.1760 | E |
| West-high | 46 | 39.7020 | S | 168 | 4.1520 | E |
| South-high | 46 | 44.8560 | S | 168 | 18.6300 | E |
| West-low | 46 | 37.3020 | S | 168 | 1.2480 | E |
| East-low | 46 | 38.1720 | S | 168 | 29.3940 | E |
| South-low | 46 | 46.7340 | S | 168 | 12.6240 | E |

Estimates of spawner densities

Because of the depth, strong currents, and hard substrate of Foveaux Strait, dredge sampling is the only method available to estimate oyster densities. Photographic, video and grab sampling methods have severe limitations in Foveaux Strait. Repeat estimates of oyster density (Doonan et al. 1992, Michael et al. 2001) and of dredge efficiency (the scalar used to estimate absolute abundance, Fu et al. 2016) show good consistency.

Many of the six sites sampled across the fishery were deeper than 40 m, too deep for divers to sample. We estimated *Ostrea chilensis* spawner densities using standard dredge sampling methods (Michael et al. 2015) before spat collectors were deployed in November 2007. After 2007, we used mean estimates of recruits to the fishery (≥ 58 mm in length) and pre-recruit- (50–57 mm in length) sized oysters as putative estimates of local spawner densities (≥ 50 mm in length) from nearby survey sites (Michael et al. 2013), because we didn't want to disturb the spat collector sites. These surveys sampled different combinations of subareas (survey strata) each year. For years when there was no sampling near the sites, we assigned spawner density as the mean of the previous and following year's estimates. Spawner densities were estimated after spawning and settlement occurred, but before significant disease mortality and any fishing.

Sampling used a 3.3 m wide commercial oyster dredge towed in a straight-line, down tide. The standard tow length was 0.2 nautical miles (371 m), and target speed of 2.5 – 3.0 knots. Estimated sampling efficiency of the dredge was 0.17 (95% confidence intervals 0.13 – 0.22, Dunn 2005). We used this scalar to calculate estimates of absolute *O. chilensis* density.

We calculated spawner densities (oysters/m²) by adjusting catches to a standard tow distance (371 m), scaling for dredge efficiency (0.17), and dividing by the area swept (1224.3 m²). Because of the low sample numbers (3 – 4 tows at each site), we estimated 95% CIs using nonparametric bootstrapping (B=1000). Fig. S1 shows estimates of spawner densities for the six sites.

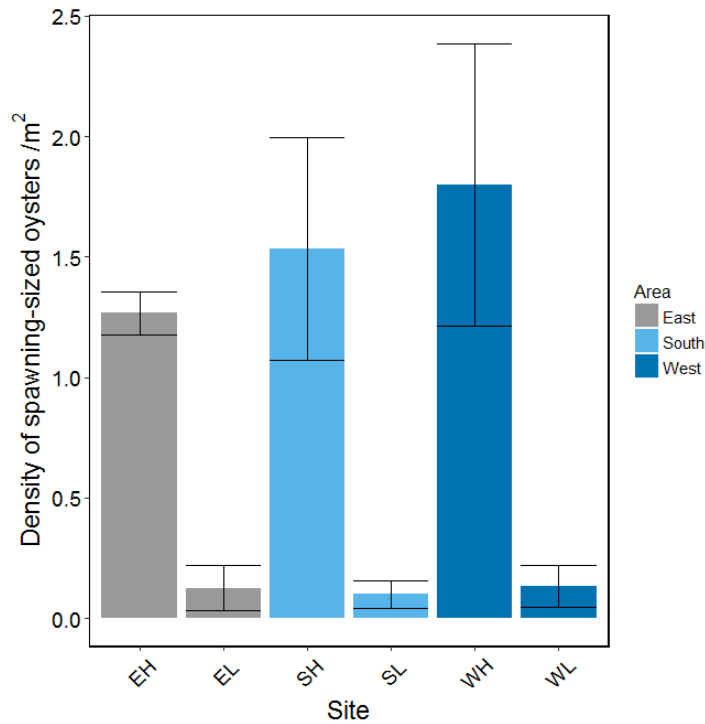


Fig. S1: Spawner densities, oysters (³ 50 mm in diameter) per m² sampled from sites across the fishery in November 2007. Site codes prefixed with “Area” West (W), South (S), and East (E); and suffixed with Category of density, high density (H), low density (L) respectively. Bars show mean densities with ±1 SE.

Putative annual estimates of spawner densities are derived from stratum level estimates from fishery independent surveys 2008–2011 (Michael et al. 2009a, 2009b, 2011, 2012, 2013), and only from those samples that were randomly allocated (Fig. S2). We made two assumptions about spawner densities at collector sites: dredge tows before sampling began were representative of localized densities; and these local densities remained the same or increased over the sampling period consistent with the estimates from fishery independent surveys.

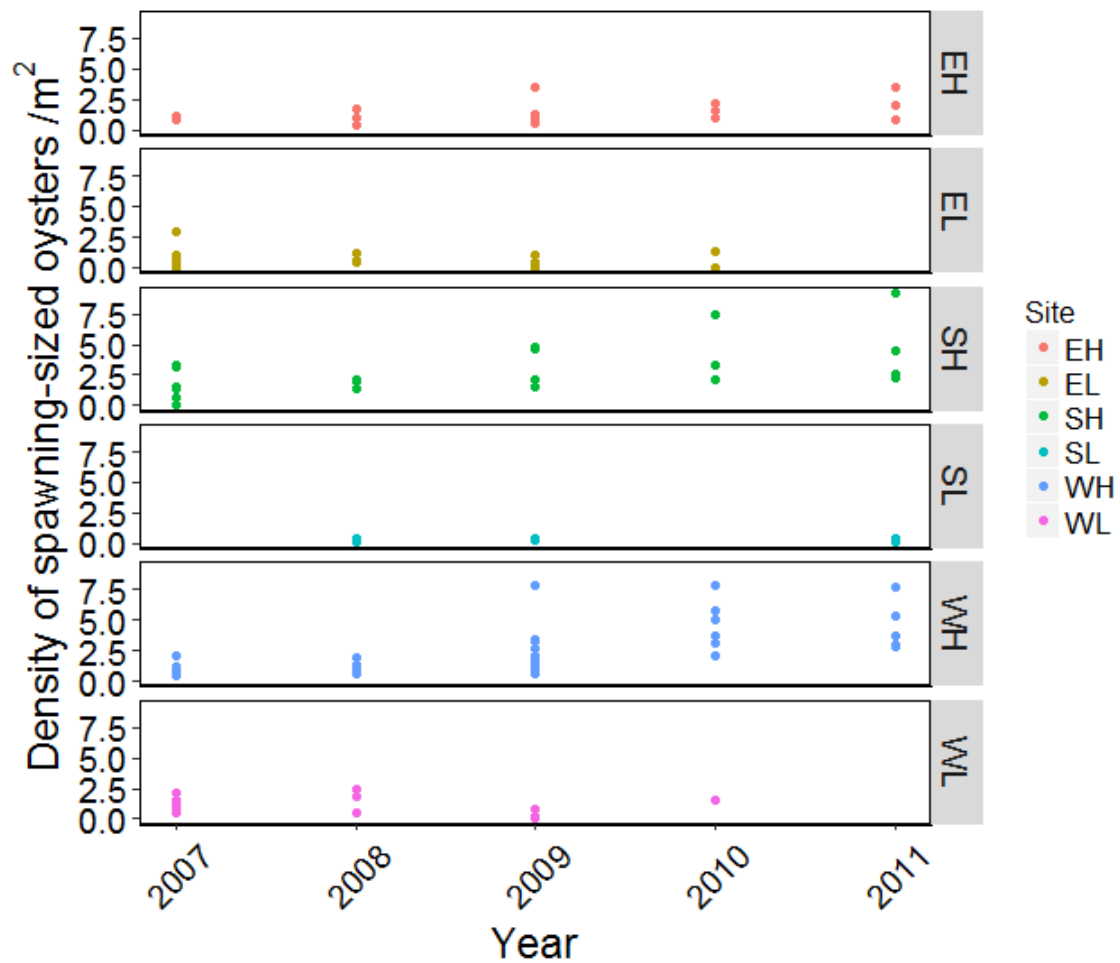


Fig. S2: Spawner densities by site from nearby, randomly allocated survey tows in strata where fishery-scale sites were located. Data from fishery independent surveys 2007–2011 (Michael et al. 2009a, 2009b, 2011, 2012, 2013).

Spawner densities sampled (Sample) in November 2007 and putative estimates from surveys in February 2008–11 (Survey) were similar at four of the six sites except the West-Low and East-Low sites (Fig. S3). Growth in *O. chilensis* occurs only in the summer months (Dun 2005), and the increase in spawner densities between November 2007 and February 2008 may more reflect recruitment of spawning-sized oysters than sampling variation alone. Moreover, fishery areas of relatively high spawner density are well defined in survey strata and the random locations of the survey samples likely to be closer to our spat collector sites. Spawner densities at West-Low and East-Low sites were similar over the study period, February 2008 to February 2011 (Fig. S2).

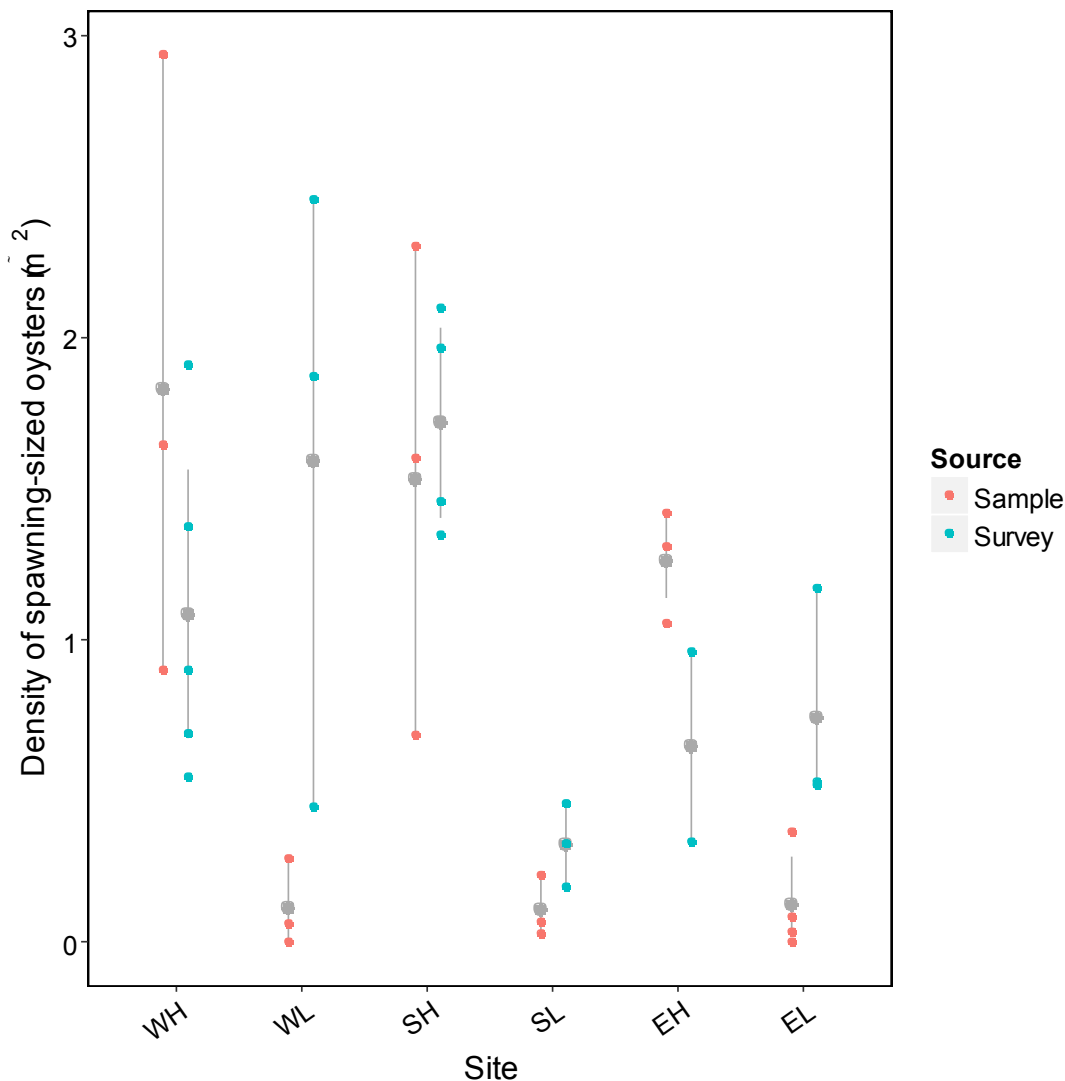


Fig. S3: Spawner densities sampled at each site before the spat collectors were deployed in November 2007 (Sample, red dots); and survey estimates sampled in February 2008 (Survey, blue dots). Growth in *O. chilensis* occurs only in the summer months (Dun 2005) and the increase in spawner densities between November and February may more reflect recruitment of spawning-sized oysters than sampling variation alone. Grey lines represent bootstrapped 95% confidence intervals for “Sample” and “Survey” estimates and grey dots are the mean densities.

Assessments of the Foveaux Strait *O. chilensis* stock (Fu 2013) shows the population size of oysters recruiting to the fishery increased 47% between 2007 and 2012, and catch per unit effort (CPUE), indicative of oyster densities in commercial fishery areas, increased 70% over the same period. Small annual surveys between stock assessments (Michael et al. 2015) show similar or increasing spawner densities 2006–2008 when recruitment was high, but higher densities in 2009–2011 when recruitment was low. A slight decline in density is shown in 2011, due to summer mortality from *B. exitiosa*, but after spawning and brooding had occurred. Estimates of spawner densities used in the study 0.1–1.8 in 2007 and 0.3–4.6 in 2011 (Table S2) are similar to the 75 percentiles of spawner densities in the fishery (Fig. S4).

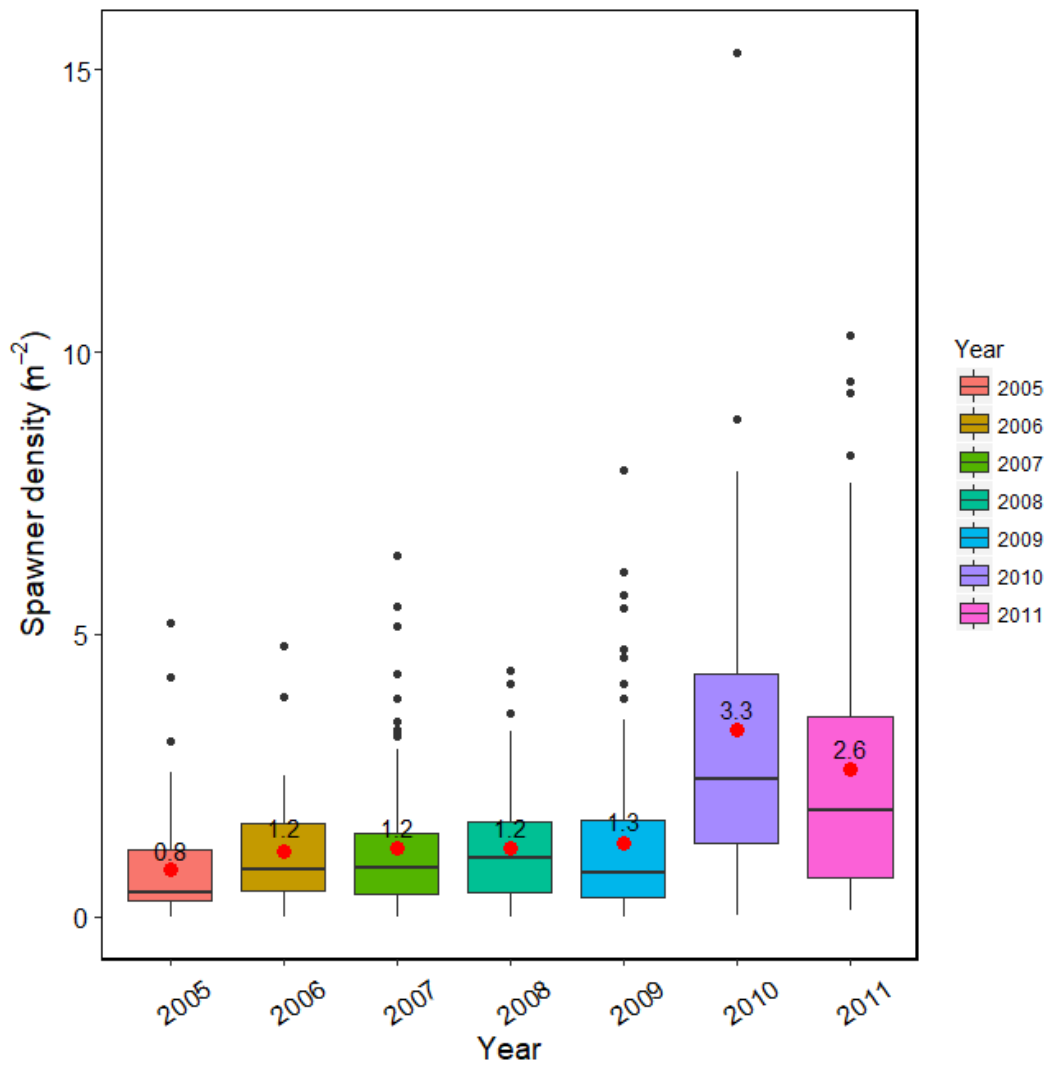


Fig. S4: The range of absolute *O. chilensis* spawner densities per m² sampled from random, fishery independent surveys 2005-2011. Boxplots show medians, boxes the 25th and 75th percentiles, and whiskers 1.5 the interquartile range. Outliers are shown as black dots. Mean spawner densities are shown as filled red circles and in black text.

Table S2: Estimates of mean spawner densities (oysters/m²) ± 1SE from pre-deployment sampling (November 2007) and annual February surveys (2007 to 2011) from strata containing the six sampling sites. Site codes prefixed with “area” west (W), south (S), and east (E); and suffixed with Category of density, high density (H), low density (L) respectively. For years when there was no sampling in the vicinity of sites, we assigned spawner density as the mean value between the previous and following year’s estimates (year before 2007 and after 2011 not shown). Missing data is shown in italics and underlined. Data from Michael et al. (2008a, 2009, 2009a, 2011, 2012). Mean distance (km) with SE, and minimum and maximum distances between dredge sample sites and collector sites.

| Pre-deployment | | | | | | | | | | | | |
|---|-------------|-----------|-------------|-----------|-------------|-----------|-------------|-----------|-------------|-----------|-------------|-----------|
| Site | EH | | EL | | SH | | SL | | WH | | WL | |
| | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| | 1.26 | 0.11 | 0.16 | 0.10 | 1.53 | 0.47 | 0.11 | 0.06 | 1.83 | 0.59 | 0.11 | 0.08 |
| Survey estimates | | | | | | | | | | | | |
| Stratum | C3 | | C6a | | C8 | | B7 | | E2 | | B2 | |
| Year | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| 2007 | 1.05 | 0.05 | 0.77 | 0.34 | 1.69 | 0.54 | <u>0.32</u> | - | 0.99 | 0.25 | 1.18 | 0.25 |
| 2008 | 1.01 | 0.40 | 0.74 | 0.22 | 1.72 | 0.18 | 0.32 | 0.08 | 1.08 | 0.25 | 1.59 | 0.60 |
| 2009 | 1.58 | 0.64 | 0.32 | 0.15 | 3.27 | 0.82 | 0.25 | 0.06 | 2.65 | 0.73 | 0.32 | 0.22 |
| 2010 | 1.62 | 0.36 | 0.70 | 0.67 | 4.28 | 1.62 | <u>0.32</u> | - | 4.61 | 0.85 | 1.53 | - |
| 2011 | 2.13 | 0.79 | <u>0.60</u> | - | 4.62 | 1.63 | 0.35 | 0.10 | 4.37 | 0.76 | <u>1.30</u> | - |
| Survey tow distances (km) from collector sites | | | | | | | | | | | | |
| Mean | 2.6 | | 4.4 | | 2.4 | | 3.4 | | 4.0 | | 4.0 | |
| SE | 1.4 | | 1.3 | | 0.9 | | 0.6 | | 1.0 | | 1.5 | |
| Minimum | 0.4 | | 2.6 | | 1.3 | | 3.0 | | 1.7 | | 1.5 | |
| Maximum | 5.3 | | 5.9 | | 3.5 | | 4.3 | | 5.5 | | 5.8 | |

Site is a location specific factor comprising Area and Category, and is a proxy for local spawner density. We substituted Factors Spawner Density and Area to test the sensitivity of the effect of Factor Year in our generalized linear model to spawner density. Year and Site were significant, as was their interaction. The year effect remained the same at 50.8% of deviance.

Table S3. Oyster recruitment modelled as a function of *Year*, *Site*, and their interactions using a Negative Binomial Generalized Linear Model. Cumulative percentage deviance (% Dev) for ranked variables and Akaike Information Criterion (AIC).

| | df | Deviance | Residual df | Residual deviance | p | %Dev | AIC |
|------------------|----|----------|-------------|-------------------|---------|-------|--------|
| | | | 66 | 1429.23 | | | 897.57 |
| <i>Year</i> | 3 | 811.96 | 63 | 617.27 | < 0.001 | 0.508 | 847.07 |
| <i>Site</i> | 5 | 472.56 | 58 | 144.71 | < 0.001 | 0.883 | 756.76 |
| <i>Year*Site</i> | 15 | 60.7 | 43 | 84.01 | < 0.001 | 0.941 | 743.92 |

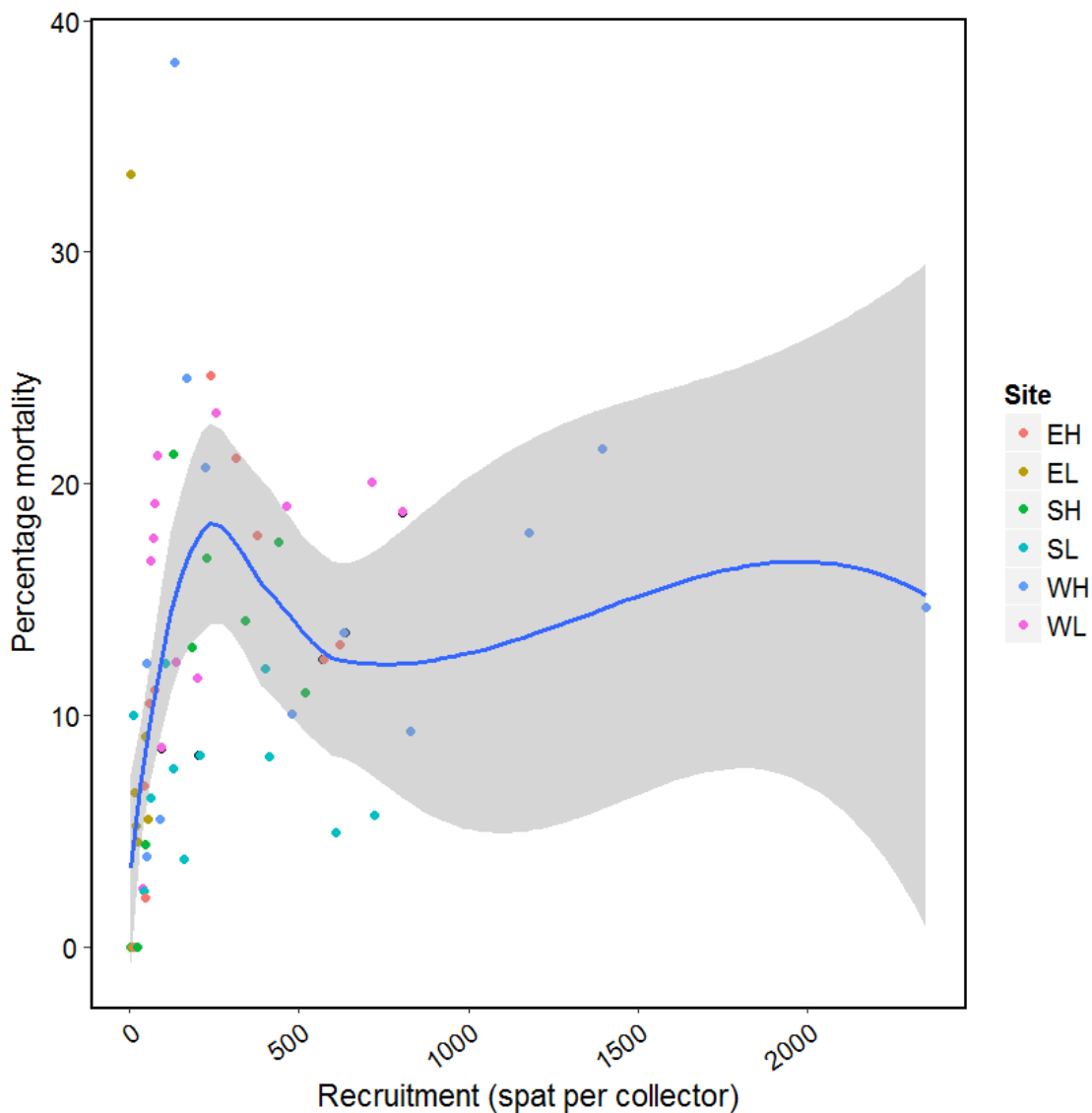


Fig. S5: The percentage mortality of *O. chilensis* spat by settler densities, by *Site*. Fitted line is a loess smoother and shaded area depicts ± 1 SE.

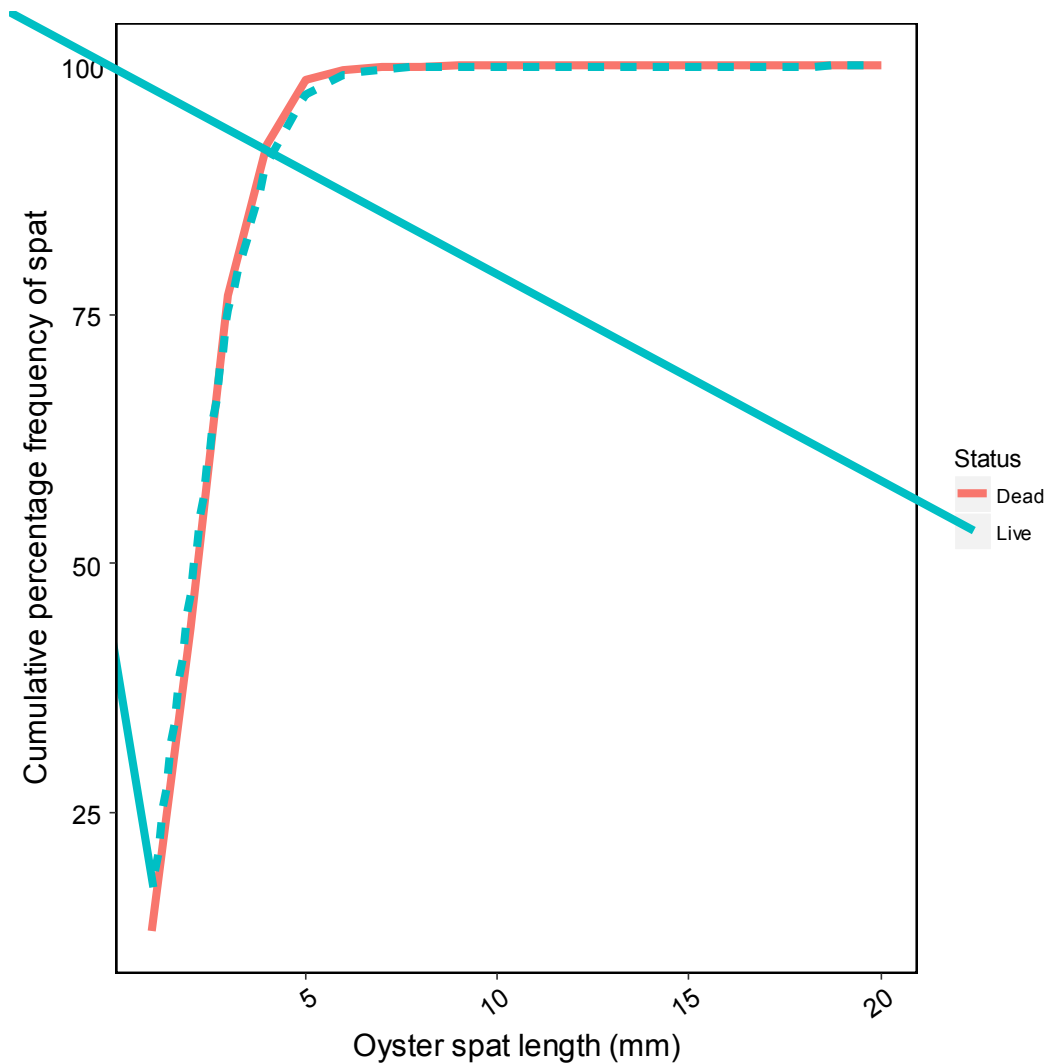


Fig. S6: The cumulative percentage frequency of lengths of live and dead *O. chilensis* spat sampled 2008-2011 in season of recruitment (B, November to February).

REFERENCES

- Broekhuizen N, Lundquist CJ, Hadfield MG, Brown SN (2011) Dispersal of oyster (*Ostrea chilensis*) larvae in Tasman Bay inferred using a verified particle tracking model that incorporates larval behavior. *Journal of Shellfish Research* 30:643-658
- Cranfield HJ, Michael KP, Doonan IJ (1999) Changes in the distribution of epifaunal reefs and oysters during 130 years of dredging for oysters in Foveaux Strait, southern New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9:461-483
- Cranfield HJ, Carbine G, Michael KP, Dunn A, Stotter DR, Smith DJ (2001) Promising signs of regeneration of blue cod and oyster habitat changed by dredging in Foveaux Strait, southern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 35: 897-908
- Cullen DJ (1962) The influence of bottom sediments upon the distribution of oysters in Foveaux Strait, New Zealand. *New Zealand Journal of Geology and Geophysics* 5(2):271-275

- Cranfield HJ, Dunn A, Doonan IJ, Michael KP (2005) *Bonamia exitiosa* epizootic in *Ostrea chilensis* from Foveaux Strait, southern New Zealand between 1986 and 1992. *ICES Journal of Marine Science: Journal du Conseil* 62:3-13
- Cullen DJ (1962) The influence of bottom sediments upon the distribution of oysters in Foveaux Strait, New Zealand. *New Zealand Journal of Geology and Geophysics* 5(2):271-275
- Doonan IJ, Cranfield HJ, Hine PM, Fisher DO, Wesney B (1992) Multi-vessel oyster surveys using a grid design conducted on Foveaux Strait oysters in 1990 and 1992. *New Zealand Fisheries Assessment Research Document* (Unpublished report held at NIWA, Wellington). MAF Fisheries, Wellington
- Dunn A (2005) Stock assessment of Foveaux Strait dredge oysters (*Ostrea chilensis*) for the 2003-04 fishing year. *New Zealand Fisheries Assessment Report 2005/25*. 63p.
- Fu, D. (2013) An updated stock assessment for Foveaux Strait dredge oysters (*Ostrea chilensis*) for the 2012 fishing year. Unpublished report held by the Ministry for Primary Industries, Wellington. Final Research Report for OYS2009-01C, Objective 1. 56 p.
- Fu D, Dunn A, Michael KP, Hills J (2016) The development and performance of a length-based stock assessment of Foveaux Strait oysters (*Ostrea chilensis*, OYU 5) in southern New Zealand, and application to management. *Fisheries Research* 183:506-517
- Gorman RM, Bryan K, Laing AK (2003) Wave hindcast for the New Zealand region: nearshore validation and coastal wave climate. *New Zealand journal of marine and freshwater research* 37(3):567-588
- Jeffs AG, Hickman RW (2000) Reproductive activity in a pre-epizootic wild population of the Chilean oyster, *Ostrea chilensis*, from southern New Zealand. *Aquaculture* 183:241-253
- Kirby MX (2004) Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. *Proceedings of the National Academy of Sciences of the United States of America* 101:13096-13099
- Knights AM, Walters K (2010) Recruit–recruit interactions, density-dependent processes and population persistence in the eastern oyster *Crassostrea virginica*. *Marine Ecology Progress Series* 404:79-90
- Lapegue S, Beaumont A, Boudry P, Gouilletquer P European flat oyster-*Ostrea edulis*. Proc GENINPACT-Evaluation of genetic impact of aquaculture activities on native population A European network, WP1 workshop Genetics of domestication, breeding and enhancement of performance of fish and shellfish
- Michael KP, Dunn A, Andrew. N. L., Breen PA (2001) Foveaux Strait dredge oyster (*Ostrea chilensis*) stock assessment, 1999. *New Zealand Fisheries Assessment Report 2001/38*:42 p.
- Michael KP, Gorman R, Hadfield M, Richardson K (2008) Summary of information in support of the Foveaux Strait Oyster Fisheries Plan: The Foveaux Strait ecosystem and effects of oyster dredging. *NIWA Information Series No 68*:18 p
- Michael KP, Dunn A, Forman J, Arlidge A (2008a) A survey of the distribution and absolute abundance of pre-recruit and recruited dredge oysters (*Ostrea chilensis*) in both non-commercial and designated commercial areas of Foveaux Strait, and estimates of the prevalence and intensity of infection by *Bonamia exitiosa*, February 2007. *New Zealand Fisheries Assessment Report 2008/61*:50 p
- Michael KP, Dunn A, Forman J (2009a) The status of infection by *Bonamia exitiosa* in Foveaux Strait oysters (*Ostrea chilensis*), changes in the distributions and densities of recruit, pre-recruit, and small oysters, and projections of disease mortality in February 2008. *New*

Zealand Fisheries Assessment Report 2009/32 (Unpublished Report held by the Ministry of Fisheries, Wellington). 50 p

Michael KP, Fu D, Forman J (2009b) Foveaux Strait oyster (*Ostrea chilensis*) 2009 stock assessment: estimates of oyster population size, the distribution of oyster densities, the status of bonamia infection in oysters, and status of the fishery. *New Zealand Fisheries Assessment Report 2009/45*. 56 p.

Michael KP, Forman J, Fu D, Hulston D (2012) The status of infection by bonamia (*Bonamia exitiosa*) in Foveaux Strait oysters (*Ostrea chilensis*) in February 2011, estimates of pre-survey and projections of post-survey disease mortality, and implications for the projections of future stock status made in the 2009 stock assessment for OYU 5. *New Zealand Fisheries Assessment Report 2012/37*. 55p.

Michael KP, Forman J, Hulston D (2015) A survey of the Foveaux Strait oyster (*Ostrea chilensis*) population (OYU5) in commercial fishery areas and the status of bonamia (*Bonamia exitiosa*) in February 2015. *New Zealand Fisheries Assessment Report 2015/73*. 86 p.

Michael KP, Forman J, Hulston D, Fu D (2011) The status of infection by bonamia (*Bonamia exitiosa*) in Foveaux Strait oysters (*Ostrea chilensis*), changes in the distributions and densities of recruit, pre-recruit, and small oysters in February 2010, and projections of disease mortality. *New Zealand Fisheries Assessment Report 2011/5*. 51 p.

Michael KP, Forman J, Fu D, Hulston D (2012) The status of infection by bonamia (*Bonamia exitiosa*) in Foveaux Strait oysters (*Ostrea chilensis*) in February 2011, estimates of pre-survey and projections of post-survey disease mortality, and implications for the projections of future stock status made in the 2009 stock assessment for OYU 5. *New Zealand Fisheries Assessment Report 2012/37*:55 p

Michael KP, Fu D, Forman J, Hulston D (2013) The Foveaux Strait oyster (*Ostrea chilensis*, OYU5) stock assessment survey and status of bonamia infection and mortality, February 2012. *New Zealand Fisheries Assessment Report 2013/09*. 64 p.

Michael KP, Forman J, Hulston D (2015) A survey of the Foveaux Strait oyster (*Ostrea chilensis*) population (OYU5) in commercial fishery areas and the status of bonamia (*Bonamia exitiosa*) in February 2015. *New Zealand Fisheries Assessment Report 2015/73*:86 p

Pascual MS, Zampatti EA (1995) Evidence of a chemically mediated adult-larval interaction triggering settlement in *Ostrea puelchana*: applications in hatchery production. *Aquaculture* 133:33-44

Powell EN, Klinck JM (2007) Is oyster shell a sustainable estuarine resource? *Journal of Shellfish Research* 26:181-194

Pritchard C, Shanks A, Rimler R, Oates M, Rumrill S (2015) The olympia oyster *Ostrea lurida*: recent advances in natural history, ecology, and restoration. *Journal of Shellfish Research* 34:259-271

Puckett BJ, Eggleston DB, Kerr PC, Luettich RA (2014) Larval dispersal and population connectivity among a network of marine reserves. *Fisheries Oceanography*

Narváez DA, Klinck JM, Powell EN, Hofmann EE, Wilkin J, Haidvogel DB (2012) Modeling the dispersal of eastern oyster (*Crassostrea virginica*) larvae in Delaware Bay. *Journal of Marine Research* 70:381-409.

Robins P E, Tita A, King JW, Jenkins SR (2017) Predicting the dispersal of wild Pacific oysters *Crassostrea gigas* (Thunberg, 1793) from an existing frontier population - a numerical study. *Aquatic Invasions* 12:117-131

Shulte DM, Burke RP, Lipcius RN (2009) Unprecedented Restoration of a Native Oyster Metapopulation. *Science* 325:1124-1127

Stead DH (1971) Observations on the biology and ecology of the Foveaux Strait dredge oyster (*Ostrea lutaria*, Hutton). N.Z. Fisheries Technical Report No.68. New Zealand Marine Department, Wellington. 49 p.

Walles B, Mann R, Ysebaert T, Troost K, Herman PMJ, Smaal AC (2015) Demography of the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef persistence. *Estuarine, Coastal and Shelf Science* 154:224-233