

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

Keith P. Michael^{1,2,3,*}, Jeffrey S. Shima^{1,2}

¹School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand

²Victoria University Coastal Ecology Laboratory (VUCCEL), PO Box 600, Wellington 6140, New Zealand

³National Institute of Water and Atmospheric Research (NIWA), PB 14901, Wellington 6021, New Zealand

ABSTRACT: Rebuilding and maintaining sufficient spawning stock to ensure recruitment is a key strategy for fisheries management and ecological restoration. We evaluated variation in *Ostrea chilensis* recruitment across seasons and sites over 4–6 yr in Foveaux Strait (New Zealand) to infer the relative importance of determinants of population recruitment. Recruitment varied significantly between seasons ($p < 0.001$). Most recruitment in any given year ($97.8 \pm 0.9\%$, mean \pm SE) occurred in the austral spring and summer (November to February). Recruitment also varied significantly between years ($p < 0.001$). In a separate fishery-wide study, we investigated the effect of spawner densities on recruitment, relative to other climatic and biological factors. We deployed spat collectors at 6 sites across 3 discrete fishery areas, and estimated densities of spawning-sized oysters from dredge samples. We modelled counts of oyster spat and spawners with a negative binomial regression to evaluate the stock–recruitment relationship. Recruitment varied between years (50.8% of the deviance explained), spawner densities (13.8%), and areas (11.6%), with further 2-way interactions among these factors. Importantly, our analysis showed a continued decline in recruits per spawner, despite similar or increasing densities of spawning-sized oysters. Average recruitment for 2010–11 when spawner densities were highest was 4.6% of the level observed in 2007–08. Our data suggest that factors other than densities of oysters play a major role in the numbers of competent larvae available for settlement. Managing oyster fisheries as a single stock and maintaining oyster densities above management reference points alone may not be sufficient to ensure recruitment to rebuild populations.

KEY WORDS: Recruitment variability · Oysters · Spatial management · Foveaux Strait · Stock–recruitment relationship

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Recruitment is notoriously variable (Caley et al. 1996, Sale & Kritzer 2003) across a wide variety of taxa in marine systems (fish: Carr & Syms 2006; algae: Vadas et al. 1992; benthic invertebrates: Underwood & Fairweather 1989, Rodriguez et al. 1993). The influence of climatic and biological factors on recruitment are well recognized. However, assumptions of static stock–recruitment relationships (Beverton & Holt

1957) underpin fisheries management (Hilborn & Walters 1992) and ecological restoration (e.g. Schulte et al. 2009). Rebuilding and maintaining sufficient spawning stock (e.g. Mace 2012) is a principal strategy to maximize larval production as a prerequisite to successful recruitment of young. However, stock–recruitment relationships remain poorly understood, and the common assumptions of constancy in stock–recruitment relationships have important consequences for the many stocks where spawning stock

size and recruitment are not positively correlated (Szuwalski et al. 2015). A mechanistic understanding of recruitment variability will better inform stock assessments and the identification of key drivers of recruitment dynamics. Here, we describe variation in the recruitment of *Ostrea chilensis* in Foveaux Strait, southern New Zealand, and evaluate its relationship with stock size and other sources of variation.

Oysters (family Ostreidae) occur globally over a wide range of habitats. They can play key roles in benthic communities (Jones et al. 1994, Grabowski & Peterson 2007) and provide important ecosystem services (Coen et al. 1999, Grabowski et al. 2012). Historically, oysters also provided highly valued fisheries, although many high-value stocks are now economically extinct (Beck et al. 2011). The *O. chilensis* fishery in Foveaux Strait is a highly valued and nationally important fishery for New Zealand (Ministry for Primary Industries 2014). *O. chilensis* biology and characteristics of the fishery differ markedly from other oyster species and fisheries (details in the Supplement at www.int-res.com/articles/suppl/m600p085_supp.pdf). *O. chilensis* brood larvae until they are ready to settle. The short pelagic larval duration (PLD) suggests limited opportunity for larval transport, and high self-recruitment to natal populations. Other commercial oyster species (*O. edulis*, *O. lurida*, *O. puelchana*, *Crassostrea virginica*, and *C. gigas*) have longer PLDs and potentially greater dispersal and connectivity. *O. chilensis* in Foveaux Strait occur in depths of 25–50 m on gravel substrates overlaid with coarse, calcareous sand (Cullen 1962, Stead 1971b). This area is exposed to oceanic swells and has swift tidal currents (Michael 2008c). *O. chilensis* habitat differs markedly from that of other commercial oyster species which occur in mainly low-energy, shallow (≤ 10 m) estuarine and embayment habitats. Moreover, *O. chilensis* does not form reefs like other species (e.g. *C. virginica*). The Foveaux Strait fishery is an entirely wild fishery with no enhancement of stock, spat, or shell. Management of this fishery assumes a single stock with a stock–recruitment relationship (Ministry for Primary Industries 2014, Fu et al. 2016). These assumptions affect projections of future stock size.

Oysters, like many marine taxa, have a pelagic larval stage and a relatively sedentary (or sessile) post-settlement stage. Both pre- and post-settlement processes (Sale & Kritzer 2003, Shima et al. 2008, Cowen & Sponaugle 2009, Hixon et al. 2012) are likely to shape their recruitment. In addition, biophysical factors may affect recruitment patterns by altering larval quality and cohort size (e.g. Pineda et al. 2007),

and/or dispersal and retention dynamics of pelagic larvae (e.g. Jones et al. 2009). A better understanding of the processes that shape recruitment will inform population models and management of the Foveaux Strait oyster fishery and have application to the management of other marine resources and communities.

Evaluations of stock–recruitment relationships through time and among locations within a population are rare. We investigated the nature and constancy of the stock–recruitment relationship that underlies management of the Foveaux Strait oyster fishery, and the significance of the combined roles of climatic and other biological factors on this relationship. Here, we operationally define recruitment as the number of *O. chilensis* spat settling from the plankton (after Carr & Syms 2006), i.e. the relationship between spawner densities and the densities of competent larvae that settled after minutes to hours in the plankton. Hence, we evaluated the stock–recruitment relationship with reduced opportunity for post-settlement mortality (which can be highly variable in time and space [Hunt & Scheibling 1997] and obscure stock–recruitment relationships). We estimated oyster recruitment across a range of spatial scales, and describe seasonal and interannual patterns to infer the relative importance of determinants of population recruitment for oysters.

MATERIALS AND METHODS

Study sites and species

The Foveaux Strait oyster fishery in southern New Zealand is a high-value, nationally significant fishery that has harvested oysters for over 140 yr. Oysters *Ostrea chilensis* are targeted by customary, recreational, and commercial fishers, and are important to the socio-economics of Southland, New Zealand (Michael et al. 2015). Before 1986, the annual commercial catch was about 80 million oysters (Dunn 2005). Since then, mortality from disease has reduced the stock size to low levels (Doonan et al. 1994, Cranfield et al. 2005). In response to the decline in oyster stock, commercial catch was reduced from 80 to 15 million oysters annually (Ministry for Primary Industries 2014).

We evaluated oyster recruitment in the Foveaux Strait oyster fishery (OYU 5, Fig. 1), which is managed as a single stock (Ministry for Primary Industries 2014). The distribution of oysters within the 3300 km² fishery area is patchy (Stead 1971b, Allen & Cranfield 1979). Most of the oysters occur in a smaller

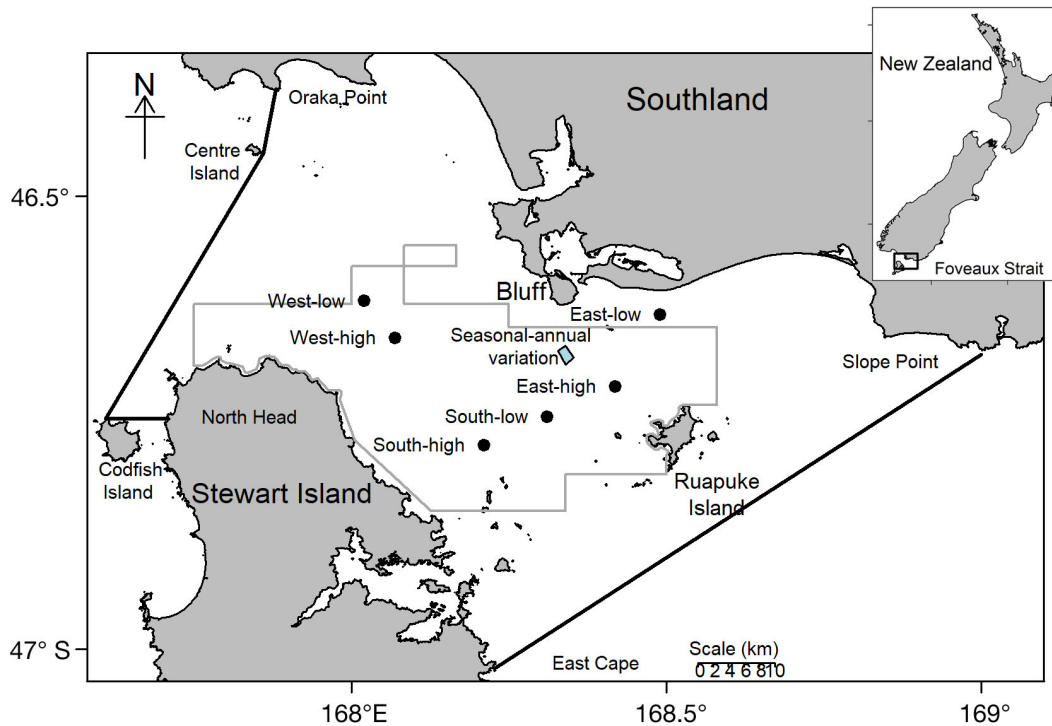


Fig. 1. Foveaux Strait oyster stock (OYU 5) boundary (heavy black lines) and the outer boundary of the 2007 stock assessment survey area (grey lines) encompassing the commercial fishery. We sampled seasonal and interannual variation in recruitment at a single site (light blue shading), and spatio-temporal variation in recruitment at 6 sites across the fishery (filled black circles). Inset shows the location of Foveaux Strait within New Zealand

region of this area (i.e. the 2007 stock assessment area; 1072 km², see Fig. 1). Fisheries-independent variation in oyster densities is mostly driven by periodic disease mortality (Doonan et al. 1994, Cranfield et al. 2005) caused by *Bonamia exitiosa* (previously *B. exitiosus*, Berthe & Hine 2003), and variability in recruitment to the oyster population (Michael et al. 2015).

O. chilensis in Foveaux Strait grows to minimum legal size (MLS, defined as oysters that are unable to pass through a 58 mm internal diameter ring) in 4 to 5 yr after settlement (Cranfield 1979). MLS equates to 58 mm in length (maximum distance measured along the anterior–posterior axis). More than 60% of the oysters landed in the commercial catch are larger than 70 mm in length (Marsh et al. 2016), 8 or more years after settlement (Fu et al. 2016). Spawners (spawning-sized oysters) are defined as individuals ≥ 50 mm in diameter (after Dunn 2005). *O. chilensis* is a protandrous, larviparous hermaphrodite. Individuals mature first as males in the summer after settlement; they transition to females and initiate brooding in their fourth summer (Cranfield 1979, Jeffs & Hickman 2000). Females typically brood larvae to late-stage pediveligers (Hollis 1962, Cranfield 1979, Chaparro et al. 2006). Cranfield & Michael (1989) suggested that most *O. chilensis* larvae released into Foveaux Strait

were competent and settle soon after release (minutes to hours, Cranfield 1979, Westerskov 1980, Chaparro et al. 2006). This putatively short PLD motivates the hypothesis that most dispersal events will occur over short distances (Cranfield 1968, Broekhuizen et al. 2011) and self-recruitment is likely to be high, leading us to hypothesize that stock–recruitment relationships may operate over relatively small spatial scales.

The nature of stock–recruitment relationships may vary from year to year (depending on biological and climatic conditions that may determine reproductive success of oysters). Here, we used an ecological definition of recruitment (i.e. the number of recently settled juveniles; Stanwell-Smith & Barnes 1997) as opposed to a standard fisheries definition (i.e. the number of harvestable adults; Hilborn & Walters 1992).

Quantifying recruitment

We quantified recruitment from counts of oyster spat that settled to artificial collectors (Cranfield 1968, Brown et al. 2010). Our spat collectors consisted of a reinforced concrete base with a steel frame holding 4 cement board settlement plates (220 × 140 mm and 4 mm thick) at heights of 10, 120, 240,

and 360 mm above the seabed. The settlement plates were not 'conditioned' before deployment because the settlement of larvae had previously been high on unconditioned plates deployed for similar periods of time. Mooring lines with floats attached to each collector facilitated location and retrieval.

We sampled oyster recruitment across years, with deployment and recovery of spat collectors at approximately 4 mo intervals (i.e. targeting 3 'seasons' per year). The sampling year (Year) began 1 July and ended the following 30 June, with Year partitioned into 3 seasons: Season A (1 July to 31 October), when brooding begins, but before any significant settlement occurs; Season B (1 November to 28 or 29 February), when most settlement is thought to occur; and Season C (1 March to 30 June), after the presumed period of peak settlement. Sampling began and ended in Season B (Season A was not sampled in the first year and Season C was not sampled in the last year). Each deployment of spat collectors used new cement board plates. Recruitment to each collector is the cumulative number of oyster spat that settled on any plate surface (top or bottom) of any of the 4 plates of a given collector. Because our focus was on competent larvae that were available for settlement (i.e. independent of sources of post-settlement mortality), we estimated recruitment as the total number of both living and dead oyster spat on plates (although we note that >85% of oysters were alive at the time of recovery). We standardized estimates of recruitment to a 122 d sampling period for each season (because actual deployment times varied around this target period by a small amount).

Seasonal and interannual variation in recruitment

We quantified seasonality and interannual variation in oyster recruitment with collectors deployed to a single site from December 2005 to February 2011. The site was closed to fishing. Specifically, we deployed a single collector to each of 9 randomly selected locations within a 2.25 km² area (see Fig. 1). We sampled collectors 3 times each year (Seasons A, B, and C).

We modelled oyster recruitment as a function of Season, Year, and the interaction between Season and Year. These count data had overdispersed distributions (chi-squared test statistic = 21323.4, $p < 0.001$ for $\alpha = 0.05$), and contained many zeros (zero-inflated: $W = 0.24$ overall, and $W = 0.85, 0.03$, and 0.12 for Seasons A, B, and C, respectively).

Zeros originated from 2 sources: structural zeros because we expected no or little settlement in Seasons A and C, and sampling zeros where collectors recorded no settlement in Season B (when we expected some settlement). We modelled these data with zero-inflated negative binomial mixed regression (ZINB) using the *pscl* package (Jackman 2008) in R (R Core Team 2016). We also evaluated a generalised linear model with negative binomial distribution (GLM.NB) using the *pscl* package and compared fits using the Vuong (1989) likelihood ratio tests function in the *pscl* package.

Spatio-temporal variation in recruitment as a function of spawner density

We quantified spatial and interannual variation in recruitment of oysters in relation to estimates of spawner densities across the wider fishery (see Fig. 1) to evaluate potential variation in stock–recruitment relationships operating over relatively small spatial scales. Six sampling sites were stratified across 3 discrete areas (Area) within the fishery (2 sites in each area: West, South, and East; for site locations, see Fig. 1 and also see Table S1 in the Supplement). Minimum distances between sites ranged between 9.0 and 35.8 km. The 2 sites within each area were selected non-randomly to establish contrasting densities of spawning-sized oysters (called 'Category' in our analysis: reflecting qualitative high versus low density). Distances between high and low paired sites ranged between 5.5 and 10.2 km. Site selection was informed by previous surveys (Michael et al. 2006, 2008a,b, 2009), fishers' catch and effort data (Michael et al. 2012), and interviews with oyster vessel skippers. We also estimated spawner densities directly at each site before deployment of spat collectors (in November 2007) using standard dredge sampling procedures for Foveaux Strait oyster surveys (Michael et al. 2015, summarized in the Supplement). We estimated mean spawner densities indirectly in subsequent years (2008–2011), using data from fishery-independent surveys conducted at nearby sites (summarized in the Supplement) because we did not want to disturb these sites once spat collectors were deployed. Mean distances (km) between dredge sample sites and collector sites ranged from 2.4 to 4.4 km (Table S2 in the Supplement).

We deployed 3 replicate spat collectors at each of the 6 sites (Fig. 1) in randomly selected locations that remained fixed during the study. We sampled oyster recruitment from November 2007 to February 2011,

sampling only Season B in each year (deployed November, recovered February) because almost all settlement occurred over this period. Foveaux Strait is closed to all oyster fishing during the period the collectors were deployed (1 September to 28 or 29 February, Ministry for Primary Industries 2014). Between the 2007 and 2011 oyster seasons, there was no fishing within at least 1 nautical mile of 4 of the 6 sites (West-low, South-high, East-high, and East-low). A small amount of fishing occurred near West-high and South-low (between 0 and 3% of the total annual catch in any one year), and some disturbance of these collector sites may have occurred.

We modelled interannual variation in recruitment, its coherence across the fishery, and its relationship to putative spawner density. Specifically, we modelled oyster recruitment as a function of Year, Spawner density, Area, and Category and the interactions between these factors. We used a GLM with a negative binomial distribution and a log link function. The effect of Spawner density was modelled as a third-order polynomial, which increases flexibility to better fit the data (e.g. Ver Hoef & Boveng 2007). Model fits and compliance with statistical assumptions were evaluated graphically (after Zuur et al. 2010). We selected the best-fit model by removing non-significant factors or interactions based on Akaike's information criterion (AIC, Akaike 1973).

RESULTS

Seasonal and interannual variation in recruitment

On average in a given year, $97.8 \pm 0.9\%$ (mean \pm SE) of all recruits settled in Season B (Fig. 2). We observed low levels of recruitment in Season C ($2.2 \pm 0.9\%$) and almost none in Season A (Fig. 2). Oyster recruitment varied significantly between Season and Year ($p < 0.001$, Table 1). Recruitment was consistently greatest in Season B, and drove between-year variation in oyster recruitment (Table 2, Fig. 2). Recruitment was relatively high in 2006–07 and 2007–08 (Fig. 2), on average 10–15% higher than in 2005–06 (Table 1). Recruitment was significantly lower ($p < 0.001$)

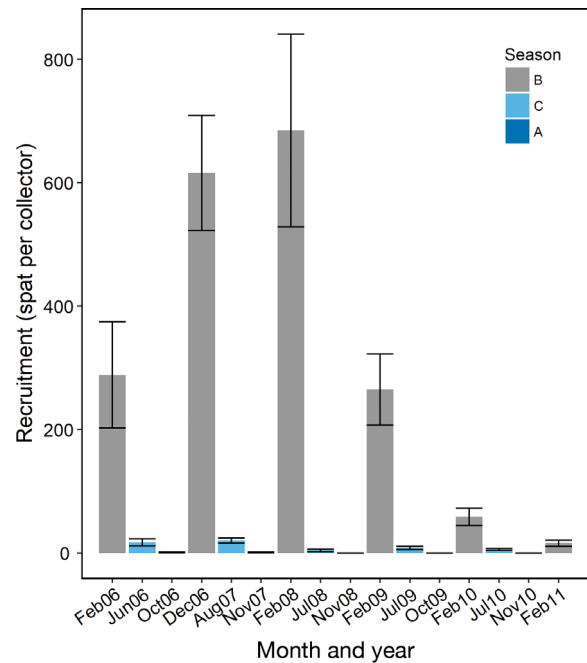


Fig. 2. Oyster recruitment (mean \pm SE) by Season (labelled A, B, and C) from December 2005 to February 2011 at a single site (light blue shading in Fig. 1). Season A: 1 July to 31 October, Season B: 1 November to 28 or 29 February, Season C: 1 March to 30 June. Recruitment was estimated as the counts of living and dead oysters per collector (sample) settling over 122 d. The x-axis gives month and year of retrieval

Table 1. Seasonal and interannual variation in recruitment of oysters at a single site in Foveaux Strait, New Zealand, between 2005 and 2011. Season A: 1 July to 31 October, Season B: 1 November to 28 or 29 February, Season C: 1 March to 30 June. Oyster recruitment is modelled as a function of Season and Year using zero-inflated negative binomial regression. Shown are the results of a negative binomial model for the count data ($\theta = 2.0943$, $df = 12$, and \log -likelihood = -492.4) and the results of a zero-inflated model with logit coefficients for predicting excess zeros. The exponents of coefficients (Exp.coeff) are shown with 95% confidence intervals (CI)

Source of variation	Coefficient	SE	Z	p	Exp.coeff (CI)
Negative binomial model					
Intercept	0.758	0.450	1.684	0.092	2.135 (0.883–5.161)
2006–2007	0.142	0.246	0.576	0.565	1.152 (0.712–1.864)
2007–2008	0.103	0.266	0.387	0.698	1.109 (0.658–1.869)
2008–2009	-0.370	0.257	-1.443	0.149	0.691 (0.418–1.142)
2009–2010	-1.643	0.281	-5.856	<0.001	0.193 (0.112–0.335)
2010–2011	-3.252	0.321	-10.139	<0.001	0.039 (0.021–0.073)
Season B	6.096	0.413	14.764	<0.001	444.081 (197.697–997.529)
Season C	2.211	0.431	5.134	<0.001	9.125 (3.923–21.224)
Log(θ)	0.739	0.164	4.506	<0.001	
Zero-inflated model					
Intercept	0.783	0.587	1.333	0.183	2.187 (0.692–6.912)
Season B	-21.271	4145.540	-0.005	0.996	0 (0–Infinity)
Season C	-2.976	0.805	-3.696	<0.001	0.051 (0.011–0.247)

Table 2. Seasonal and interannual variation in recruitment of oysters at a single site in Foveaux Strait, between 2005 and 2011. Recruitment is modelled by factors Season, Year, and the interaction between Season and Year, using a negative binomial regression with a log link function. %Dev: cumulative percentage deviance explained, AIC: Akaike's information criterion

	df	Deviance	Residual df	Residual deviance	p	%Dev	AIC
Season	2	1108.39	124	280.18	<0.001	0.767	1082.3
Year	5	114.37	119	165.82	<0.001	0.872	1027.5
Season×Year	8	42.24	111	123.58	<0.001	0.911	1004.7

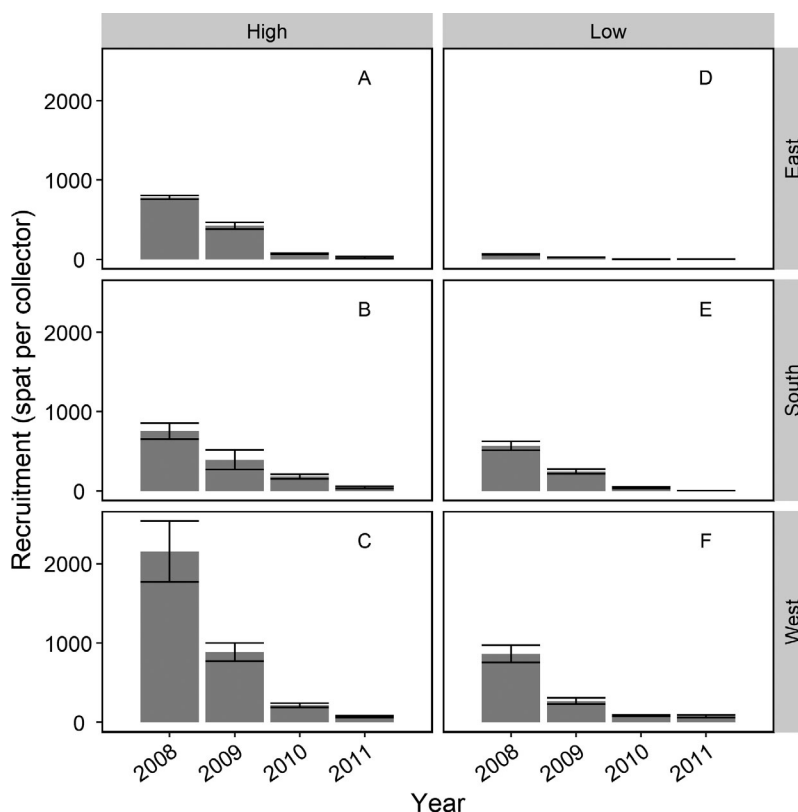


Fig. 3. Interannual and spatial variation in oyster recruitment (mean \pm SE) assessed for the primary season of recruitment (November to February). Means and SE were estimated from total counts of living and dead oysters from each collector (sample) which settled over 122 d. Recruitment for sites with (A–C) putatively high and (D–F) putatively low spawner densities for areas East, South, and West, respectively

in 2009–10 and 2010–11 (relative to 2005–06; Table 1), on average declining to 4% in 2010–11 compared to 2005–06 (Table 1).

There was no significant difference between the zero-inflated negative binomial and negative binomial models (AIC-corrected Vuong z-statistic = -0.007 , $p = 0.497$). Season explained 76.7% of the

deviance in the best-fit model, with less of the deviance explained by interannual variation (10.5%) and the interaction between Season and Year (3.9%, Table 2).

Spatio-temporal variation in recruitment as a function of spawner density

Spawner densities remained the same or increased over the study period. Spawner densities sampled directly from focal sites before deployment of the spat collectors were 0.1–1.8 oysters m^{-2} (Fig. S1 in the Supplement). For other times, spawner densities were estimated indirectly (Figs. S2 & S3, Table S2) and were 0.3–4.6 oysters m^{-2} .

For the commercial fishery area, recruitment during Season B varied between years ($p < 0.001$, $df = 3$, deviance = 811.96), spawner density estimates ($p < 0.001$, $df = 2$, deviance = 189.76), and area ($p < 0.001$, $df = 2$, deviance = 140.90) (Fig. 3). There were also significant 2-way interactions between Spawner density and Area ($p < 0.001$, $df = 6$, deviance = 114.04), and Spawner density and Year ($p < 0.001$, $df = 9$, deviance = 88.56). These interactions imply that recruitment patterns between years differed subtly by area and spawner densities (see Tables 3 & 4 for the best-fit model). Factor Year explained 50.8% of the deviance, Spawner density 13.8%, Area 11.6%, and the 2-way interactions Spawner density and Area (9.9%) and Spawner density and Year (8.0%).

The stock–recruitment relationship for oysters in the fishery (Fig. 4) varied significantly between years. We dropped factor Area, forcing the

model to use Spawner density and Year as predictors of recruitment variation. Spawner density remained significant ($p < 0.001$, $df = 3$, deviance = 39.778) when among-year variation in recruitment was taken into account ($p < 0.001$, $df = 3$, deviance = 155.767). The interaction term (Year and Spawner density) also remained significant ($p < 0.001$, $df = 9$, deviance =

Table 3. Spatio-temporal variation in oyster recruitment across the Foveaux Strait fishery between 2007 and 2011. Oyster recruitment is modelled as a function of Year, Spawner density, and Area, and their interactions, using data from Season B (settlement season) only. The best-fit negative binomial regression is shown. %Dev: cumulative percentage deviance explained, AIC: Akaike's information criterion

	df	Deviance	Residual df	Residual deviance	p	%Dev	AIC
			66	1429.23			
Year	3	811.96	63	617.27	<0.001	0.508	847.07
Spawner density	3	189.76	60	427.51	<0.001	0.646	828.57
Area	2	140.90	58	286.61	<0.001	0.762	804.33
Spawner density×Area	6	114.04	52	172.57	<0.001	0.861	780.00
Spawner density×Year	9	88.56	43	84.00	<0.001	0.941	743.92

Table 4. Spatio-temporal variation in oyster recruitment across the Foveaux Strait fishery, 2007–08 to 2010–11. Oyster recruitment is modelled as a function of Year, Spawner density, and Area, and their interactions, using data from Season B (settlement period) only. Paired comparisons for the best-fit negative binomial model ($\theta = 10.3658$, $df = 43$, and $\log\text{-likelihood} = -693.92$) are shown. Spawner densities (1), (2), (3) denote first- to third-order polynomials, respectively

Source of variation	Coefficient	SE	Z	p
Intercept	-132.635	23.586	-5.624	<0.001
Year 2008–2009	152.523	28.681	5.318	<0.001
Year 2009–2010	146.811	27.943	5.254	<0.001
Year 2010–2011	144.964	27.707	5.232	<0.001
Spawner density (1)	-2027.245	348.405	-5.819	<0.001
Spawner density (2)	-946.14	161.371	-5.863	<0.001
Spawner density (3)	-193.297	35.046	-5.516	<0.001
Area (South)	-8.474	15.205	-0.557	0.577
Area (West)	-9.23	15.097	-0.611	0.541
Spawner density (1)×Area (South)	-179.327	230.635	-0.778	0.437
Spawner density (2) ×Area (South)	-80.289	109.138	-0.736	0.462
Spawner density (3) ×Area (South)	-15.656	26.731	-0.586	0.558
Spawner density (1) ×Area (West)	-163.622	226.701	-0.722	0.470
Spawner density (2) ×Area (West)	-72.673	106.96	-0.679	0.497
Spawner density (3) ×Area (West)	-26.837	26.751	-1.003	0.316
Year2008–2009×Spawner–density (1)	2256.905	422.251	5.345	<0.001
Year2009–2010×Spawner–density (1)	2206.942	412.938	5.344	<0.001
Year2010–2011×Spawner–density (1)	2201.309	411.929	5.344	<0.001
Year2008–2009×Spawner density (2)	1048.731	197.343	5.314	<0.001
Year2009–2010×Spawner density (2)	1010.256	190.359	5.307	<0.001
Year2010–2011×Spawner density (2)	1012.736	192.724	5.255	<0.001
Year2008–2009×Spawner density (3)	232.837	45.889	5.074	<0.001
Year2009–2010×Spawner–density (3)	205.719	40.991	5.019	<0.001
Year2010–2011×Spawner density (3)	229.67	45.355	5.064	<0.001

26.288), and accounted for a larger percentage of explained deviance (from 8.0% by the best-fit model with factor Area included, to 9.5% without). Recruitment was greatest overall, and highest with higher spawner densities in 2007–08. In all successive years, overall recruitment and the slope of the relationship between recruitment and Spawner density decreased, despite fishery-wide increases in spawner densities (see Fig. 4).

DISCUSSION

Ostrea chilensis recruits per spawner declined over the successive 4 years of our fishery-wide study, despite spawner densities that remained similar or increased. The high recruitment observed in 2007–08 and the subsequent decline in recruits per spawner was consistent with recruitment in our 6 yr study at a single site (2005–06 to 2010–11, see Figs. 2 & 3). The oyster stock–recruitment relationships differed between years (Fig. 4), and by the significant interaction between Spawner density and Year in our model. Our inference of a diminishing stock–recruitment relationship is based on the assumptions that settler densities represent recruitment at the sites where larvae were brooded, and that our estimates of spawner densities from dredge sampling represent spawner densities at sites.

We infer recruitment from settler densities based on the assumption that *O. chilensis* in Foveaux Strait releases larvae that are competent and settled within minutes to hours

after release (Cranfield 1968, 1979, Westerskov 1980, Cranfield & Michael 1989), as they do elsewhere (Chaparro et al. 2006, Broekhuizen et al. 2011). The putatively short pelagic larval duration suggests that most dispersal events will occur over short distances (Cranfield 1968, Broekhuizen et al. 2011). Moreover, *O. chilensis* readily settles on manmade substrates (e.g. cement board, Cranfield 1968, Brown et al. 2010), and in the absence of conspecifics (our obser-

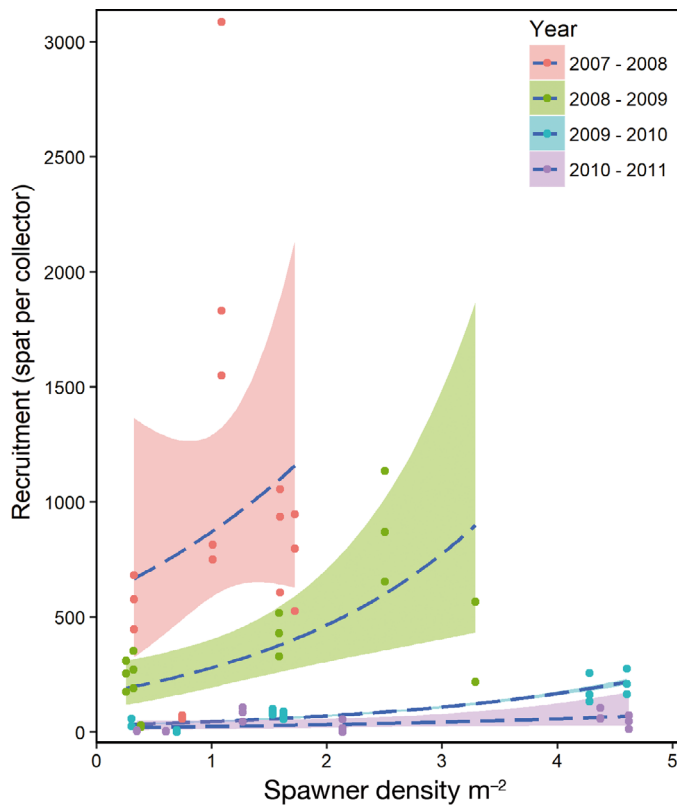


Fig. 4. Stock–recruitment relationships for oysters sampled at fixed locations across the fishery over successive years (2007–08 to 2010–11). Estimates of oyster recruitment (spat collector⁻¹) are for the primary season (November to February). Each point represents counts from a single collector ($n = 3$ collectors deployed at each of 6 sites, each year). A few spat collectors were lost. Spawner densities were estimated from dredge samples. Colours correspond to years as given in the key; fitted lines are from a negative binomial regression model, and shaded areas depict \pm SE

vations). We therefore infer that settler densities represent mostly self-recruitment to sampling sites. During high settlement years, recruitment at sites was consistent with spawner densities (see Fig. 3), and therefore is consistent with the brooding and the release of competent larvae ready to settle. These assumptions underpin our hypothesis of a stock–recruit relationship.

Our sampling in Season B represents annual recruitment. The timing of peak settlement relative to the time over which sampling occurs can affect estimates of settler densities. *O. chilensis* broods throughout the year (Jeffs & Hickman 2000). The levels of factors that determine peak brooding and subsequent settlement (e.g. temperature and primary productivity) are unknown. Before the *Bonamia exitiosa* epizootic in 1986 (Doonan et al. 1994, Cranfield et al.

2005), the highest numbers of brooders were recorded in November and December (Stead 1971a, Jeffs & Hickman 2000), and 80–90% of settlement occurred from mid-December to mid-February (Cranfield 1979). As the timing of peak settlement may have changed, we sampled recruitment in all 3 seasons (A, B, C) in the separate 6 yr study to ensure that our sampling of the spatio-temporal variation in recruitment in Season B (November to February) gave reliable estimates of annual settler densities. The seasonality of *O. chilensis* recruitment in Foveaux Strait was consistent with previous studies. In our study, 97.8% of settlement occurred in November to February (Season B), consistent with percentages of spat settling over that period during the 1960s and 1970s (Cranfield 1979).

An important assumption of our study is that settler densities represent the densities of competent larvae ready to settle at the sampling sites, and therefore represent putative recruitment. Post-settlement mortality can affect estimates of settler densities, especially over the 4 mo that our spat collectors were deployed (after Knights & Walters 2010). In *Crassostrea virginica*, both density-dependent and density-independent mortality determined the numbers of settlers surviving post-settlement (Knights & Walters 2010). *C. virginica* population growth was negative after high recruitment events, when density-dependent mortality reduced oyster densities and cohort strengths. We recorded low post-settlement mortality. Dead *O. chilensis* spat leave a record on the collector plates (see the Supplement). Overall, percent mortality was relatively low (14.6%) and did not differ greatly between high settlement years 2007–2008 and 2008–2009 (15.1 and 13.7%, respectively) and low settlement years 2009–2010 and 2010–2011 (16.6 and 7.6%, respectively). Higher settler densities did not incur increased mortality (Fig. S5), and there was no difference in the percentage mortality amongst sites (Fig. S5). Additionally, more than 95% of spat (live and dead) were less than 5 mm in length (Fig. S6), suggesting recent settlement, and by inference, less opportunity for density-dependent mortality. The percentage mortality remained consistent by spat length (Fig. S6). We infer from these data that our estimates of *O. chilensis* recruitment were not affected by density-dependent mortality, and in contrast to the findings of Knights & Walters (2010), *O. chilensis* settler densities appeared to be determined mainly by larval supply.

Estimates of *O. chilensis* recruits per spawner from our study are sensitive to our estimates of spawner densities. We evaluated the effect of spawner density

inferred from dredge estimates averaged from sampling at larger spatial scales, and not precisely at the locations where we sampled recruitment. The depth, strong currents, and hard substrate of Foveaux Strait (Michael et al. 2008c) limit the sampling methods available to effectively estimate spawner densities across the fishery area (described in the Supplement). Dredge sampling has been deemed the most reliable method for stock assessments of the Foveaux Strait oyster fishery (Ministry for Primary Industries 2014, Fu et al. 2016). Dredge sampling has limitations in Foveaux Strait and elsewhere. Chai et al. (1992) found that dredge sampling gave poor estimates of market-sized *C. virginica* densities in Chesapeake Bay (USA) because of the relatively low and variable dredge efficiency. Dredge efficiency estimates for sampling of *C. virginica* densities in the New Jersey waters of Delaware Bay (USA) showed non-random spatial and temporal variability for market-sized oysters (Powell et al. 2007). Additionally, the patchy distribution of oysters suggests that low dredge sample numbers at each site may, on average, underestimate spawner density (after Powell et al. 2017). We used the best available estimates of spawner densities, and suggest that they represent differences in the spawner densities between sites and years (see Fig. S4). 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 in Foveaux Strait.

Manipulative studies to investigate the effects of spawner density on recruitment have been undertaken for *O. chilensis* in Tasman Bay, New Zealand (Brown 2011), and elsewhere for *C. gigas* and *Saccostrea glomerata* (Wilkie et al. 2013), and for the bay scallop *Argopecten irradians* (Tettelbach & Wenczel 1993, Peterson et al. 1996). The effects of increased spawner density on recruitment were mixed. Recruitment varied markedly between 2 sites with the same brooder densities (Brown 2011), with the complexity in the arrangement of settlement surfaces and oyster species (Wilkie et al. 2013), and recruitment increased markedly in enhanced areas receiving translocated bay scallops (Peterson et al. 1996). We did not consider manipulative studies because of the depth (25–50 m), strong tides, and exposure to large oceanic swell, and also because handling of oysters may exacerbate disease mortality from *B. exitiosa*. Instead, we modelled Site as a proxy for Spawner density that incorporated sites of putatively high and low densities of spawners and an Area effect. Year, Site, and their interaction were significant ($p < 0.001$, Table S3 in the Supplement). These sensitivity ana-

lyses showed that the effect size of Year was robust to combinations of other factors representing spawner densities in alternative models, suggesting that factors other than spawner densities drove recruitment in Foveaux Strait in some years.

There were significant interactions between Year, Area, and Spawner density, suggesting different patterns of recruitment through space and time with respect to putative spawner density. Recruitment scaled most strongly with Spawner density in 2007–08. In this year, recruitment was relatively high at all sites even though spawner densities were less than 2 oysters m^{-2} . By 2010–11, spawner densities were similar or had increased to over 5 oysters m^{-2} , but average recruitment was only 4.6% of levels observed in 2007–08. There were also marked spatial differences. Recruitment to the West-high site was initially high (more than 2000 oyster recruits collector⁻¹), but recruitment declined markedly in successive years (Fig. 3). In comparison, the East-low site was chronically low across all years of the study (see Fig. 3). This may be an example of a localised population where spawner densities were too low to take advantage of favourable climatic and biological conditions for heightened recruitment, and suggests a need to maintain spawner densities to prevent serial depletion of stocks. Since the 1940s, spawner densities at East-low have been low, most likely the result of disease mortality (Cranfield et al. 2005, Dunn 2005), or possibly because of fishing effects (Cranfield et al. 1999). Both hypotheses implicate low spawner densities in low recruitment. Many other commercial fishery areas in Foveaux Strait have sustained high effort and catch, and have been subjected to high *B. exitiosa* mortality, but have remained productive (Michael 2007).

Biological reference point based fisheries management has maintained or improved stocks in New Zealand (Ministry for Primary Industries 2017) and elsewhere, e.g. in the U.S. (Soniati et al. 2014). Reference points (e.g. Mace 2012) used to rebuild stocks towards maximum sustainable yield rely on a positive relationship between spawning stock sizes and recruitment (i.e. recruitment varies positively in relation to spawning stock size). Stock–recruitment relationships are difficult to estimate for most species (Maunder 2012) because there are few data for most stocks (Maunder & Piner 2015); moreover, estimates from models are often uncertain (Lee et al. 2012). The lack of relationship between stock size, spawner density, and recruitment in oysters with long PLDs is well known (e.g. Knights & Walters 2010, Soniati et al. 2014). The long PLD of *C. virginica* contributes to the

high interannual variation in oyster numbers and biomass. *C. virginica* also form oyster reefs, thereby creating their own habitat important to recruitment and post-settlement survival (shell abundance is an important biological reference point, Powell & Klinck 2007, Soniat et al. 2012). In contrast, *O. chilensis* in Foveaux Strait are assumed to have a stock–recruitment relationship because of their biology and habitat. *O. chilensis* do not form reefs, but occur as individuals and small clusters on sand and gravel habitat (see the Supplement). The lack of a stock–recruitment relationship in oysters and other sessile invertebrate stocks suggests that single biological reference point based management may not be appropriate for many of these stocks (after Powell et al. 2012). The diminishing stock–recruitment relationship in Foveaux Strait oysters has important implications for the management of Foveaux Strait oyster fishery and invertebrate stocks generally. Our results show that other factors not measured in this study, most likely climatic and biological factors, more strongly influenced recruitment than spawning biomass in some years, consistent with the findings of Szuwalski et al. (2015).

The Foveaux Strait oyster stock assessment model (Dunn 2005) uses a Beverton-Holt stock–recruitment relationship with steepness of 0.9 (i.e. high levels of recruitment are plausible during periods of low spawner density). High levels of recruitment observed during a period of low spawner abundance and density between 2005–06 and 2007–08 (spawning stock biomass 16% of the virgin spawning stock population size (B_0) in 2005, Fu & Dunn 2009) were consistent with the stock–recruitment assumptions of Dunn (2005) based on survey data from 1992 to 2001. However, recruits per spawner decreased in times of relatively high spawner densities (2008–09 to 2010–11, see Fig. 4); spawning stock biomass was 34.5% of B_0 in 2012 (Fu 2013). Our data did not show a stock–recruitment relationship consistent with the Beverton-Holt function used in the OYU 5 stock assessment model of Dunn (2005). While projections of future stock size were corroborated by subsequent surveys, i.e. the assessment model has performed well (Fu 2013), our data suggest that factors other than spawner density strongly influence recruitment. Fishery indices of recruitment, catch sampling (Marsh et al. 2016) and population surveys (Michael et al. 2017), show the low recruitment observed during our study continued through to 2016–2017, indicating a regime shift in recruitment. This regime shift suggests that the Beverton-Holt function may not predict recruitment well, and therefore estimates of

future stock size may be more uncertain for longer projections. Maintaining spawning stock size at or above reference points alone may not ensure recruitment and rebuilding of the fishery.

O. chilensis in Foveaux Strait is generally considered to comprise localised, self-recruiting populations that occur over small spatial scales (Allen & Cranfield 1979, Cranfield 1979), typical of other invertebrate fisheries. Management of many of these fisheries is by ‘unit stocks’ over large areas. A mismatch of the spatial scales of recruitment and fisheries management in other systems has led to overfishing, recruitment failure, serial depletion, and the eventual collapse of many invertebrate fisheries (Hilborn et al. 2005). Moreover, a persistent reduction in recruits per spawner may have flow-on effects on spawning success: consecutive years of low recruitment could reduce the density of *O. chilensis* spawning as males, potentially limiting sperm availability and fertilisation success (e.g. urchins: Levitan et al. 1992; lobsters: MacDiarmid & Butler 1999).

The diminishing stock–recruitment relationship in Foveaux Strait oysters may be due to climatic and biological (non-mutually exclusive) factors that can reduce cohort strength of competent larvae, and reduce recruitment to localised populations. Climate variability affects recruitment in fisheries (Hjort 1914), in oysters (Kimmel & Newell 2007, Kimmel et al. 2014), and in other species (Anderson et al. 2011, Miller et al. 2016). Models of population dynamics (Hilborn & Walters 1992), and other models of varying complexity used in management approaches (e.g. ecosystem-based fisheries management, EBFM), Fulton 2010; Management Strategy Evaluation, Fulton et al. 2014, Punt et al. 2014; and extended frameworks for fisheries assessments, Hollowed et al. 2009) should ideally incorporate climate variability. However, these approaches are rarely implemented (Punt et al. 2014, Skern-Mauritzen et al. 2016). ‘Fisheries management is still predominantly single-species-oriented taking little account of ecosystem processes, implicitly ignoring that fish stock production depends on the physical and biological conditions of the ecosystem’ (Skern-Mauritzen et al. 2016, p. 165). The focus on EBFM will hasten the need to understand the effects of climate and to predict the long-term effects on recruitment (Collie et al. 2016).

Heightened recruitment, i.e. high numbers of recruits per spawner, can occur in oysters (Dunn 2005) and in other species (e.g. scallops, Bethoney et al. 2016). In this study, we suggest that prolonged (9 yr) recruitment failure in oysters began at a time despite seemingly sufficient spawner densities (0.3 m^{-2}) that

have supported high recruitment in the past (Dunn 2005). Low recruitment continued after our study (Michael et al. 2017) when mean spawner densities were 0.4–0.9 m⁻², above those reported by Dunn (2005). The climatic and biological factors contributing to reduced recruits per spawner are the focus of future study. Climatic and biological factors with complex interactions may drive fishery-wide recruitment variability and may determine the persistence of their effects. However, careful consideration is required in the choice of climate data sets for analysis (Menge et al. 2011), and in the interpretation of correlations between climate and recruitment (e.g. Pacific sardine, McClatchie et al. 2010, Lindegren et al. 2013). Long time series of recruitment data at appropriate spatial scales, along with biological and climatic data, are required to better explain the changes in stock–recruitment relationships observed during our study, and for the management of other marine populations and fisheries. An understanding of these effects will better inform stock assessment models to predict changes in populations, and to underpin EBFM (Hilborn & Walters 1992, Fulton 2010, Punt et al. 2014, Collie et al. 2016, Koenigstein et al. 2016).

Acknowledgements. Seafood Innovations Limited and the Bluff Oyster Management Company Limited (New Zealand) funded this research programme (SIL07301). We thank David Skeggs, Graeme Wright, Victoria Pearsey, and the Bluff Oyster Management Company Limited crews and staff for their assistance with sampling; Sophie Mormede for discussion of the analysis; and Rosemary Hurst, Susan Jane Baird, Peter McMillan, and Charles T. T. Edwards for their comments on the manuscript.

LITERATURE CITED

- Akaike H (1973) Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika* 60:255–265
- Allen RL, Cranfield HJ (1979) A dredge survey of the oyster population in Foveaux Strait. *Rapp p-v Réun* 175:50–62
- Anderson SC, Flemming JM, Watson R, Lotze HK (2011) Serial exploitation of global sea cucumber fisheries. *Fish Fish* 12:317–339
- Beck MW, Brumbaugh RD, Airoidi L, Carranza A and others (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience* 61: 107–116
- Berthe FCJ, Hine PM (2003) *Bonamia exitiosa* Hine et al. 2001 is proposed instead of *B. exitiosus* as the valid name of *Bonamia* sp. infecting flat oysters *Ostrea chilensis* in New Zealand. *Dis Aquat Org* 57:181
- Bethoney ND, Ascì S, Stokesbury KDE (2016) Implications of extremely high recruitment events into the US sea scallop fishery. *Mar Ecol Prog Ser* 547:137–147
- Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. Her Majesty's Stationery Office, London
- 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. *J Shellfish Res* 30: 643–658
- Brown SN (2011) Ecology and enhancement of the flat oyster *Ostrea chilensis* (Philippi, 1845) in central New Zealand. PhD thesis, University of Canterbury, Christchurch
- Brown SN, Handley S, Michael K, Schiel D (2010) Annual pattern of brooding and settlement in a population of the flat oyster *Ostrea chilensis* from central New Zealand. *NZ J Mar Freshw Res* 44:217–227
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. *Annu Rev Ecol Syst* 27:477–500
- Carr M, Syms C (2006) Recruitment. In: Allen LG, Pondella DJ, Horn MH (eds) *The ecology of marine fishes: California and adjacent waters*. University of California Press, Berkeley, CA, p 411–427
- Chai AL, Homer M, Tsai CF, Gouletquier P (1992) Evaluation of oyster sampling efficiency of patent tongs and an oyster dredge. *N Am J Fish Manag* 12:825–832
- Chaparro OR, Navarrete LR, Thompson RJ (2006) The physiology of the larva of the Chilean oyster *Ostrea chilensis* and the utilisation of biochemical energy reserves during development: an extreme case of the brooding habit. *J Sea Res* 55:292–300
- Coen LD, Luckenbach MW, Breitbart DL (1999) The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. *Am Fish Soc Symp* 22:438–454
- Collie JS, Botsford LW, Hastings A, Kaplan IC, Largier JL, Livingston PA, Werner FE (2016) Ecosystem models for fisheries management: finding the sweet spot. *Fish Fish* 17:101–125
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annu Rev Mar Sci* 1:443–466
- Cranfield HJ (1968) An unexploited population of oysters *Ostrea lutaria* Hutton, from Foveaux Strait. Part 1. Adult stocks and spatfall distribution. *NZ J Mar Freshw Res* 2: 3–22
- Cranfield HJ (1979) The biology of the oyster, *Ostrea lutaria*, and the oyster fishery of Foveaux Strait. *Rapp p-v Réun* 175:44–49
- Cranfield HJ, Michael KP (1989) Larvae of the incubatory oyster *Tiostrea chilensis* (Bivalvia: Ostreidae) in the plankton of central and southern New Zealand. *NZ J Mar Freshw Res* 23:51–60
- 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. *Aquat Conserv* 9:461–483
- 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 J Mar Sci* 62:3–13
- Cullen DJ (1962) The influence of bottom sediments upon the distribution of oysters in Foveaux Strait, New Zealand. *NZ J Geol Geophys* 5:271–275
- 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 (Unpubl. report held at NIWA, Wellington)

- Doonan IJ, Cranfield HJ, Michael KP (1994) Catastrophic reduction of the oyster, *Tiostrea chilensis* (Bivalvia: Ostreidae), in Foveaux Strait, New Zealand, due to infestation by the protistan *Bonamia* sp. NZ J Mar Freshw Res 28: 335–344
- 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. Ministry of Fisheries, Wellington
- Fu D (2013) An updated stock assessment for Foveaux Strait dredge oysters (*Ostrea chilensis*) for the 2012 fishing year. Final Research Report for OYS2009-01C, Objective 1. Ministry for Primary Industries, Wellington
- Fu D, Dunn A (2009) An updated stock assessment for Foveaux Strait dredge oysters (*Ostrea chilensis*) for the 2008-09 fishing year. New Zealand Fisheries Assessment Report 2009/53. Ministry of Fisheries, Wellington
- 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. Fish Res 183:506–517
- Fulton EA (2010) Approaches to end-to-end ecosystem models. J Mar Syst 81:171–183
- Fulton EA, Smith AD, Smith DC, Johnson P (2014) An integrated approach is needed for ecosystem based fisheries management: insights from ecosystem-level management strategy evaluation. PLOS ONE 9:e84242
- Grabowski JH, Peterson CH (2007) Restoring oyster reefs to recover ecosystem services. In: Cuddington K, Byers J, Wilson W, Hastings A (eds) Ecosystem engineers. Theoretical Ecology Series Vol 4. Academic Press, New York, NY, p 281–298
- Grabowski JH, Brumbaugh RD, Conrad RF, Keeler AG and others (2012) Economic valuation of ecosystem services provided by oyster reefs. BioScience 62:900–909
- Hilborn R, Walters CJ (1992) Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Chapman and Hall, New York, NY
- Hilborn R, Orensanz JM, Parma AM (2005) Institutions, incentives and the future of fisheries. Philos Trans R Soc B 360:47–57
- Hixon MA, Anderson TW, Buch KL, Johnson DW, McLeod JB, Stallings CD (2012) Density dependence and population regulation in marine fish: a large scale, long term field manipulation. Ecol Monogr 82:467–489
- Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp p-v Réun 20:1–228
- Hollis PJ (1962) Studies on the New Zealand mud-oyster, *Ostrea lutaria*, Hutton, 1873. MSc thesis, Victoria University, Wellington
- Hollowed AB, Bond NA, Wilderbuer TK, Stockhausen WT and others (2009) A framework for modelling fish and shellfish responses to future climate change. ICES J Mar Sci 66:1584–1594
- Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar Ecol Prog Ser 155:269–301
- Jackman S (2008) pscl: Classes and methods for R developed in the Political Science Computational Laboratory, Stanford University. Department of Political Science, Stanford University, Stanford, CA. R package version 0.95, <http://CRAN.R-project.org/package=pscl>
- 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
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386
- Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28:307–325
- Kimmel DG, Newell RIE (2007) The influence of climate variation on eastern oyster (*Crassostrea virginica*) juvenile abundance in Chesapeake Bay. Limnol Oceanogr 52:959–965
- Kimmel DG, Tarnowski M, Newell RIE (2014) The relationship between interannual climate variability and juvenile eastern oyster abundance at a regional scale in Chesapeake Bay. N Am J Fish Manag 34:1–15
- Knights AM, Walters K (2010) Recruit–recruit interactions, density-dependent processes and population persistence in the eastern oyster *Crassostrea virginica*. Mar Ecol Prog Ser 404:79–90
- Koenigstein S, Mark FC, Göbbling Reisemann S, Reuter H, Poertner HO (2016) Modelling climate change impacts on marine fish populations: process based integration of ocean warming, acidification and other environmental drivers. Fish Fish 17:972–1004
- Lee HH, Maunder MN, Piner KR, Methot RD (2012) Can steepness of the stock–recruitment relationship be estimated in fishery stock assessment models? Fish Res 125–126:254–261
- Levitan DR, Sewell MA, Chia FS (1992) How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus* [sic] *franciscanus*. Ecology 73: 248–254
- Lindegren M, Checkley DM Jr, Quinn T (2013) Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. Can J Fish Aquat Sci 70:245–252
- MacDiarmid AB, Butler MJ (1999) Sperm economy and limitation in spiny lobsters. Behav Ecol Sociobiol 46:14–24
- Mace PM (2012) Evolution of New Zealand’s fisheries management frameworks to prevent overfishing. International Council for the Exploration of the Sea Document CM 50:09. ICES, Copenhagen
- Marsh C, Michael KP, Wright G, Fu D (2016) Estimates of the length frequency from commercial catch sampling of Foveaux Strait dredge oysters (*Ostrea chilensis*) in 2015. Final Research Report for Ministry of Fisheries research project OYS2013-01, objective 9. Ministry for Primary Industries, Wellington
- Maunder MN (2012) Evaluating the stock–recruitment relationship and management reference points: application to summer flounder (*Paralichthys dentatus*) in the US mid-Atlantic. Fish Res 125–126:20–26
- Maunder MN, Piner KR (2015) Contemporary fisheries stock assessment: Many issues still remain. ICES J Mar Sci 72: 7–18
- McClatchie S, Goericke R, Auad G, Hill K (2010) Re-assessment of the stock–recruit and temperature–recruit relationships for Pacific sardine (*Sardinops sagax*). Can J Fish Aquat Sci 67:1782–1790
- Menge BA, Gouhier TC, Freidenburg T, Lubchenco J (2011) Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: toward explaining ‘unexplained’ variation. J Exp

- Mar Biol Ecol 400:236–249
- Michael KP (2007) Summary of information in support of the Foveaux Strait Oyster Fishery Plan: the Foveaux Strait ecosystem and effects of oyster dredging. Final Research Report for the Ministry of Fisheries for project ZBD200504. Ministry of Fisheries, Wellington
- Michael KP, Dunn A, Andrew N L, Breen PA (2001) Foveaux Strait dredge oyster (*Tiostrea chilensis*) stock assessment, 1999. New Zealand Fisheries Assessment Report 2001/38
- Michael KP, Dunn A, Forman J (2006) A survey of *Bonamia exitiosa* infection, and oyster density and recruitment in Foveaux Strait dredge oyster (*Ostrea chilensis*), January 2005. New Zealand Fisheries Assessment Report 2006/40. Ministry of Fisheries, Wellington
- Michael KP, Dunn A, Forman J (2008a) A survey of *Bonamia exitiosa* infection, and oyster density and recruitment in Foveaux Strait dredge oysters (*Ostrea chilensis*), February 2006. New Zealand Fisheries Assessment Report 2008/47. Ministry of Fisheries, Wellington
- Michael KP, Dunn A, Forman J, Arlidge A (2008b) 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. NIWA, Wellington
- Michael KP, Gorman R, Hadfield M, Richardson K (2008c) 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. NIWA, Wellington
- Michael KP, Dunn A, Forman J (2009) 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. Ministry of Fisheries, Wellington
- Michael KP, Fu D, Wright G (2012) Increasing production and revenue of Foveaux Strait oysters through the development of management strategies, technology, and industry capability. To develop the capability of the Bluff oyster industry to develop, evaluate, and manage harvest and fishery management strategies. 1 April 2009–30 June 2011. NIWA Client Report: WLG2012-44 (Project SIL07301, Objective 4). Ministry for Primary Industries, Wellington
- 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. Ministry for Primary Industries, Wellington
- Michael KP, Forman J, Hulston D, Bilewitch J, Moss G (2017) The Foveaux Strait oyster and *Bonamia* surveys, February 2017. NIWA Client Report 2017374WN for project BOM17302, prepared for the Bluff Oyster Management Company Ltd. NIWA, Wellington
- ✦ Miller MJ, Feunteun E, Tsukamoto K (2016) Did a 'perfect storm' of oceanic changes and continental anthropogenic impacts cause northern hemisphere anguillid recruitment reductions? ICES J Mar Sci 73:43–56
- Ministry for Primary Industries (2014) Dredge oysters (OYS 5). In: Fisheries Science Group (comps) Fisheries Assessment Plenary, November 2014: stock assessments and stock status. Ministry for Primary Industries, Wellington, p 128–150
- Ministry for Primary Industries (2017) Status of stocks as at December 2016 or 'Last Assessment Date'. www.mpi.govt.nz/growing-and-harvesting/fisheries/fisheries-management/fish-stock-status/ (accessed 4 January 2018)
- ✦ Peterson CH, Summerson HC, Luettich RA Jr (1996) Response of bay scallops to spawner transplants: a test of recruitment limitation. Mar Ecol Prog Ser 132:93–107
- ✦ Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20:22–39
- ✦ Powell EN, Klinck JM (2007) Is oyster shell a sustainable estuarine resource? J Shellfish Res 26:181–194
- ✦ Powell EN, Ashton-Alcox KA, Kraeuter JN (2007) Reevaluation of eastern oyster dredge efficiency in survey mode: application in stock assessment. N Am J Fish Manag 27: 492–511
- ✦ Powell EN, Klinck JM, Ashton-Alcox K, Hofmann EE, Morrison J (2012) The rise and fall of *Crassostrea virginica* oyster reefs: the role of disease and fishing in their demise and a vignette on their management. J Mar Res 70: 505–558
- Powell EN, Mann R, Ashton-Alcox KA, Kuykendall KM, Long MC (2017) Can we estimate molluscan abundance and biomass on the continental shelf? Estuar Coast Shelf Sci 198:213–224
- ✦ Punt AE, A'mar T, Bond NA, Butterworth DS and others (2014) Fisheries management under climate and environmental uncertainty: control rules and performance simulation. ICES J Mar Sci 71:2208–2220
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Rodriguez SR, Ojeda FP, Inestrosa NC (1993) Settlement of benthic marine invertebrates. Mar Ecol Prog Ser 97: 193–207
- ✦ Sale PF, Kritzer JP (2003) Determining the extent and spatial scale of population connectivity: decapods and coral reef fishes compared. Fish Res 65:153–172
- ✦ Schulte DM, Burke RP, Lipcius RN (2009) Unprecedented restoration of a native oyster metapopulation. Science 325:1124–1128
- ✦ Shima JS, Osenberg CW, St Mary CM (2008) Quantifying site quality in a heterogeneous landscape: recruitment of a reef fish. Ecology 89:86–94
- ✦ Skern Mauritzen M, Ottersen G, Handegard NO, Huse G, Dingsør GE, Stenseth NC, Kjesbu OS (2016) Ecosystem processes are rarely included in tactical fisheries management. Fish Fish 17:165–175
- ✦ Sóniat TM, Klinck JM, Powell EN, Cooper N and others (2012) A shell-neutral modeling approach yields sustainable oyster harvest estimates: a retrospective analysis of the Louisiana state primary seed grounds. J Shellfish Res 31:1103–1112
- ✦ Sóniat TM, Cooper N, Powell EN, Klinck JM and others (2014) Estimating sustainable harvests of eastern oysters, *Crassostrea virginica*. J Shellfish Res 33:381–394
- ✦ Stanwell-Smith D, Barnes DKA (1997) Benthic community development in Antarctica: recruitment and growth on settlement panels at Signy Island. J Exp Mar Biol Ecol 212:61–79
- Stead DH (1971a) Observations on the biology and ecology

- of the Foveaux Strait dredge oyster (*Ostrea lutaria*, Hutton). NZ Fish Tech Rep 68. New Zealand Marine Department, Wellington
- Stead DH (1971b) Survey of Foveaux Strait oyster beds 1960–64. NZ Fish Tech Rep 16. New Zealand Marine Department, Wellington
- ✦ Szuwalski CS, Vert-Pre KA, Punt AE, Branch TA, Hilborn R (2015) Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish Fish* 16:633–648
- Tettelbach S, Wenczel P (1993) Reseeding efforts and the status of bay scallop *Argopecten irradians* (Lamarck, 1819) populations in New York following the occurrence of 'brown tide' algal blooms. *J Shellfish Res* 12: 423–431
- ✦ Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine assemblages. *Trends Ecol Evol* 4: 16–20
- ✦ Vadas RL, Johnson S, Norton TA (1992) Recruitment and mortality of early post-settlement stages of benthic algae. *Br Phycol J* 27:331–351
- ✦ Ver Hoef JM, Boveng PL (2007) Quasi-Poisson vs. negative binomial regression: How should we model overdispersed count data? *Ecology* 88:2766–2772
- ✦ Vuong QH (1989) Likelihood ratio tests for model selection and non-nested hypotheses. *Econometrica* 57:307–333
- Westerskov K (1980) Aspects of the biology of the dredge oyster *Ostrea lutaria* Hutton, 1873. PhD thesis, University of Otago, Dunedin
- ✦ Wilkie EM, Bishop MJ, O'Connor WA (2013) The density and spatial arrangement of the invasive oyster *Crassostrea gigas* determines its impact on settlement of native oyster larvae. *Ecol Evol* 3:4851–4860
- ✦ Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14

Editorial responsibility: Romuald N. Lipcius, Gloucester Point, VA, USA

*Submitted: September 11, 2017; Accepted: May 15, 2018
Proofs received from author(s): July 20, 2018*