Evaluating the effectiveness of a seasonal spawning area closure

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Abstract

Fish that aggregate at predictable locations and times to spawn are often vulnerable to over-exploitation. Seasonal closures have often been implemented in an attempt to alleviate such impacts but the effectiveness of these measures is rarely tested. This study evaluates the effectiveness of a spawning closure for Atlantic cod (*Gadus* morhua) in the Firth of Clyde off the Scottish West Coast (ICES area VIa). This closure was introduced in March 2001 as an emergency measure to allow as many cod as possible to spawn and avoid the build-up of displaced effort from another spawning closure. Genetic, tagging and otolith microchemistry investigations indicate that cod inhabiting the Clyde are reproductively isolated from other resident groups in the central and northern part of the Scottish West Coast stock. This study used a beyond-BACI (Before-After, Control-Impact) approach to compare population trends of the Clyde spawning aggregation before and after the introduced area closure, using two other sub-population spawning grounds as control areas. There was no evidence of local recovery in terms of abundance, biomass or reduced mortality in the Clyde more than a decade after establishing the closure. Mortality may have remained high because young cod are still caught as bycatch in the *Nephrops* fishery in the area and the predation rate may have increased due to an expanding whiting population. Considering the state of the already severely depleted Clyde sub-population when the closure was implemented the measure appears to have been too little and too late. The tendency to implement such spawning closures on nearly collapsed stocks may be why these measures often appear to have been ineffective.

Key words

Fisheries closure; Spawning aggregations; Atlantic cod; BACI

Introduction

Catch control measures for commercial species are often at a spatial scale greater than that of local population dynamics, making individual spawning components vulnerable to extirpation (Stephenson, 1999; Hutchinson, 2008; Armstrong *et al.*, 2013). Area closures have been suggested as a tool to support fisheries management, particularly for areas where key life history stages congregate (Halliday, 1988; Murawski *et al.*, 2000; Pickett *et al.*, 2004), such as spawning aggregations. Spawning aggregations often occur at times and places that are predictable making them vulnerable to exploitation (Sadovy and Domeier, 2005). Aggregative behaviour can cause localised increases in catchability which can lead to higher fishing mortality (Halliday, 1988; van Overzee and Rijnsdorp, 2015). High catch rates during spawning can mask overall stock declines as the aggregation fisheries exhibit catch per unit (CPUE) hyperstability (Rose and Kulka, 1999; Erisman *et al.*, 2011). This is where catch rates remain high even when the actual stock abundance is in steep decline through the spatial concentration of fish and fishery (Hilborn and Walters, 1992). Consequently, many spawning aggregations have at first appeared inexhaustible and this has led to their depletion (Ames, 2004) and in some cases near extirpation (Beets and Friedlander, 1998; Aguilar-Perera, 2006; Erisman *et al*., 2011; Armstrong *et al.*, 2013). Therefore the introduction of a spawning area closure timed to the period when fish aggregate to spawn can reduce fishing mortality directly, whilst permitting sustainable exploitation outside of the spawning period (Murawski *et al.*, 2000). However, for a spawning closure to have a net benefit to population growth there should be a reduction in the annual fishing mortality (Heppell *et al.*, 2006). Hence, if fish are not particularly susceptible to capture during spawning or there is a change in fishing effort that negates the seasonal reduction in mortality, a spawning closure may have no effect (Gruss *et al.*, 2013; Gruss and Robinson, 2015).

If the catchability is greater during the spawning period than at other times of the year, then reducing overall fishing effort through the introduction of a spawning area closure can benefit the fish population by reducing fishing mortality (Gruss *et al.*, 2013; Gruss and Robinson, 2015) and

also by reducing disturbance (Morgan *et al.*, 1997). Disturbance from fishing can alter spawning aggregation behaviour and interrupt the spawning process with some fish not returning to spawn until after the disturbance has stopped (Dean *et al.*, 2012). Loss of spawning areas may impact recruitment since the diversity and location of sites where eggs are released may help mitigate against the effects of local mortality events and promote favourable egg and larval transport (Marteinsdottir, 2000; Jonasson *et al.*, 2009). Re-colonisation of extirpated spawning grounds may take many generations in species where spawning migrations are related to social learning, as inexperienced recruits learn the routes to grounds by following older experienced individuals (Rose, 1993). High fishing mortality on spawning individuals will also lead to a size and age truncation, which can affect the viability of offspring produced and the timing of spawning (Birkeland and Dayton, 2005; Wright and Trippel, 2009). Ultimately, the removal of larger individuals during spawning may also create a strong selection pressure for fish that mature at a smaller size and younger ages and so may have evolutionary consequences (Law, 2007; Devine *et al.*, 2012). Therefore the cessation of fishing of spawning aggregations can lead to a recovery of demographic structure (Wright and Trippel, 2009), sex ratios (Beets and Friedlander, 1998), prevent the extirpation of distinct spawning components (Ames, 2004; Armstrong *et al.*, 2013) and reduce negative selection pressures (Law, 2007).

Despite theoretical models predicting potential benefits of spawning area closures for fish conservation (Sadovy and Domeier, 2005; Gruss *et al.*, 2014) this management approach remains controversial due to the frequent lack of clear objectives, monitoring and empirical impact studies (Sadovy and Domeier, 2005; STECF, 2007; Gruss *et al.*, 2014). Although many spawning area closures have been established, the effectiveness of this approach has rarely been evaluated (van Overzee and Rijnsdorp, 2015). Whilst potential impacts of spawning fidelity and effort redistribution have been examined there is still comparatively few empirical studies of spawning closures. The Before/After, Control/Impact (BACI) survey design has been widely accepted as an appropriate method of directly assessing the effects of area closures (Claudet and Guidetti, 2010; Ojeda-Martinez *et al.*, 2011; Osenberg *et al.*, 2011; Fenberg *et al.*, 2012). Of those studies that have examined the effect of area closures to protect spawning aggregations (Beets and

Friedlander, 1998; Murawski *et al.*, 2000; Rhodes and Sadovy, 2002; Pet *et al.*, 2005), none have used a BACI survey design.

Atlantic cod, *Gadus morhua*, are particularly relevant to the debate about spawning area closures as this measure has been applied to many stocks (Murawski *et al.*, 2000; Hu and Wroblewski, 2009; Armstrong *et al.*, 2013). They are broadcast spawners (Hutchings *et al.*, 1999) that aggregate in high numbers to spawn (Rose, 1993; Rose and Kulka, 1999; Wright *et al.*, 2006a; Siceloff and Howell, 2013). Aggregations are persistent from year to year and form in specific locations for set periods of time. Cod exhibit a diversity of migratory behaviour associated with differing degrees of reproductive isolation among spawning aggregations (Knutsen *et al.*, 2003; Wright *et al.*, 2006b; Skjaeraasen *et al.*, 2011). Many resident populations often exhibit differences in life history traits over comparatively small spatial scales (Olsen *et al.*, 2004; Yoneda and Wright, 2004; Wright *et al.*, 2011).

Cod off the West Coast of Scotland in ICES Area VIa are managed as a single stock (ICES, 2013). However evidence on the connectivity between nursery and spawning areas from otolith microchemistry and home ranges based on tag-recapture experiments suggest that this stock is composed of three sub-populations; the Clyde, Minch and South West (Wright *et al.*, 2006a; 2006b). Cod from the Clyde were shown to be reproductively isolated having little detectable exchange with the northern spawning aggregations. Genetic evidence also supports this population structure as Clyde cod were found to have a greater affinity to those from the Irish Sea than the cod from the northern aggregations (Heath *et al.*, 2014). Different trends in spawning stock biomass (SSB) among the sub-populations further supports the existence of this population structure (Holmes *et al.*, 2014). A fishery closure was introduced to the Firth of Clyde in 2001 to coincide with the cod spawning period (6th March to 30th April) to allow as many cod as possible to spawn (Commission Regulation (EC) No 456/2001) and was subsequently continued by the Scottish Government (The Sea Fish (Prohibited Methods of Fishing) (Firth of Clyde) Order 2002) . The location was known as an important spawning area for cod identified by a high catch rate of mature individuals (age 3 and 4) (Armstrong *et al.*, 2006), and spawning individuals (Wright *et al.*, 2006a) and the area is vulnerable to increased fishing efforts during the spawning period (Hislop,

1986). In addition, the Clyde closure was intended to avoid an increase in local fishing mortality as a consequence of fishing effort being displaced from an Irish Sea closure (Commission Regulation (EC) No 304/2000). The closure has two zones (Figure 1), Area 2 prohibits gears that target fish and trawling for *Nephrops* (*Nephrops norvegicus*), but allows creeling and dredging for scallops (*Pecten maximus*) whilst Area 1 also prohibits gears targeting fish but permits trawling for *Nephrops*, creeling and scallop dredging.

Given the apparent reproductive isolation of Clyde cod, the seasonal closure was expected to reduce the sub-population mortality rate and aid the recovery of spawning stock biomass, although it was not expected to affect the other sub-populations within ICES Area VIa. The aim of this study was to investigate the rationale and effectiveness of the area closure. The rationale that the closure reduced catchability was examined from changes in commercial landings and fishing effort before and after the closure. Effectiveness, in terms of the closure allowing the recovery of the Clyde sub-population, was assessed by applying an asymmetric "beyond-BACI" design (Underwood, 1992) to analyse survey based indices of spawning stock biomass (SSB) and CPUE. The fine scale sub-population structure within the stock with a relatively long time series of standardised survey data, lends itself to a BACI analysis, by providing one sub-population with a putative impact (the area closure) and two comparable control spawning areas. To establish whether the closure had an effect on total mortality the same beyond-BACI methodology was applied to a linearised catch curve of the length composition for each sub-population, before and after the measure was introduced.

Methods

The three sub-populations and their associated spawning aggregations used in this study were identified from Wright *et al*. (2006b). Landings of cod and fishing effort (hours fished) data for each vessel type greater than 10m were extracted from the Marine Scotland FIN database by ICES rectangle (1° longitude x 0.5° latitude). Data were summed for multiple ICES rectangles corresponding to each of the three sub-populations (Table 1), then effort was displayed as monthly proportions for the period "Before" (1986-2000) and "After" (2001-2010) the Clyde cod closure was introduced. Landings per unit effort were calculated using a correction factor for each of the seven

gear types based on that used by Wright *et al.*, (2006a) and displayed as corrected landings per unit effort (CLPUE) monthly total for each sub-population for each time period . The sum effort and landings for the two gears that accounted for most landings; light otter trawls (LTR) and *Nephrops* trawls (NTR) was calculated for each sub-population area for each year.

Seasonal and annual variation in catch rates

Data on catch per unit effort and length composition were obtained from the 1st quarter (February to April) Scottish West Coast Bottom Trawl Survey conducted by Marine Scotland Science from 1986 until 2010, during the March-April spawning period for cod. Due to a change in the survey design after this date later data were not used in the analysis. The surveys used a Grande Overture Vertical trawl with a high-headline bottom trawl fitted with a 20 mm cod end liner. The distance of the tow, wingspread and speed was recorded so that the catch per unit effort (CPUE) could be standardised to the number of cod caught at each 1 cm size class per hour. The surveys within ICES area VIa were replicated at a spatial scale of an ICES rectangle (1° longitude x 0.5° latitude). All trawls used in the Minch were within 65 km of the identified spawning site; 60 km of the SW spawning site and 35 km of the Clyde spawning site (Figure 1)**.** Sample sizes for each sub-population can be seen in Table 1.

Changes in CPUE and SSB from scientific trawls

Generalised Linear Models were used to test for different trends in both CPUE and SSB before (1986-2000) and after (2001–2010) the closure. As the closed area was expected to reduce fishing mortality of spawning cod only mature sized cod were used in the analysis. The length at which 25% of cod off the West coast of Scotland are mature is 35 cm according to Yoneda and Wright (2004), and so this length threshold was used in the estimation of mature cod CPUE. 25 % length at maturity rather than 50 % was used due to the low abundance of larger sized cod during the after period, which would not have allowed for a robust analysis. SSB was calculated by using data on length and weight from ICES Area VIa extracted from the DATRAS website. A linear model was fitted to the natural logarithm (base e) of the length and weight of all cod sampled. The intercept (-1.9307) and slope (2.9831) from this model were then used to calculate the weight from

the measured length of all mature fish. The SSB for each trawl was then calculated by summing the total biomass of mature fish for each trawl.

Analysis of both SSB and CPUE started with a saturated model, including all interaction terms based on *a priori* hypotheses for the inclusion of a third order interaction (β_7,spy) between period (p), sub-population (s) and year (y) (Equation 1).

$$Log(Response) = \beta_0 + \beta_1, s + \beta_2, p + \beta_3, y + \beta_4, sp + \beta_5, py + \beta_6, sy + \beta_7, spy \qquad (1)$$

Both sub-population and period were modelled as factors, where sub-population (s) included three levels: (i) Clyde closed area, (ii) Minch control area, and (iii) SW control area. Period (p) included two levels for the time period (i) “before” the area closure from 1986 until 2000; and (ii) “after” including 2001 until 2010. Year (y) was modelled as a continuous variable. Generalised linear models were implemented using the glm() function in the R package “nLME ”(Pinheiro *et al.*, 2013). The model of best fit was identified using backward model selection from the fully saturated model using likelihood ratio tests (Zuur *et al.*, 2009), and checking residual plots. If the model of best fit includes the third order interaction (spy) this would indicate that the trend in response variable differed for each sub-population, and the trend differed for each sub-population for each of the time periods, “before” and “after” the area closure. A difference in trend for the Clyde sub-population in the “after” period compared to the other sub-populations could then be inferred as an effect of the closure.

Changes in length composition and total mortality

Changes in length composition “Before” and “After” the closure in each sub-population were compared using a Kolmogorov-Smirnoff (K-S) test from the function clus.lf() from the R package “fishmethods” (Nelson, 2014) applied to calculated CPUE per 5 cm length bin. Total mortality (Z) before and after the closure was calculated from the slope of a linearised catch curve, modelling the relationship between the natural logarithm of CPUE and length (Jensen, 1984) implemented using the function glmer() in the R package “lme4” (Douglas *et al.*, 2015). A general linear mixed model was used to analyse mortality using the following model structure:

$$Z = \beta_0 + \beta_1, s + \beta_2, p + \beta_3, l + \beta_4, sp + \beta_5, sl + \beta_6, lp + \beta_7, spl + b_0 + b_1, y + b_2, l \qquad (2)$$

Both sub-population (s) and period (p) were modelled as factors as in the preceding analysis. Length was modelled as a continuous variable between 45 cm and 70 cm. This range was chosen as the catch curve indicated that smaller sizes were not fully vulnerable to the fishing gear and larger fish were not regularly caught in all areas. A random intercept and slope effect was included in the model to account for different mortality rates each year. Year was modelled as a random factor with 25 levels. A significant interaction effect would imply that the CPUE of different size fish changes for different sub-populations during the different time periods. The model of best fit was identified using backward model selection from the fully saturated model using likelihood ratio tests (Zuur *et al.*, 2009), and checking residual plots. If the model of best fit includes the third order interaction and a positive coefficient for the Clyde sub-population then this would indicate a reduction in total mortality (Z) and could be inferred as an effect of the area closure.

Results

Seasonal and annual variation in catch rates

CLPUE and proportion of fishing effort varied significantly over the year in all three sub-population areas (Kruskall-Wallis; $p < 0.01$). In the Clyde and SW area there was a peak in the CLPUE and proportion of fishing effort related to spawning time during the “Before” period (Figure 2). In the “Before” period in the Clyde area, there was a 3 times difference in catchability (CLPUE) between the spawning and non-spawning period; 70% of annual landings were taken during these two months and 45% of the total annual effort for Light Otter Trawls in this area was accounted for during these two months (Figure 2). During the “After” period effort in the Clyde peaked in October although there was a small peak in cod landings during the spawning period. In the SW and Minch there was no peak in either landings or fishing effort around spawning time in the “After” period. Landings and effort by the light otter trawls decreased from the start of the study period until the end with a clear decline from the 1990s for all areas (Figure 3). Importantly, there was no redistribution of light otter trawl in the Clyde area following the closure, the effort was effectively removed from this area (Figure 8 Supplementary Information). The effort of *Nephrops* trawls

remained fairly constant throughout the study period (Figure 9 Supplementary Information) although the landings of cod showed a decline in each of the areas, which was particularly steep after 2000. As a result, landings and effort by 2001 represented < 12% of the peak (Figure 3).

Changes in CPUE and SSB from scientific trawl

Model selection for estimating changes in CPUE and SSB did not support the three-way interaction term between year, time and sub-population. The absence of evidence supporting a three-way interaction indicates that there was no effect of the Clyde closure on CPUE or SSB. The model of best fit (Equation 3) for both CPUE and SSB supported interactions between time period and year, and sub-population and year (CPUE in Table 2 and SSB in Table 3). For the "Before" time period the gradient of the slope for CPUE (Figure 4) and SSB (Figure 5) was negative for all areas. For the "After" period the gradient of the slope was more negative, but the degree of decline was equal for each area, indicating no effect of the Clyde area closure.

$$Log(Response) = \beta 0 + \beta 1,s + \beta 2,p + \beta 3,y + \beta 4,py + \beta 5,sy \qquad (3)$$

Changes in length composition and total mortality

There was no significant change in length structure in any of the three sub-populations before and after the closure (Kolmogorov-Smirnov test, $p > 0.1$). In the Clyde population the most frequently caught length classes were 15-20 cm and 45-50 cm before and after the closure. The population did show signs of size truncation with no fish greater than 70 cm caught after 2001, whereas prior to 2001 cod up to the size of 100 cm were caught (Figure 6). Both the Minch and SW sub-populations also showed signs of size truncation and the most frequently caught size classes can be seen in Figure 6.

Model selection for the estimation of total mortality did not support the three-way interaction between sub-population, time and length. The model of best fit included the slope intercept random effect and both of the two way interactions between sub-population and period, and sub-population and length (Equation 4). Hence whilst there were different gradients for the slope for each sub-population, the gradient did not differ between the "Before" and "After" periods. This suggests that

total mortality is different for each sub-population but that this did not change between the “Before” and “After” time period (Table 4). The steepest slope, which can be inferred as the highest rate of total mortality was for the Minch, followed by the Clyde and then the SW (Figure 7).

$$Z = \beta_0 + \beta_1, s + \beta_2, p + \beta_3, l + \beta_4, sp + \beta_5, sl + b_0 + b_1, y + b_2, l \qquad (4)$$

Discussion

The Clyde seasonal closure did stop the seasonal build-up of fishing effort on spawning cod and probably prevented a build-up that might have been even more intense given the concurrent displacement of fishing effort from a similar closure in the Irish Sea. Before the closure, there was a clear seasonal peak in effort corresponding to the spawning time of cod in this area (Yoneda and Wright, 2004; Wright *et al.*, 2006a). This peak in effort corresponded with an increase in catchability as evident from the elevated corrected landings per unit effort (CLPUE) during the spawning months of March and April. The closure stopped this seasonal build up in effort, although increased catchability could still be seen from the elevated CLPUE in March and April. Hence even with the marked decline in local population abundance, catch rates remained high consistent with aggregations exhibiting hyperstability (Rose and Kulka, 1999; Erisman *et al*., 2011). The seasonal trend in monthly CLPUE was consistent with an earlier study by Hislop (1986), which showed a 10-fold increase in LPUE during March and April for the time period 1971-80. Many fishers are known to capitalize on the predictable nature and high catch rate of such spawning aggregations by concentrating their effort on spawning fish (Sadovy and Domeier, 2005; Erisman *et al.*, 2012). Management measures to reduce mortality on cod have often included spawning closures for this very reason. For example, in the Gulf of Maine a series of large “Rolling Closures” were introduced (Armstrong *et al.*, 2013). In the Irish Sea seasonal closures were introduced in 2000 (Kelly *et al.*, 2006) and temporary spawning closures have been applied in the North Sea (Holmes *et al.*, 2011). Consequently, the Clyde spawning closure seemed appropriate and would have been expected to benefit the local population of cod because this area encloses the major spawning component for this region (Wright *et al*., 2006b).

This is the first study that has used a beyond-BACI (Underwood, 1992) approach to compare the trends within a spawning aggregation before and after the introduction of an area closure. In the wider field of fisheries area closures and marine protected areas the beyond-BACI methodology has been identified as the most robust method to monitor the trajectory of populations over time (Sale *et al.*, 2005; Claudet and Guidetti, 2010; Fenberg *et al.*, 2012). In this study spawning areas of three distinct sub-populations were used for the analysis, each of which has a high level of self-recruitment (Wright *et al*., 2006b). Therefore any localised reduction in fishing mortality due to the spawning aggregation area closure would be expected to affect the local sub-population without influencing any of the control sub-populations. Particularly in spawning aggregation studies it is difficult to find representative control populations, which may be why other studies have been unable to take a similar approach to this study.

Despite the potential benefits of a seasonal closure there was no evidence of a local recovery on the Clyde cod sub-population more than a decade after its implementation. We can infer this because the beyond BACI approach (Underwood, 1992) allows us to account for before/after differences in both the area where management was implemented and other control sites that are likely to be exposed to the same natural drivers of change. There was a greater rate of decline in SSB and CPUE for all the three sub-populations after 2001 compared to before, but the change in rate of decline was the same for each of the three sub-populations. This implies that there was no detectable effect of the area closure on the Clyde sub-population of cod. Although spawning area closures have been used for a wide-range of species throughout the world's oceans, there have been few studies that have attempted to evaluate the effectiveness of this measure (see Van Overzee and Rinsdorp, 2015). Those empirical studies that have looked at the effects of spawning aggregation closures are mostly descriptive, comparing changes in length composition, sex ratios, abundance and biomass, but generally lack baseline and/or temporal data (Beets and Friedlander, 1998; Murawski *et al*., 2000; Rhodes and Sadovy, 2002; Pet *et al*., 2005; Heppell *et al*., 2012). Theoretical studies have suggested that a combination of spawning aggregation reserves and reduced fishing effort are required to maintain or promote the recovery of fish populations (Heppell *et al.*, 2006; Ellis and Powers, 2012), whilst others have suggested that the use of spawning aggregation closures over normal residence closures is dependent on the catchability during the

spawning period (Gruss *et al.*, 2013; Gruss and Robinson, 2015). Model simulations show that redistribution of effort, particularly when it exceeds that which occurred prior to a closure, can negate any benefit of a spawning closure (Heppell *et al.*, 2006; Gruss *et al.*, 2013; Gruss and Robinson, 2015). However, for a highly exploited population where a seasonal closure removes a large proportion of fishing effort that targets spawners without redistribution of this effort this would be predicted to benefit population growth (Gruss *et al.*, 2013, 2014; Gruss and Robinson, 2015). This was expected to be the case for the Clyde spawning area closure where fishing effort was reduced and not redistributed, at least for the main gear targeting cod. Landings have similarly declined in all three sub-population areas although by 2006 estimated discards did exceed landings across the entire west of Scotland stock region (ICES, 2013).

As cod in the Clyde are largely self-recruiting (Wright *et al*., 2006b), recovery depends on the intrinsic population growth rate of this sub-population. Without any fishing mortality the median population growth rate of cod from the Scottish west coast has been estimated to be 26% per year (Wright, 2014). Based on such a rate of population growth and in the absence of density dependent recruitment or fishing mortality, the local sub-population may have been expected to recover to near 1980s levels within 10 years of closure. It would be expected that such a fast recovery rate would be evident well within the study period based on estimates of the power to detect changes in cod abundance from surveys (Maxwell and Jennings, 2005). The lack of recovery in the Clyde sub-population after the introduction of the area closure may therefore indicate a number of possibilities such as sustained fishing mortality, increasing natural mortality, reproductive failure and/or low recruitment.

Total mortality or length composition did not change in the Clyde after the area closure was introduced, although there was evidence of size truncation. Reductions in mortality would have been expected to lead to a recovery in the length composition, such as in the study by Beets and Friedlander (1998) who found a recovery of length composition of the grouper, *Epinephelus guttatus*, after the introduction of a seasonal spawning area closure. Cod are vulnerable to fishing gears outside of the seasonal area closure and as there was not a substantial change in effort and landings by light otter trawls (Supplementary Information Figures 8 and 10) immediately associated with the Clyde closure and effort for the Nephrops trawls remained steady until 2009

(Supplementary Information Figure 9), fishing mortality may not have been significantly reduced by this measure. Catchability remained high during the spawning period after the closure had been introduced, so it is likely that cod migrating to spawning sites still appeared particularly vulnerable. Whilst the demersal fishery ceased in the Clyde during the early 2000s there were still landings coming from the *Nephrops* trawl fishery, which has a derogation to fish all year in most of the closed area. Cod landings from the *Nephrops* fishery peaked in March and April both before and after the closed area was introduced indicating that some fishing induced mortality on spawning cod continued. Similarly reduced but continued fishing within a closure was not associated with any change in length composition or trend in abundance in an area closure designed to protect groupers (*Epinephelus fuscoguttatus* and *Plectropomus areolatus*) whilst aggregating to spawn in Komodo National Park, Eastern Indonesia (Pet *et al*., 2005).

Across the Scottish west coast cod catches were less than a tenth of the peak by 2000 and SSB was below Blim (ICES 2013). As there is strong evidence that cod at low SSB can be subject to depensation, i.e. the Allee effect (Keith and Hutchings, 2012) the apparent ineffectiveness of the closure may reflect the poor state of the Clyde sub-population by the time this measure was implemented. Several mechanisms have been hypothesized as to how the Allee effect impacts marine fishes such as altered food-web dynamics ("cultivation-depensation") (Walters and Kitchell, 2001); increased predator mortality (Kuparinen and Hutchings, 2014) and reduced mating success (Rowe et al., 2004).

It is possible that the change in the Clyde fish community from highly diverse to one dominated by whiting (*Merlangius merlangus*) could have increased the natural mortality of an already depleted population of cod. Since 1995, whiting, a piscivorous gadoid, has dominated the biomass of fish within the Clyde (Heath and Speirs, 2012). Young of the year whiting have been shown to compete with other gadoids for food and through predation on smaller size classes (Bromley *et al.*, 1997) and adult whiting have also been shown to be a voracious predator of juvenile cod (Temming *et al.*, 2007). Hence a key predator and competitor of young cod may have impeded the recovery of cod. A recent study has also suggested that another key predator of cod, Grey seals (*Halichoerus grypus*) could be a contributing factor to the lack of recovery of cod off the west coast

of Scotland (Cook *et al.*, 2015), although the population of this predator is relatively low in the Clyde.

Disturbance from fishing can change the behaviour of spawning fish compromising reproduction (Morgan *et al.,* 1997; Dean *et al.,* 2012). The reduction in targeted fishing on spawning cod is likely to have reduced the overall level of disturbance on the Clyde cod sub-population. However, whilst cod are unlikely to be spawning on the grounds targeted by *Nephrops* trawl fishing, as spawning cod tend to avoid mud (González-Irusta & Wright, in review), it is possible that shoals moving to those spawning sites could have continued to be disturbed. Recruitment success may have also decreased in Clyde cod as a result of poor environmental conditions and the combined effect of truncated size structure of the spawning stock (Stige *et al.*, 2006). A positive correlation between spawner mean age and offspring survival was found in the Irish Sea and North Sea cod (Wright, 2014). Possible reasons for an effect of spawner age on reproductive success include maternal effects on larval viability (Marteinsdottir and Steinarsson, 1998) and/or the potential for a mismatch between spawning and optimal conditions for larval survival (Wright and Trippel, 2009), as there are age related differences in the onset of cod spawning (Morgan *et al.*, 2013).

The GOIS (Goals, Objectives, Indices and Success Criteria) approach has been used to provide a framework for objective setting, planning, and governance of closed areas (Rice *et al.*, 2012).

The goal of the Clyde closure was to protect adult cod during the spawning period, but no explicit objectives or indices of success were defined at the time of the closure. STECF (2007) suggested that the criteria to indicate that the Clyde closure had been a success was the extent of reduction in fishing mortality on mature cod and a local increase in SSB. Based on these criteria the closure has not been a success. Even though there has been no sign of recovery of cod in the Clyde, the rationale for an area closure to protect spawning cod appears justified on the basis that it did reduce targeted fishing effort on spawning cod and prevented additional fishing effort displaced from the Irish Sea Closure. Considering the state of the already severely depleted population when the closure was introduced, it could be argued that a) the area closure was implemented too late, b) the closure alone was not sufficient and c) that it did not go far enough to protect spawning cod. We cannot change the past but we can address the future by managing populations within an ecosystem context, like that being discussed through the Clyde 2020 project (The Scottish

Government, 2014). Spawning area closures alone are not enough to manage populations when numbers are too low to withstand environmental fluctuations and additional sources of mortality. Other measures will be required to protect all life stages and prevent unintentional sources of fishing mortality. However, the current Clyde spawning area closure permits disturbance of aggregations with derogations allowing the continued use of some types of fishing gear with the possibility of incidental bycatch of spawning cod. Hence, whilst it is unclear what combination of factors are preventing the recovery of the local cod population, at the very least what can be done is to allow those remaining to spawn undisturbed to improve the chances of successful reproduction.

Supplementary Information

Supplementary material is available at ICESJMS online version of the manuscript giving further details on model selection.

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Table Legends

Table 1. List of ICES rectangles used for each sub-population. Values represent the number of trawl surveys conducted by Marine Scotland Science in quarter 1 within each sub-population area in each time period.

Table 2 . Output from the model of best fit for the response variable CPUE. Fixed effects show treatment contrast coefficients and diagnostics (z- and p-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference levels for each term are: Time, After and Sub-population, Clyde.

Table 3. Output from the model of best fit for the response variable SSB. Fixed effects show treatment contrast coefficients and diagnostics (z- and p-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference levels for each term are: Time, After and Sub-population, Clyde

Table 4 . Output from the model of best fit for the response variable estimating mortality (CPUE). Fixed effects show treatment contrast coefficients and diagnostics (t- and p-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level for each term are: Time, After and Sub-population, Clyde

Tables

Table 1

Sub-population	ICES Rectangle	Before	After	Total
Clyde	39E4 and 39E5	32	21	53
Minch	45E4, 45E3, 46E4	109	64	173
SW	42E3, 42E2, 41E2	41	39	80

Table 2

CPUE	Estimate	Standard Error	z value	p value
(Intercept)	2.085	0.289	7.222	<0.001
Time(Before)	-0.233	0.304	-0.765	0.444
Sub-population(Minch)	-0.202	0.054	-3.761	<0.001
Sub-population(SW)	-1.086	0.220	-4.929	<0.001
Year	-1.618	0.278	-5.81	<0.001
Time(Before) : Year	0.149	0.055	2.711	0.007
Year : Sub-population(Minch)	0.027	0.028	0.943	0.346
Year : Sub-population(SW)	-0.110	0.035	-3.098	0.002

Table 3

SSB	Estimate	Standard Error	z value	p value
(Intercept)	2.855	0.352	8.115	<0.001
Time(Before)	-0.582	0.367	-1.584	0.113
Sub-population(Minch)	-0.267	0.063	-4.229	< 0.001
Sub-population(SW)	-0.667	0.270	-2.471	0.013
Year	-1.697	0.335	-5.069	<0.001
Time(Before) : Year	0.180	0.064	2.832	0.004
Year : Sub-population(Minch)	0.066	0.035	1.884	0.060
Year : Sub-population(SW)	-0.165	0.044	-3.75	<0.001

Table 4

Mortality	Value	Standard Error	t value	p value
(Intercept)	1.243	0.513	2.422	0.016
Length	-0.026	0.009	-3.074	0.002
Sub-population(Minch)	-1.227	0.588	-2.086	0.038
Sub-population(SW)	-2.153	0.615	-3.498	<0.001
Time(Before)	0.095	0.201	0.472	0.641
Length:Sub-population(Minch)	-0.002	0.010	-0.157	0.875
Length:Sub-population(SW)	0.022	0.011	2.032	0.043
Sub-population(Minch):Time(Before)	0.551	0.196	2.808	0.005
Sub-population(SW):Time(Before)	0.361	0.215	1.683	0.093

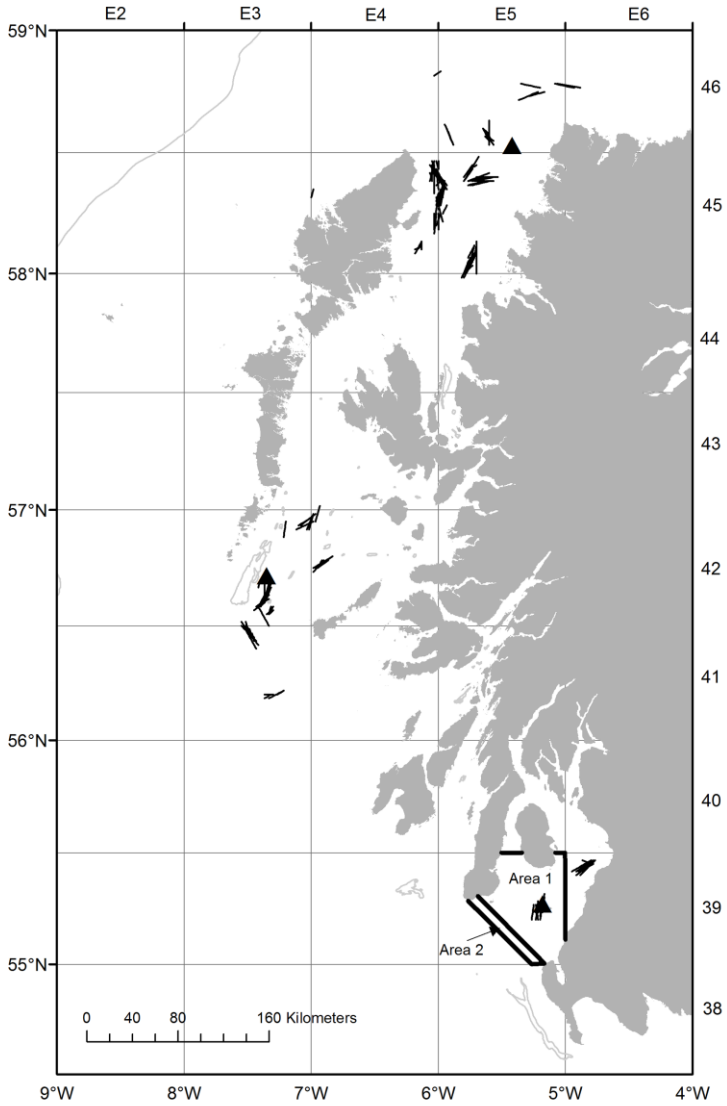

Figure 1 Map of survey area to the west of Scotland. Lines indicate all trawls conducted during the study period and used in the analysis. Black triangles indicate spawning locations taken from surveys conducted by (Wright et al., 2006a). The Clyde closure is split into two zones, Area 1 prohibits gear that targets fish and Area 2 prohibits gear that targets fish and *Nephrops* during the spawning period.

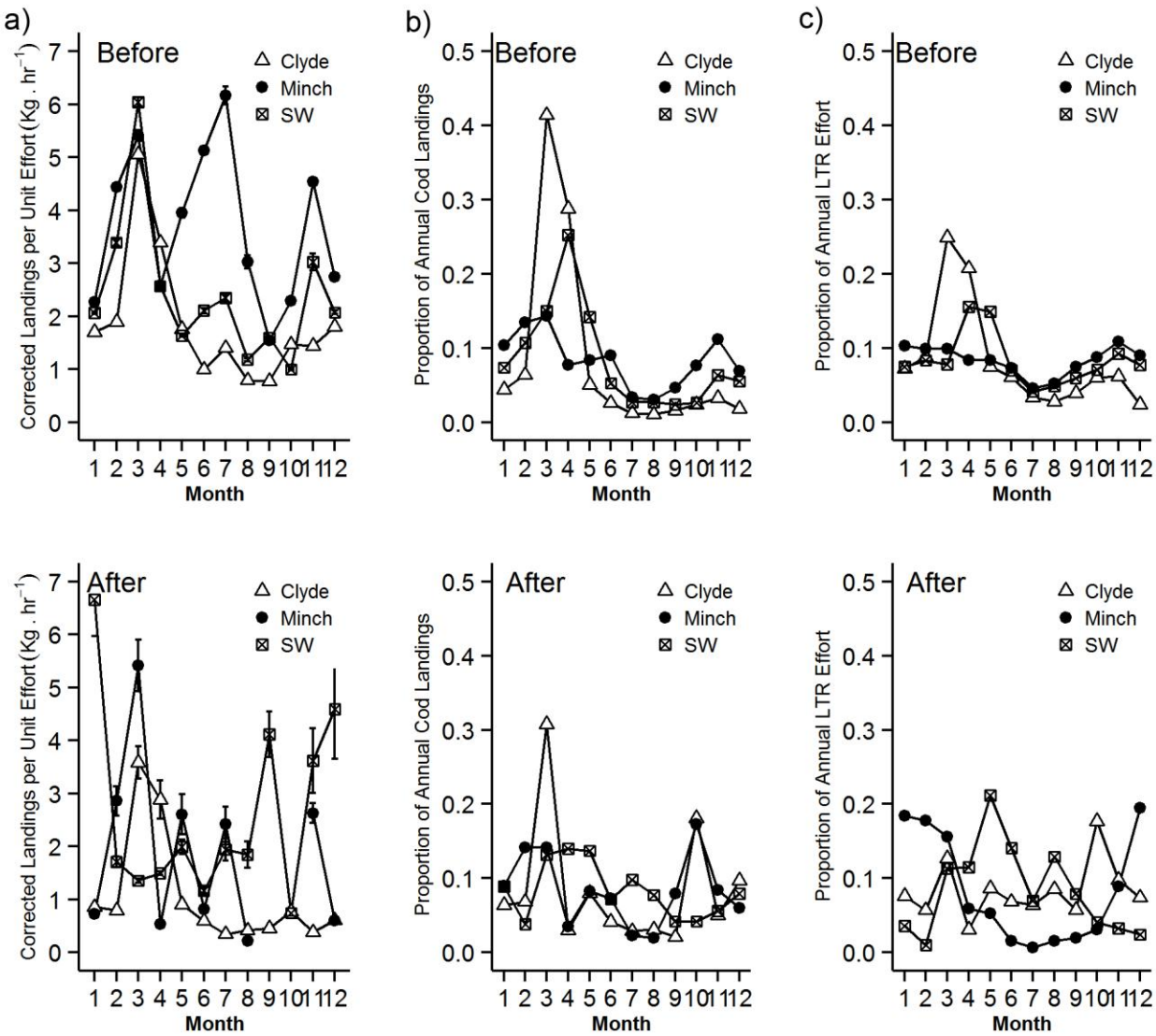

Figure 2 Solid lines show corrected landings per unit effort (CLPUE) (kg.h^{-1}) for each location for each month during the “Before” time period (upper graph) and “After” (lower graph) for all vessel types. The dashed lines show the proportion of effort for each area, for each month for all gear types during the “Before” time period (upper graph) and “After” (lower graph).

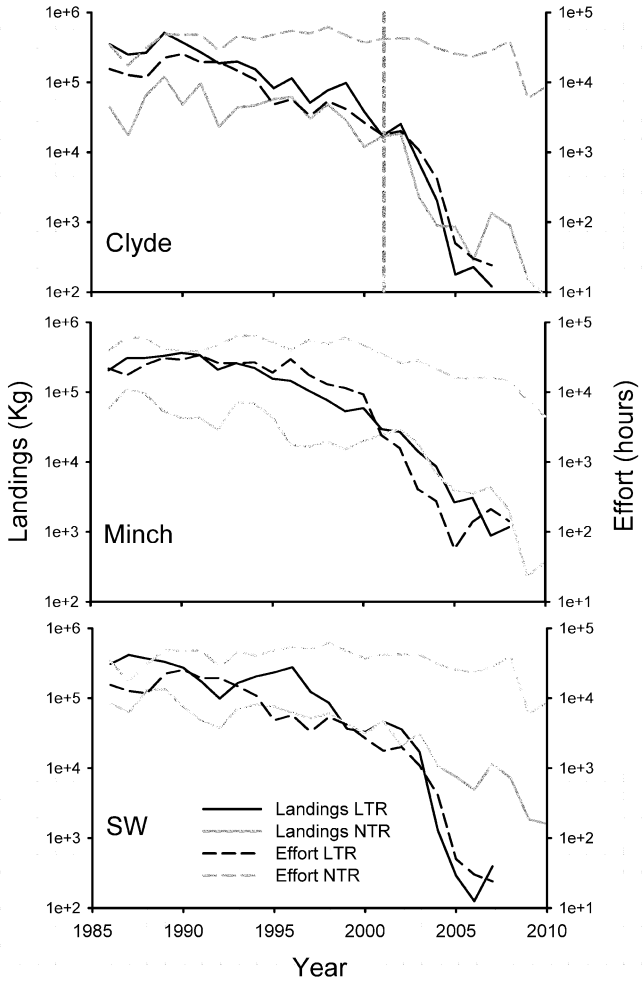

Figure 3. Solid lines indicates the sum landings of cod in kilograms and the dashed lines indicate the sum of the effort in number of hours fished for each location for each year. Black lines are the sum total for Light Otter Trawls (LTR) and the grey lines are the sum total for Nephrops Trawls

(NTR). Vertical dashed line in the Clyde graph indicates the year the area closure was

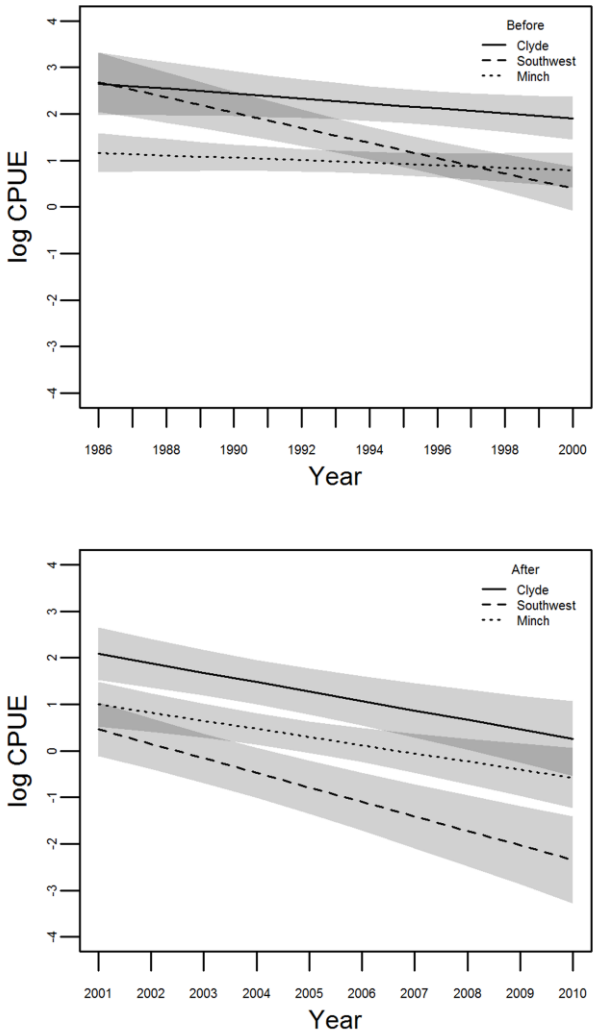

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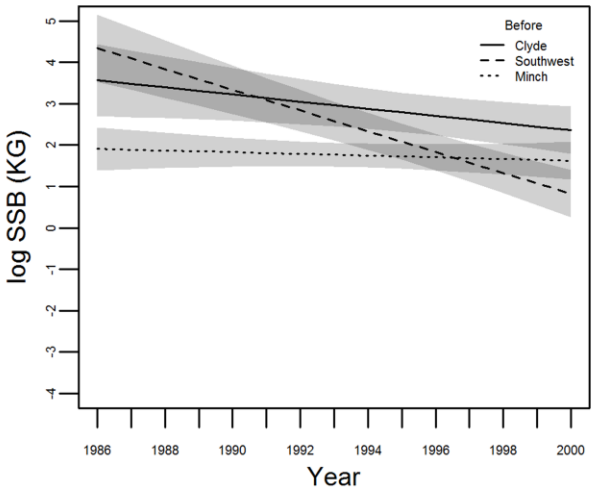
Figure 4. Fitted values taken from the model of best fit of the logarithm Catch per unit Effort (CPUE) versus year for each sub-population with 95% confidence intervals shaded in grey. The upper figure is for the “Before” time period and the lower figure is for the “After” time period.



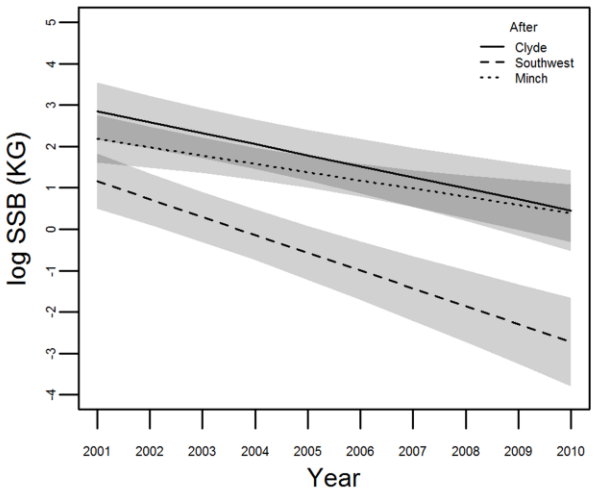


Figure 5. Fitted values taken from the model of best fit of the logarithm of Spawning Stock Biomass (SSB) versus year for each sub-population with 95% confidence intervals shaded in grey. The upper figure is for the “Before” time period and the lower figure is for the “After” time period.

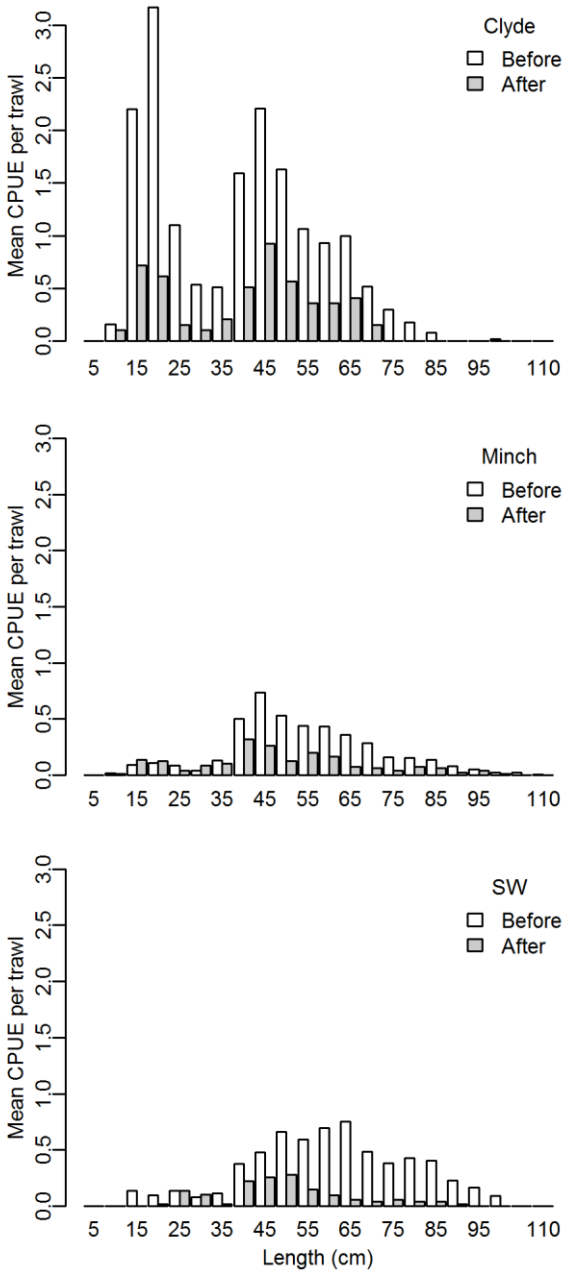


Figure 6. Length frequency plots of mean number of cod caught per trawl in 5cm length bins for each sub-population for each time period. The top figure is the Clyde, middle is the Minch and the bottom is the SW.

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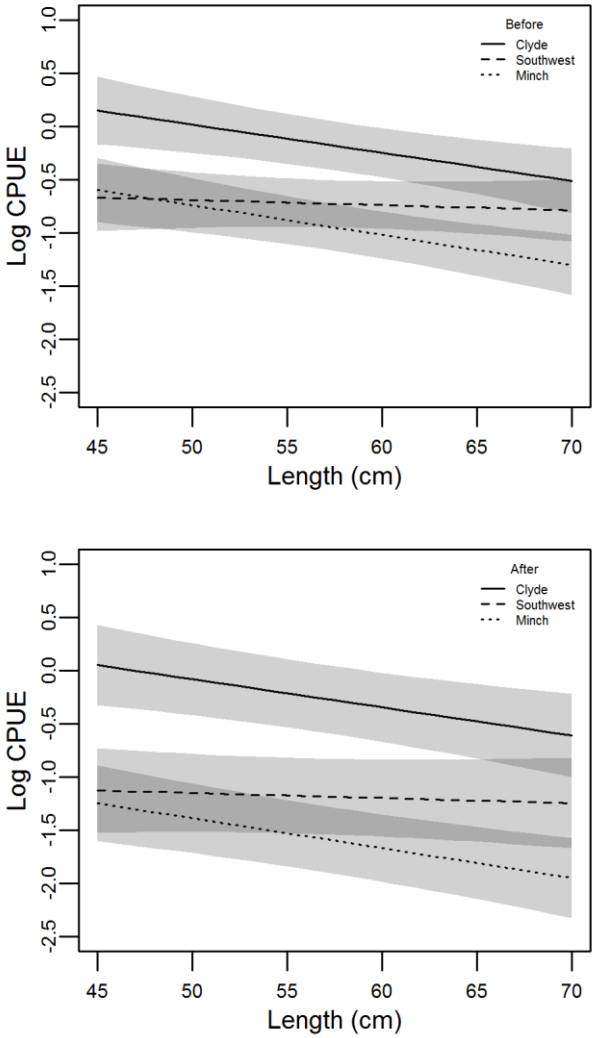

Figure 7. Fitted values taken from the model of best fit for the logarithm of Catch per unit effort (CPUE) for each sub-population across length from the time period “Before” (upper figure) and “After” (lower figure).