Received: 25 July 2017 | Revised: 8 April 2018 | Accepted: 11 April 2018
DOI: 10.1002/aqc.2938

RESEARCH ARTICLE

WILEY

The importance of nonnative Pacific oyster reefs as supplementary feeding areas for coastal birds on estuary mudflats

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Abstract

1. A combined empirical and modelling approach was used to investigate the value of a Pacific oyster reef to feeding shorebirds and to observe and predict the impact of reef clearance on bird populations in the Colne Estuary, a protected area in south-east England. Macro-invertebrate biomass and numbers of feeding birds were measured on a Pacific oyster reef, an adjacent uncolonized mudflat, and an area of mudflat that had been cleared of oysters 6 months previously. These data were used to parameterize an individual-based model (MORPH) to predict the impact of clearance of the reef on winter bird survival. Feeding success and intake rates of Eurasian oystercatcher, Eurasian curlew, and Eurasian common redshank were also recorded during the course of a winter.
2. The macro-invertebrate diversity and biomass within both the oyster reef and the cleared area were significantly greater than the adjacent uncolonized mudflat. The density and biomass of large invertebrate prey in the mudflat were low, yet the Pacific oyster reef had much higher densities and biomass of large prey, especially annelids and shore crabs.
3. The winter assemblage of feeding birds differed significantly between each of the areas. The mean total number of feeding birds was significantly greater on the uncolonized mudflat; however, mean peak counts, feeding success rate and prey intake rate of Eurasian oystercatcher were greater on the reef. Significantly greater intake rates and feeding success rates were also observed on the reef for Eurasian curlew, a species of conservation concern.
4. Field data and model predictions show that Pacific oyster reefs can provide valuable supplementary feeding areas for some shorebirds, yet other species avoided the reef. However, as estuaries vary in available feeding resources, it is important that the value of reefs and their management is determined regionally.

KEYWORDS

aquaculture, behaviour, estuaries, fisheries, individual-based models, intertidal, invasive species, management measures, marine protected areas, *Megallana* (*Crassostrea*) *gigas*, wading birds

1 | INTRODUCTION

The impact of non-native species upon ecosystems is one of the most serious issues facing the conservation of biodiversity (IUCN, 2000). Along coasts of many temperate regions, the Pacific oyster, *Magallana* (*Crassostrea*) *gigas*, has been introduced and cultivated outside its native range (FAO, 2016a, 2016b; Humphreys, Herbert, Roberts, & Fletcher, 2014; Ruesink et al., 2005). In some areas, wild settlement of oysters is now occurring that can result in the formation of extensive reefs on intertidal mudflats (Lejart & Hily, 2005, 2011; Reise, 1998; Smaal, Kater, & Wijsman, 2009; Troost, 2010). Reef formation on soft-sediment habitats commences when two or more oysters that have settled in proximity come into contact to form a "clump." These clumps may merge with other clumps and form a larger patch. When oyster densities become so high that little space exists for new settlement on the substrate surface other than upon the oysters themselves, then a reef is formed. On soft sediments, these areas may have in excess of 200 live oysters per square metre, which are usually mixed with dead shell. Oyster densities over 700 m^{-2}, which have created a hard substratum, have been reported in the Wadden Sea (Markert, Wehrmann, & Kröncke, 2010; Walles et al., 2015). The area, height, and thickness of the reef vary and are likely to be dependent on larval supply and settlement success in different parts of the site, which may depend on local variation in substrate. Most Pacific oyster reefs are patchy and may include areas of bare substrate and pools (Herbert et al., 2016; Troost, 2010).

Pacific oysters are ecosystem engineers (Padilla, 2010), and reef formation can transform benthic invertebrate assemblages (Herbert et al., 2016; Lejart & Hily, 2011), yet the potential impact of these oyster reefs on coastal bird populations is largely unknown. In the UK and elsewhere in Europe, soft-sediment intertidal habitats are key feeding areas for overwintering migratory birds on the East Atlantic flyway (Goss-Custard, West, et al., 2006; Stroud et al., 2004), and many areas are protected. Winter survival and fitness determine the number of birds able to return to breeding grounds and reproduce successfully (Goss-Custard, Burton, et al., 2006). Most overwintering wading birds (Charadrii) rely on benthic invertebrates in intertidal areas, and terrestrial resources, such as earthworms in surrounding fields, may be exploited by some species (Zwarts & Wanink, 1993). Yet the formation of dense reefs of *M. gigas* could pose a threat to winter survival and fitness of the birds as they may be unable to reach food due to the size and shell thickness of the oysters (Nehring, Reise, Dankers, & Kristensen, 2009). In the Wadden Sea, European herring gull (*Larus argentatus*) and European oystercatcher (*Haematopus ostralegus*) are currently the only birds that feed directly on *M. gigas* (Cadée, 2008a, 2008b; Nehring et al., 2009; Troost, 2010). As waders use visual, tactile, and sweeping strategies to locate prey (Thomas, Szekely, Powells, & Cuthills, 2006) it is uncertain to what extent *M. gigas* settlement will affect the birds' abilities to feed efficiently.

Although there have been attempts to remove wild Pacific oysters from rocky habitats where density has been low (Guy & Roberts, 2010; Herbert et al., 2016; McKnight & Chudleigh, 2015), mechanical dredging of oysters would appear to be the only practical solution to reef removal on soft-sediment habitats. However, mobile gears can cause significant disturbance to intertidal benthic habitats and both target and non-target species (Clarke, Hughes, Herbert, Esteves, & Stillman, 2017; Ferns, Rostron, & Sima, 2000; Piersma et al., 2001; Spencer, Kaiser, & Edwards, 1998). In the Wadden Sea, where wild settlement is extensive, total eradication of Pacific oysters through dredging has not occurred owing to concerns that it would harm the ecosystem (Reise, Wegener, Sea, & List, 2010). Elsewhere, however, it could be feasible to remove smaller reefs using mechanical methods if they threaten particularly sensitive habitats, or amenities such as navigation and recreation (Herbert et al., 2016). Yet, as many of these habitats are within protected areas, an assessment of the impact and potential benefits of these measures needs to be carefully established. An integrated approach utilizing field observations to inform predictive modelling tools can be beneficial to evaluate such interventions (Wonham & Lewis, 2009).

Here, the impact of a small area of Pacific oyster reef that has become established on an estuary mudflat on the distribution and feeding behaviour of coastal birds is investigated.

The study aims to answer the following questions:

1. Is the Pacific oyster reef a beneficial feeding area for all species of birds?
2. What impact does *M. gigas* reef removal have on the number of birds and bird feeding behaviour?
3. What effect does reef clearance have on the predicted survival of birds?

Field observations of bird distribution and feeding behaviour and macro-invertebrate resources were used to parameterize an individual-based model (IBM) to predict species fitness and winter survival of birds on the cleared and uncleared areas of Pacific oyster reef and natural mudflat habitats.

2 | METHODS

2.1 | Study site

The field study was carried out within Brightlingsea Creek on the Colne Estuary in south-east England (Figure 1) between September 2013 and March 2014. The Colne Estuary is a Marine Conservation Zone, Special Protection Area (SPA), and Ramsar site. The estuary includes extensive saltmarshes, is surrounded by farmland, and supports over 20 000 overwintering waterfowl, including nationally and internationally important populations. Pacific oysters have been introduced to the region at various times since 1926 (Utting & Spencer, 1992) and are now both cultivated and create valuable fisheries. Wild settlement has been observed over several decades, usually following warm summers; however, since the mid-2000s this had become more frequent and has resulted in localized reef formation (Herbert, Roberts, Humphreys, & Fletcher, 2012). On a mudflat in proximity to a boat slipway at Brightlingsea, an area of reef, which had developed between 2008 and 2012 and attained a live oysters density of 200 m^{-2}, had become a public safety concern due to injuries sustained from sharp oyster shells. To safeguard the public and amenity, the harbour authority and local fishermen agreed to clear a small area

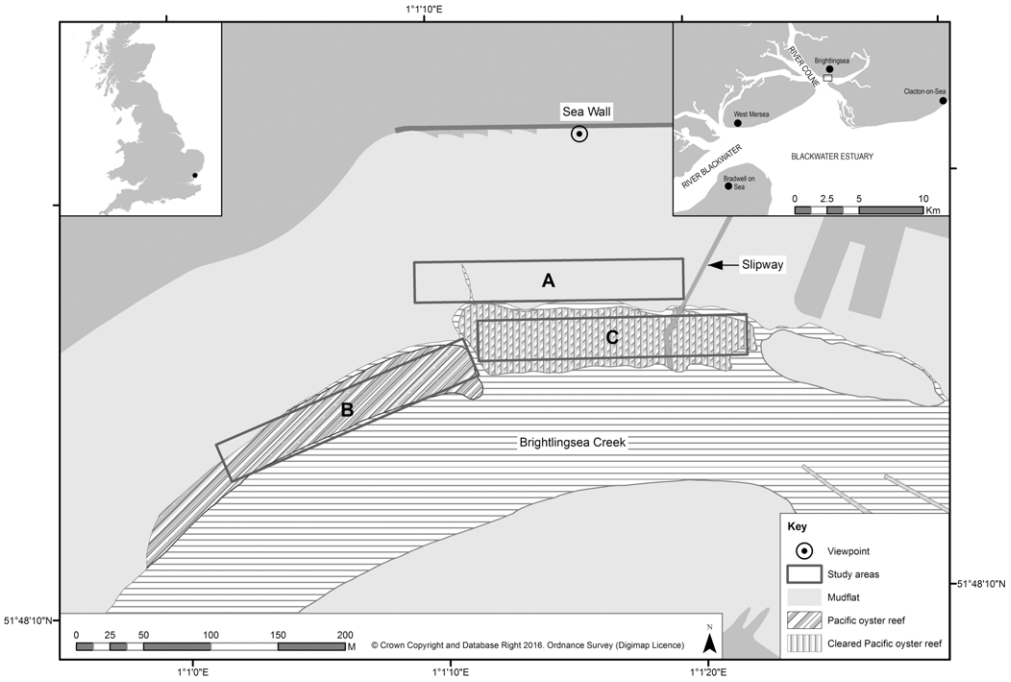

FIGURE 1 Study site at Brightlingsea Creek (Essex) indicating the three study areas from which benthic invertebrate samples were taken and counts and observations of feeding behaviour of birds were obtained

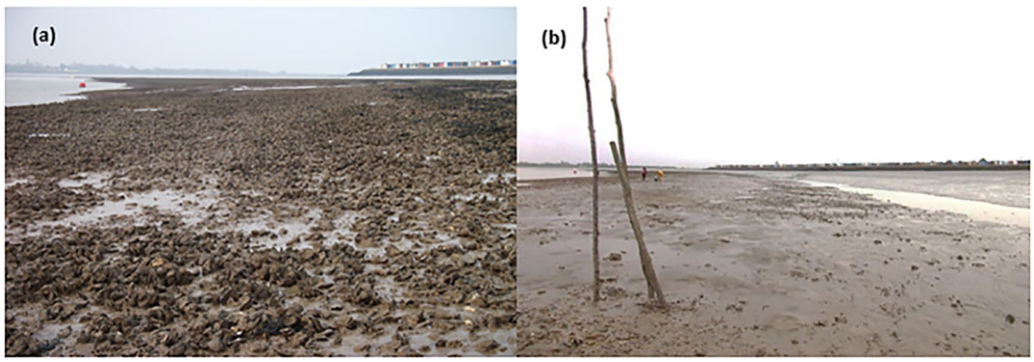

FIGURE 2 Removal of *Magallana gigas* reef at Brightlingsea, Essex. (a) Area C in foreground prior to clearance in February 2013 viewing west from slipway. Area B is just visible near the orange buoy. (b) Site C in foreground following clearance. The mudflat (area A) is visible to the right of creek

(~6000 m^2) of this reef using an oyster dredge deployed from a boat (Figures 1, 2). This was carried out as part of regular fishing operations between February and April 2013. At low tide, fishermen also accessed the site on foot and collected remaining clumps of oysters by hand-picking down to the extreme low water spring tide mark. Once cleared, no further dredging was undertaken. No patches of oysters could be identified on the site during a visual inspection and in aerial imagery obtained in autumn 2013 (Channel Coastal Observatory, http://www.channelcoast.org). A few small clumps, containing a mix of 5–10 live and dead oysters, were seen at the extreme low water spring tide mark; however, these were mainly loose and may have originated from other areas.

The study site, for which samples and field observations were made, comprised equal areas of intertidal habitat (Figure 1): site A, mudflat; site B, *M. gigas* reef; and site C, an area where *M. gigas* reef had been cleared. Each area is separated by a small creek and is of similar tidal elevation between mean tide level and mean low water (2.5–3.0 m above chart datum).

2.2 | Species abundance

To analyse habitat use by birds in the three areas, low-tide counts were carried out on 19 days from a viewpoint on the sea wall during the main overwintering season (October 2013–March 2014). Within each area (A, B, C), all birds were identified and abundances recorded at intervals of 30 min for the duration of reef exposure, which was 2.5 h either side of low water. Birds were observed by using a telescope (Swarovski Optik ATS 80 HD, 25–50× wide angle), and the peak abundance of each feeding species was determined over each low-tide period.

2.3 | Behaviour

Measuring the quantity and size of available prey is important for predicting survival of birds (Bowgen, Stillman, & Herbert, 2015). The study focused on five target species: (i) Eurasian oystercatcher (*H. ostralegus*); (ii) Eurasian curlew (*Numenius arquata*); (iii) black-tailed godwit (*Limosa limosa*); (iv) bar-tailed godwit (*Limosa lapponica*); and (v) redshank (*Tringa totanus*). All target species are carnivorous feeders that forage on benthic and epibenthic invertebrates. Populations of curlew, black-tailed godwit, and redshank are of international or national importance in the Colne Estuary (JNCC, 2017). Foraging behaviour was recorded using a video camera (Pentax K30 DSLR) mounted on the telescope, and random individual birds were observed and recorded for 2–3 min in each area. Analysis of videos (Supporting Information Table S1) was carried out on a PC using Windows Media Player. The species "pecking rate" on potential prey and feeding "success" rate were measured over the duration of each video, which was confirmed if the prey was visibly removed and swallowed. The size of prey items was initially measured as a proportion of the lengths of the bird's beak, and then allocated an actual length category based on bird bill lengths. The prey size was then converted to ash-free dry mass (AFDM) using regression lines from Thomas et al. (2004).

2.4 | Prey availability

Samples of benthic fauna were obtained in September 2013, which represents the commencement of the winter feeding period for many migratory bird species. In each of the three areas A, B, and C, a predefined sampling grid of approximately 20 m × 40 m was established within which 15 sampling points were located approximately 10 m apart. At low tide, sampling of the Pacific oyster reef (site B) was carried out in two stages. At each sampling point, oysters were removed within a 25 cm × 25 cm quadrat (0.0625 m^2) and oysters together with any trapped sediment were placed into plastic bags. Upon removal of the oysters, three cores (10 cm diameter, 15 cm depth) of the underlying sediment were taken using a metal corer. Three cores were also obtained at each sampling point from site C using a similar procedure. At the mudflat (site A), three full cores were obtained at each sampling point by boat at high tide using a metal cylindrical suction corer (10 cm diameter, 15 cm depth). All core samples and samples of oysters were washed through a 0.5 mm mesh sieve and fixed with 4% formal saline. In the laboratory, samples were washed through with clean water and all invertebrates were "picked" and placed into 70% ethanol (industrial methylated spirits). All specimens were identified to species level, enumerated, and measured with calipers to the nearest millimetre except for worms <10 mm, which were grouped into this size category. The AFDM of each individual prey item was determined from linear regression equations of size and AFDM in Thomas et al. (2004).

To establish the size-frequency of the Pacific oyster population, the maximum shell length of live Pacific oysters collected from quadrats was measured to the nearest millimetre. To determine AFDM per square metre of the Pacific oysters, samples of different sizes were collected (n = 113), the shell length was measured, and the contents extracted and placed in a muffle furnace at 550°C. Upon removal from the furnace, each oyster was weighed and the relationship between shell length and AFDM was calculated by regression. From data obtained on the size and density of live oysters on the reef the AFDM per square metre of the different size classes of oysters was calculated.

At each sampling point, an additional core was taken for analysis of sediment organic content and particle size distribution. The core samples from the oyster reef were obtained from beneath the oysters; that is, oysters were removed from the surface prior to obtaining the cores. Sediment samples were initially frozen (−5°C) within 24 h and then defrosted and mixed thoroughly prior to analysis. Samples were dried at 80°C and then placed in a muffle furnace at 560°C for 48 h. The percentage organic content of each sample from areas A, B, and C were determined from loss on ignition. Samples were then passed through a 2 mm mesh sieve and all particles >2 mm were retained and weighed. The remainder of particles were passed through a laser diffraction particle analyser (Mastersizer 3000, Malvern, UK) and the proportion of each size class determined.

2.5 | Statistical analysis

Statistical analysis was carried out using SPSS and PRIMER-e version 6 (Clarke & Gorley, 2006). The mean benthic prey biomass, bird abundances, intake rates, and species richness of the bird feeding assemblage at the three sites were compared using a one-way analysis of variance (ANOVA) followed by Tukey post-hoc tests. Where statistical assumptions could not be met and data could not be transformed, then analysis was conducted using a nonparametric Kruskall–Wallace test. Ordination using nonmetric multidimensional scaling (nMDS) was used to produce a graphical representation of the bird feeding assemblages based on Bray–Curtis similarity measures calculated using square-root-transformed data in PRIMER. Analysis of similarity (ANOSIM) was used to test for statistical differences in the bird feeding assemblage in each area.

2.6 | Individual-based modelling

To predict the impact of reef clearance on the winter survival of birds, the individual-based model MORPH (Stillman, 2008; Stillman & Goss-Custard, 2010; Stillman, Railsback, Giske, Berger, & Grimm, 2015) was parameterized for the areas of mudflat, oyster reef, and cleared oyster. Full details of MORPH's assumptions and how it was parameterized are given in the Supporting Information, and so just brief details are given here. MORPH follows the individual decisions of each animal within a population as it attempts to meet its daily energy requirements by feeding in the different locations and on the prey that maximize its rate of energy consumption. MORPH predicts the tidal changes in the distribution of animals, the percentage of time spent feeding to meet energy requirements, changes in body mass, and end-of-winter survival. The model was parameterized for common birds within the feeding assemblages observed in the study areas: dunlin (*Calidris alpine*), ringed plover (*Charadrius hiaticula*), redshank, turnstone (*Arenaria interpres*), bar-tailed godwit, black-tailed godwit, Eurasian oystercatcher, and Eurasian curlew. The model comprised the three intertidal patches observed during the field study: mudflat, oyster reef, and cleared oyster reef. Three other notional patches

were included: a roost to which birds moved when they were not feeding during a time step, a terrestrial patch (fields), and alternative mudflat on which some species fed to supplement their food consumption. Intertidal habitats were available to the birds while they were exposed by the tide, the roost was always available, and the fields were available during the hours of daylight. The following prey types were included in the model: marine worms (e.g. ragworm *Hediste diversicolor*), cockles (*Cerastoderma edule*), winkles (*Littorina* sp.), mud snails (*Peringia* sp.), mussels (*Mytilus edulis*), Pacific oysters (*M. gigas*), crustacean's, including crabs (*Carcinus maenas*), other bivalves, and earthworms (*Lumbricus* sp.). Size ranges of prey consumed by shorebirds are shown in Supporting Information Table S2. The model included the tidal exposure of each of the intertidal areas and prey species abundance and size distribution as measured from the core sampling (Supporting Information Table S3). Bird species population sizes and body masses used in the model are in Supporting Information Table S4. Parameters used to calculate the energy expenditure by birds are in Supporting Information Table S5. Simulations were run with the present-day oyster reef area and with future changes in reef area resulting from clearance or new settlement.

3 | RESULTS

3.1 | Sediment analysis

Sediment samples from each area were dominated by fine clay and silt fractions (Supporting Information Figure S1), and particle size frequency in the three areas showed no statistically significant differences Larger particles (>2 mm) from the cleared area (C) mainly consisted of shell fragments, yet the percentage dry masses of larger particles were comparable between the three areas (23–31%) and were not significantly different. However, there was significantly less ($p < 0.001$) percentage organic content of the mud in the cleared area (4.3%) compared with the other sites (A, 7.2%; B, 8.8%).

3.2 | Benthic invertebrate prey

The reef largely consists of oysters more than 70 mm length (Figure 3) which is usually attained in 1–2 years (Fey, Dankers, Steenbergen, & Goudswaard, 2010). Smaller oysters, which are most likely to be preyed upon by shorebirds, occurred at relatively low density. Amongst the live oysters were empty oysters and dead shells of varied size. Collectively, the core samples from the cleared area had the greatest macro-invertebrate species richness (22 species), followed by samples beneath the oyster reef (13 species) and mudflat (nine species), yet the oyster washings revealed a total of 37 species. The mudflat was characterized by a high density of small oligochaete worms (*Tubificoides* spp.) and low densities of polychaete worms and the bivalve *Limecola balthica* (Table 1). Larger polychaetes (Nereididae, Nephtyidae, and *Cirriformia tentaculata*) were found in both cores and oyster washings from the oyster reef and cleared reef. Mussels (*M. edulis*) and the Manila clam (*Ruditapes philippinarum*) were present amongst the oysters, albeit at low density. A broader range of molluscs were found in the cleared area, including *Peringia ulvae*, *Abra tenuis*,

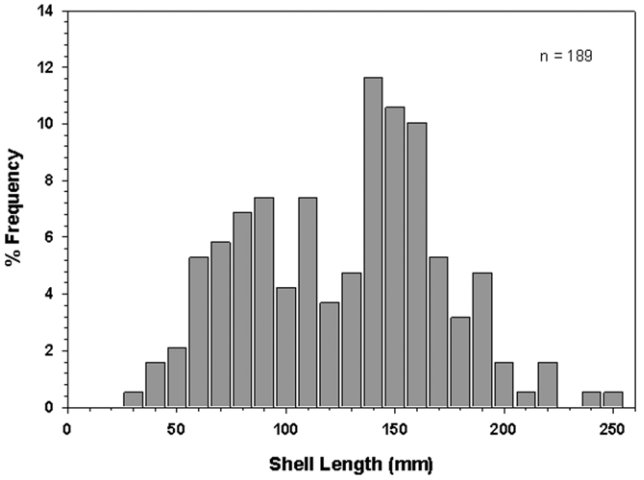

FIGURE 3 Length frequency of live oysters (n = 189) on the reef (area B) sampled within 25 cm × 25 cm quadrats (n = 15) located on a 5 m × 3 m grid in May 2013. Mean density of live oysters was 202 m^{-2}

and *Cerastoderma edule*. Crustacea, particularly the shore crab *C. maenas*, were most prominent on the reef. Excluding Pacific oysters, mean values of benthic prey biomass (g AFDM m^{-2}) between the three areas (Figure 4) were significantly different ($p < 0.001$), with pairwise tests indicating significant differences between the mudflat and the other two areas (A vs B, $p < 0.001$; B vs C, $p = 0.66$; A vs C, $p = 0.002$).

3.3 | Field observations of birds

Seventeen species of birds were observed across the three study areas during the 19 surveys between October 2013 and March 2014. All species except lapwing (*Vanellus vanellus*) and mute swan (*Cygnus olor*) were observed feeding in one or more study areas. Black-tailed godwits were more prevalent in the early and later winter periods, and there was a significant increase in numbers of shellduck and lapwing between January and March. On the ebbing tide, most of the birds "arrived" from field roosts or other mudflat feeding areas at the time the oyster reef was exposed, as opposed to following the water edge from upper levels of the adjacent mudflat. Apart from occasional boat-wash, there were no visible or audible disturbances to birds in any of the feeding areas during the study. There was hardly any use of the sailing club slipway during the winter period, and when it did occur there was no visible impact on bird numbers or foraging behaviour. The mudflat (site A) was used extensively by black-tailed godwits and bar-tailed godwits, although they did not appear to consume large prey; redshanks were observed foraging in small groups or singly. Curlew were seen frequently and occasionally observed to consume large polychaete worms (>100 mm). It was unclear what shellduck (*Tadorna tadorna*) were feeding upon as populations of their preferred food, the mud snail *Peringia ulvae*, were low. Oystercatchers were only seen occasionally on the mudflat, and when observed they were consuming worms.

On the Pacific oyster reef (site B), a large variety of bird species were observed, including oystercatcher, curlew, turnstone, dunlin, redshank, and ringed plover; however, very few black-tailed and

TABLE 1 Mean density of the large and most common benthic invertebrate fauna found in samples that comprise important bird prey

	Mean density (m^{-2})			
		Oyster reef (area B)		
Taxon	Mudflat (area A)	Cores	Washings	Cleared area (area C)
Annelida				
Alitta succinea	0	0	1	0
Alitta virens	0	0	3	0
Cirriformia tentaculata	0	93	35	43
Eunereis longissima	0	9	13	0
Hediste diversicolor	9	0	5	280
Neoamphitrite figulus	0	9	1	0
Nephtys hombergii	26	0	1	17
Tubificoides benedii	3074	323	939	314
Crustacea				
Carcinus maenas	0	9	60	9
Corophium volutator	0	68	50	0
Cyathura carinata	0	0	0	17
Gammarus locusta	0	9	16	0
Melita palmata	0	0	65	9
Mollusca				
Abra tenuis	0	0	0	17
Cerastoderma edule	0	0	0	9
Limecola balthica	60	0	0	17
Mytilus edulis	0	0	5	0
Peringia ulvae	17	0	0	43
Ruditapes philippinarum	0	0	1	0

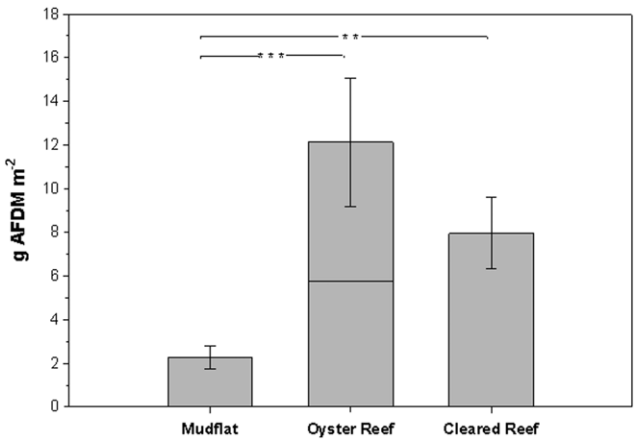

FIGURE 4 Mean benthic invertebrate biomass (excluding Pacific oysters) within the three study areas. Error bars show plus/minus SE. The proportion of biomass in the oyster reef obtained from the washings and cores is shown above and below the horizontal bar respectively. Significant differences are denoted as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

bar-tailed godwits were seen. Black-headed gulls (*Chroicocephalus ridibundus*) were recorded in large numbers, though mainly roosting. Oystercatcher and curlew were frequently observed feeding on large polychaete worms (>100 mm) and shore crabs (*C. maenas*). Herring gull and black-headed gull would occasionally follow curlew and oystercatcher to steal prey. Herring gulls were also observed dropping Manila clams (*Ruditapes phillipinarum*), cockles (*C. edule*), and Pacific oysters on the reef to crack shells. Brent geese (*Branta bernicula*) were seen feeding over the reef when it was partially submerged; it is possible that they were grazing on algae (*Ulva* spp. and *Fucus* spp.), which had colonized the reef extensively. Lapwings were observed roosting but not feeding on the reef. This was particularly evident during high winds, where they may have benefited from shelter provided by the large oysters. No species favoured the cleared area (site C) specifically. Birds observed feeding included oystercatcher, curlew, redshank, turnstone, ringed plover, and grey plover (*Pluvialis squatarola*) Oystercatchers and curlew were observed primarily on the perimeter of this site, feeding on worms and crabs associated with small clumps of *M. gigas* that had either remained following clearance or had broken off parts of the reef.

3.4 | Comparison of bird abundance and diversity

To determine whether the overall feeding assemblage of birds was different between the three areas, a one-way ANOSIM was conducted using the peak counts of all feeding species across the 19 surveys. Birds that were observed roosting were excluded from the analysis. The nMDS plot (Figure 5) and pairwise comparison tests indicate that the species assemblages between each of the three areas are significantly different from each other (Table 2), with variation in dispersion also evident. The individual bird species contributing to the separation between the communities were analysed using the similarity percentages routine (SIMPER) in PRIMER (Table 3). Species contributing most to the mean dissimilarity between the mudflat and oyster reef were

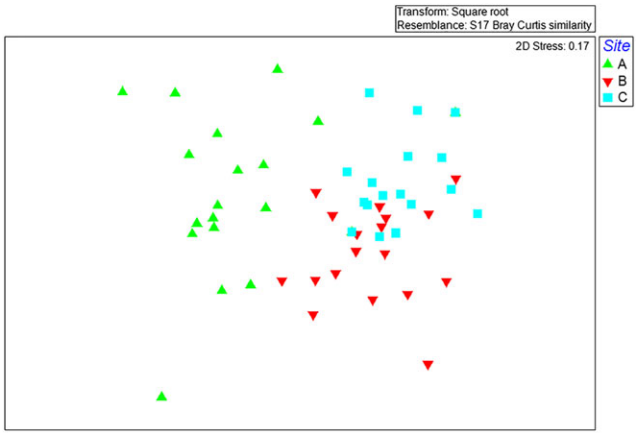

FIGURE 5 An nMDS plot showing different feeding bird assemblages across the three sites (A, mudflat; B, Pacific oyster reef; C, cleared reef). Data based on mean count of each species per survey (n = 19). Each point represents a survey on one of the three areas. One-way ANOSIM showed significant separation between the assemblages (global R = 0.41, p = 0.001, 999 permutations). See Table 2 for pairwise comparisons

TABLE 2 Pairwise tests on sample data from one-way ANOSIM performed on bird assemblage. Data based on mean count of each species per survey (n = 19). A – mudflat; B – oyster reef; C – cleared reef. Each pairwise test between each of the different areas showed significant differences in assemblages

Groups	R	p
A vs B	0.51	0.001
A vs C	0.58	0.001
B vs C	0.12	0.003

shellduck and black-tailed godwit, which were mostly on the mudflat. Between the cleared reef and oyster reef, the greatest mean dissimilarity was the abundance of herring gulls, which favoured the cleared area, whereas oystercatcher and redshank were most abundant on the reef. Compared with the mudflat, oystercatchers were significantly more abundant on both the oyster reef and cleared area (Figure 6). The highest abundance of redshank was recorded on the mudflat, where mean numbers were significantly greater than on the cleared area (Tukey pairwise test following one-way ANOVA, p = 0.029), but not significantly different to the oyster reef. Curlew was recorded independently foraging on all sites, and no statistically significant difference in abundance was found between areas. Mean numbers of black-tailed godwit were significantly higher on the mudflat than on the reef (Tukey pairwise test following ANOVA, p = 0.012), where they were often observed feeding in large groups (maximum 32), and also significantly higher than on the cleared area (Tukey pairwise test, p = 0.01). There was no significant difference in the abundances of bar-tailed godwit between sites, and numbers were generally low. Overall, there was no significant difference in species richness between the three areas (Kruskall–Wallace one-way ANOVA, H = 4.96, df = 2, p = 0.084). However, owing to the larger flocks of black-tailed and bar-tailed godwits and shellduck, the mean peak counts of all feeding bird species were significantly higher on the mudflat than on the other two areas (Figure 6).

3.5 | Feeding success rates

From the video analysis, the oystercatcher, redshank, and curlew were seen to feed within each of the three areas; however, for redshank it was difficult to confirm whether the food had been

TABLE 3 Bird species contributing most to the dissimilarity of pairs of each of the three habitats using the SIMPER routine in PRIMER: (i) mudflat and oyster reef; (ii) mudflat and cleared reef; and (iii) oyster reef and cleared reef. Only top four feeding species shown. Abundance data are square-root transformed

			Dissimilarity			
Species	Mean abundance		Mean	SD	Contribution (%)	Cumulative (%)
(i) Mudflat (area A) and oyster reef (area B)						
	Area A	*Area B*				
Shellduck	1.56	0.00	18.65	1.11	24.66	24.66
Black-tailed godwit	1.12	0.13	12.04	0.97	15.92	40.58
Redshank	0.87	0.85	9.24	1.22	12.21	52.79
Oystercatcher	0.08	0.65	7.82	1.45	10.34	63.13
(ii) Mudflat (area A) and cleared reef (area C)						
	Area A	*Area C*				
Shellduck	1.56	0.00	19.22	1.12	25.04	25.04
Black-tailed godwit	1.12	0.06	12.41	0.98	16.17	41.21
Herring gull	0.34	1.04	10.12	1.30	13.18	54.39
Redshank	0.87	0.49	8.96	1.25	11.67	66.06
(iii) Oyster reef (area B) and cleared reef (area C)						
	Area B	*Area C*				
Herring gull	0.46	1.04	11.58	1.39	21.53	21.53
Redshank	0.85	0.49	9.59	1.31	17.83	39.36
Oystercatcher	0.65	0.56	6.56	1.08	12.20	51.55
Turnstone	0.27	0.29	5.79	1.03	10.76	62.32

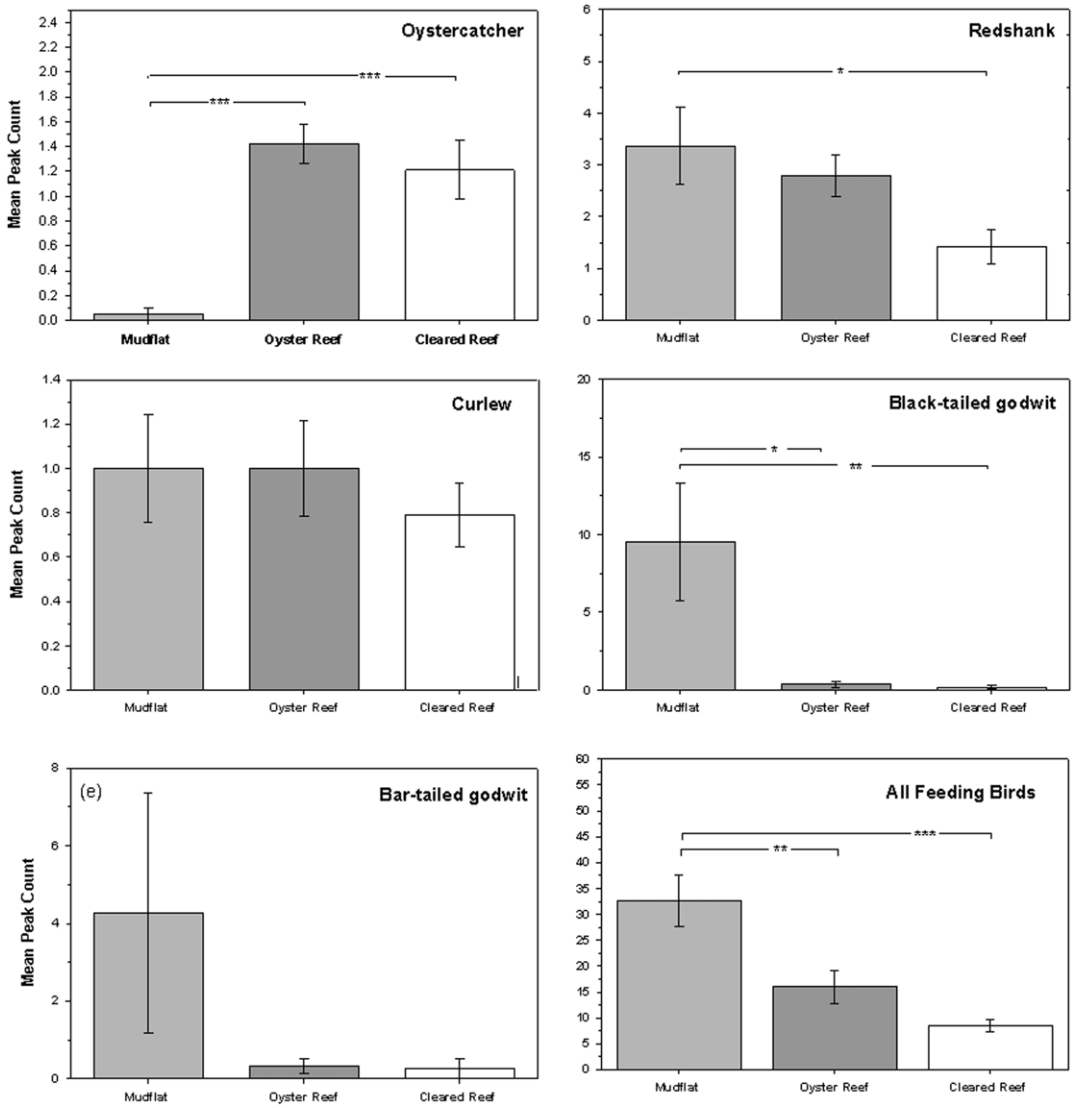

FIGURE 6 Mean of "peak" low-tide counts (n = 19) for selected species feeding across each of the study sites between September 2013 and March 2014. Counts made on spring tides. Each study site is approximately 6000 m^2. Error bars show plus/minus SE. Significant differences are denoted as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

swallowed and ingested. Pairwise tests following one-way ANOVA of the mean number of prey captures (visible swallowing per minute) observed showed that success rates of both curlew and oystercatcher were significantly greater on the reef than on the other two areas (Figure 7). For redshank, there were no statistically significant differences in feeding success between areas (p = 0.91), although the number of videos examined was relatively small. There were too few observations of both black-tailed and bar-tailed godwits feeding on the reef or cleared area for any meaningful comparison of feeding success rates.

From the videos it was only possible to determine the type of prey caught across each of the three study areas for oystercatcher and curlew, as redshank prey is smaller, was quickly swallowed, and the birds were often hidden behind oysters. Both birds are visual feeders, and they predated primarily on polychaetes in each of the three areas (Figure 8), although oystercatchers were seldom observed feeding on the mudflats. Only oystercatchers were observed prising open and feeding on the Pacific oysters; however, the number of birds was small (n = 3). These included birds feeding on the "cleared" reef; some clumps of oysters persisted at lower tidal levels, where access to hand-gatherers is more limited. Both curlew and oystercatcher were observed to target the bottom of oyster clumps, where worms could be found quickly and extracted relatively easily. Although not quantified, the edges of the reef, rather than the top, appeared to be favoured most, where densities of oysters are less. The second most favoured prey of both species was shore crabs (*C. maenas*) that were found in high numbers on the oyster reef, with large individuals (>40 mm across carapace) taken together with smaller sizes. Occasionally, larger crabs taken by oystercatchers were stolen by herring gull, although not all the crab appeared to be eaten. Curlew obtained proportionally more crabs than oystercatchers, and this was occasionally supplemented by shrimps obtained in pools that formed on the reef and in channels around the edges of the reef. On the mudflat, large worms in excess of 100 mm length were occasionally taken by curlew.

The biomass intake rate of oystercatcher and curlew was calculated from the size and type of prey observed in the videos analysis

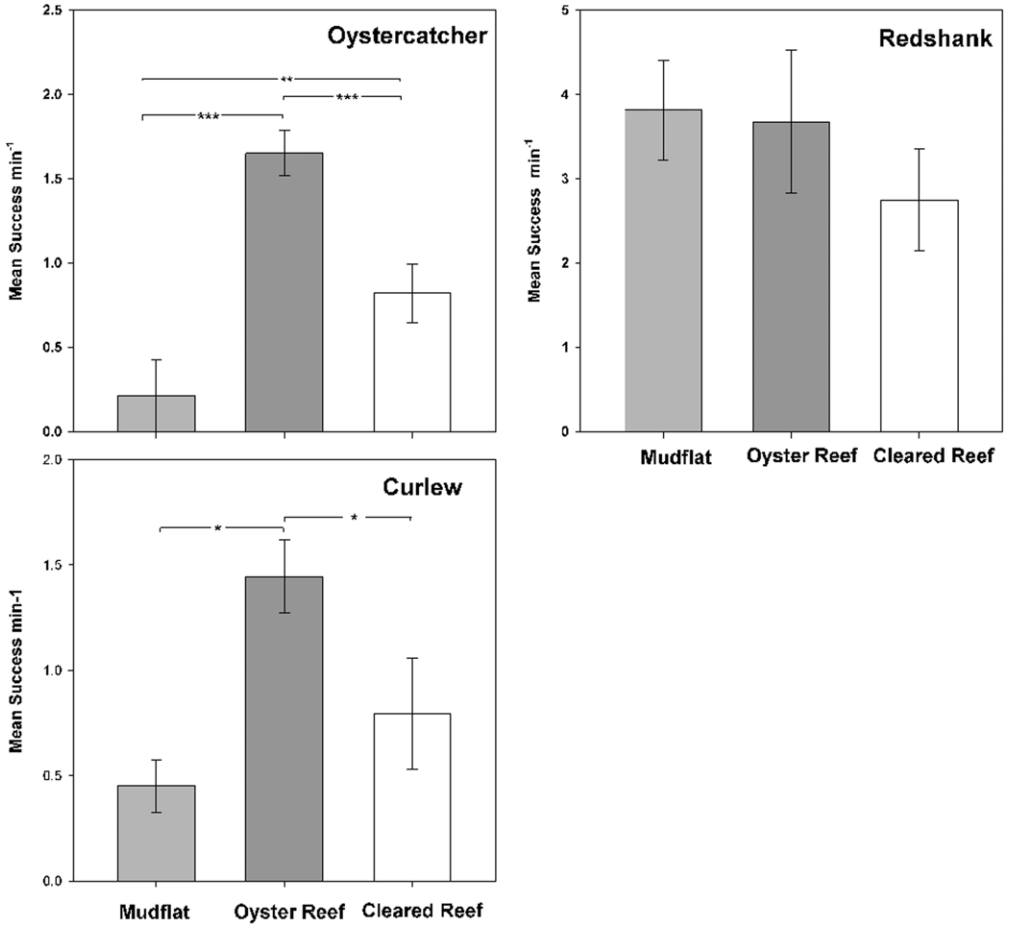

FIGURE 7 Mean feeding success rate for oystercatcher, curlew, and redshank across the three areas. Error bars show plus/minus SE. Significance levels are denoted as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

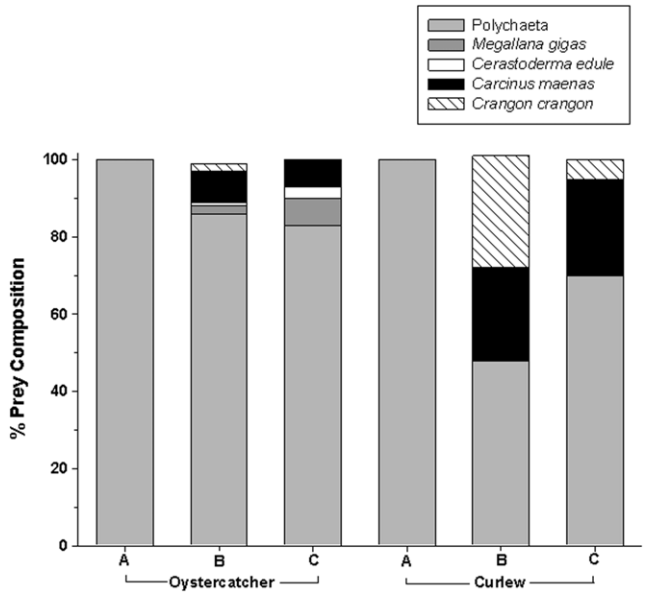

FIGURE 8 Percentage composition of prey types observed in feeding oystercatcher and curlew determined from video analysis (A – mudflat; B – Pacific oyster reef; C – cleared reef). See Supporting Information Table 1 for number of videos analysed in each area

(Figure 9). For both bird species, the intake rate was greatest on the oyster reef, although significant differences in intake rate across the three areas were found for curlew only (Kruskal–Wallace one-way ANOVA, $H = 6.856$, df = 2, $p = 0.032$), with pairwise tests showing differences between the mudflat and the reef ($p = 0.05$).

3.6 | Predictions of the present-day model

The food resources in the model were not able to support bar-tailed godwit and black-tailed godwit throughout winter in all simulations (Table 4). For these species, other prey and habitats not included in the model must be available in the real system to allow these birds to survive throughout winter. Additionally, species were included in the model throughout the course of winter, whereas godwits in particular were not present throughout in the real system. Only dunlin, ringed plover, turnstone, oystercatcher, curlew, and redshank were supported over the winter.

With the exception of oystercatcher, most species were predicted to need to spend about 50% of the time feeding in order to meet their energy requirements. This included the time that the birds needed to roost; for example, when no feeding habitats were available. Oystercatcher spent about 30% of the time feeding, implying that this species was able to meet its energy requirements by feeding for less time. In model simulations, marine worms, crustacea, and earthworms comprised the main prey items in the diets of all species except oystercatcher. Oystercatchers have a wider range of prey species than other shorebirds, and in the model also consumed mussels, winkles,

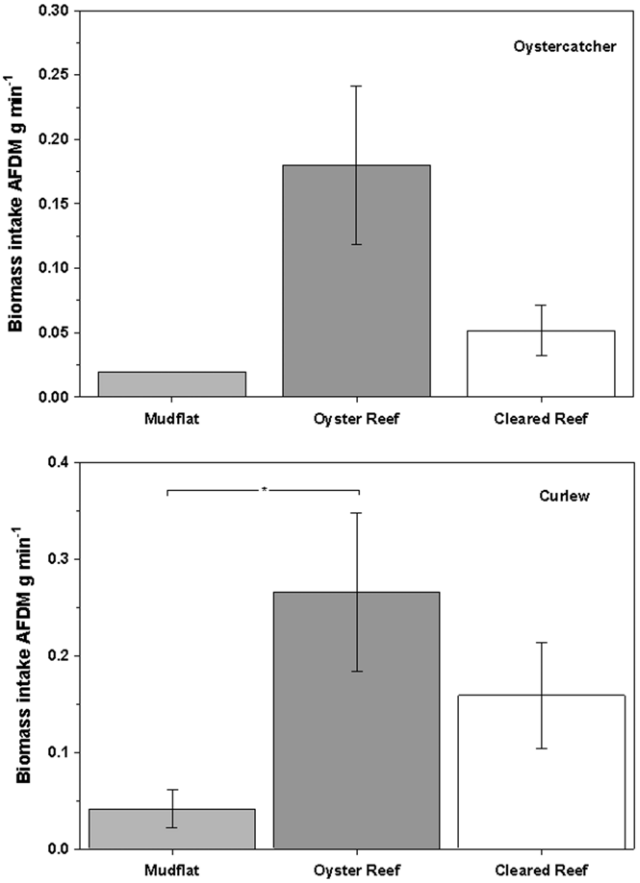

FIGURE 9 Prey biomass intake rate of oystercatcher and curlew across each habitat at Brightlingsea during winter 2013–2014. Data obtained from video analysis of feeding behavior and observed prey. Error bars show plus/minus SE. Significance levels are denoted as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

and oysters. The larger range of prey consumed by oystercatcher meant that relatively more food was available to this species, and competition for food resources was less than the remaining birds.

The oyster reef, alternative mudflat, and fields were the only feeding patches exploited by birds in the model. The mudflat was not exploited because the alternative mudflat was available at the same time and provided a higher biomass of prey. The cleared reef was available at the same time as the oyster reef but was not exploited as it had a lower biomass of prey within the size ranges consumed by each species. In the real system, birds tended to exploit the cleared reef, whereas they did not in the model. This implies that some prey exploited by birds on the cleared reef may have been underestimated in the field survey; for example, small-scale patches of high prey abundance, such as clumps of oysters that had not been cleared. Alternatively, it is possible that the real birds were less selective than the model birds (i.e. the model birds always occupied the patch on which their energy assimilation rate was greatest, but real birds may have occupied any patch in which energy assimilation rate was above a threshold level).

3.7 | Predicted effect of changes in reef area

In simulations that decreased reef area it was assumed that reef was replaced by the cleared reef habitat and the same prey abundance. In simulations that increased the reef area it was assumed that the cleared reef habitat was replaced by reef, in effect simulating the situation before the reef was cleared from this area. The model predicted the effect of changes in reef area on the maximum number of birds of each species that could be supported (found by increasing the number of birds in simulations until no individuals of a species are able to survive). Results (Table 5) are presented for dunlin, ringed plover, turnstone, redshank, oystercatcher, and curlew, as the remaining species were not supported throughout the course of winter.

The model predicted that up to twice the observed number of ringed plover and turnstone, four times the number of dunlin, and five times the number of redshank, curlew, and oystercatcher could be supported. Removing the reef reduced the number of redshank, oystercatcher, and curlew that could be supported, but it did not change the number of dunlin, ringed plover, and turnstone that could be supported. This implies that a greater amount of redshank, oystercatcher, and curlew prey was found in the reef than in the cleared reef. Increasing the reef area (by removing the cleared area and "replacing" it with reef) increased the number of oystercatcher and turnstone that could be supported, also implying that a greater amount of prey was found in the reef than in the cleared reef. The key prey of turnstone, redshank, oystercatcher,and/or curlew that were more abundant in the reef were marine worms, oysters and mussels (oystercatcher prey only), and crustacea.

4 | DISCUSSION

Although the study was limited to a single site, field observations showed that the presence of a Pacific oyster reef can affect the distribution and feeding behaviour of coastal birds. Results from the model also indicated that the reef can provide valuable supplementary feeding areas for some species, such as curlew and oystercatcher, and yet was avoided by others, notably the godwits. Densities of birds were generally comparable to other estuaries (Goss-Custard et al., 1991); however, compared with the uncolonized mudflats, there was a higher frequency and abundance of oystercatchers and herring gulls on the oyster reef and cleared area, and fewer black-tailed and bar-tailed godwits. For oystercatcher, these differences can be attributed to the greater amount of benthic prey available on the oyster reef and cleared areas. Both oystercatcher and curlew were observed to target the undersides of oyster clumps searching for food, and they had greater success and biomass intake rates on the oyster reef and cleared reef than on the mudflat. Polychaetes dominate the prey of both species, although curlew were also seen foraging on mobile fauna within small pools and creeks on the reef. These features, which may add important diversity to the foraging potential of the reef, were prevalent and yet were not accounted for in the model. However, should there be higher oyster settlement, these features may eventually become colonized and lost. It was observed that some very large worms taken by curlew and oystercatcher were not sampled within sediment cores, and variance between observed and simulated feeding behavior could suggest that benthic food resources of the reef may have been underestimated. It is recommended that longer (30 cm) cores are utilized or that larger areas are dug out below the

TABLE 4 Predictions of the present-day model

Species	Mean no. individuals on each patch	Mean no. individuals consuming each diet	Mean proportion of time spent feeding	All individuals supported throughout winter?
Dunlin	AM = 0.54 F = 0.05 *R* = 0.41	MW = 0.54 EW = 0.05	0.53	Yes
Ringed plover	AM = 0.54 *R* = 0.46	MW = 0.54	0.52	Yes
Turnstone	OR = 0.73 AM = 0.35 *R* = 0.92	MW = 0.35 CR = 0.73	0.50	Yes
Redshank	AM = 4.33 *R* = 3.67	MW = 4.33	0.42	Yes
Black-tailed godwit	AM = 4.24 F = 3.12 *R* = 2.63	MW = 4.24 EW = 3.12	0.70	No
Bar-tailed godwit	AM = 2.67 *R* = 2.31	MW = 2.67	0.54	No
Oystercatcher	OR = 1.30 AM = 0.19 *R* = 1.51	MW = 0.19 M = 0.05 O = 0.95 W = 0.28 CR = 0.02	0.30	Yes
Curlew	OR = 0.30 AM = 1.32 F = 0.29 *R* = 1.09	MW = 1.32 CR = 0.30 EW = 0.29	0.58	Yes

Patch name codes: MF – mudflat; AM – alternative mudflat; OR – oyster reef; CR – cleared reef; F – field; R – roost.

Diet codes: MW – marine worms; M – mussels; C – cockles; O – oysters; W – winkles; OM – other molluscs; CR – crustacea; P – *Peringia*; EW – earthworm.

TABLE 5 Predicted effect of clearance of the oyster reef to the maximum number of individuals of each species that can be supported. The present-day simulations included the presence of both the reef and cleared area. The values represent the increase in population size from baseline (i.e., 31 individuals across all species) at which all individuals of a species are supported. Predictions are only presented for dunlin, ringed plover, turnstone, redshank, oystercatcher, and curlew as other species were not supported throughout winter even with the present-day observed population size

	Clearing current oyster reef (12 000 m^2 cleared reef)	Present day (6000 m^2 cleared reef and 6000 m^2 oyster reef)	Reef not removed (12 000 m^2 oyster reef)
Dunlin	×4.0	×4.0	×4.0
Ringed plover	×2.0	×2.0	×2.0
Turnstone	×2.0	×2.0	×2.5
Redshank	×4.5	×5.0	×5.0
Oystercatcher	×4.0	×5.0	×6.5
Curlew	×4.5	×5.0	×5.0

oysters to establish more accurately the extent of larger worms that occupy deeper levels. Some oysters that had remained on the "cleared" area or had been dislodged from other reefs were targeted by oystercatcher and curlew when foraging for worms and crabs. In Argentina, Escapa et al. (2004) found that epifaunal species were greater within Pacific oyster reefs and had a positive effect on the abundance of certain foraging birds; for example, American oystercatcher (*Haematopus palliatus*) and lesser yellowlegs (*Tringa flavipes*). However, no difference was observed in the feeding efficiency of these species between colonized and uncolonized areas.

There was very little evidence of birds feeding directly on *M. gigas*, even by oystercatchers. Studies in the Wadden Sea have indicated that the only birds to feed directly on *M. gigas* are herring gulls and oystercatchers (Fey et al., 2010; Markert et al., 2010; Markert, Esser, Frank, Wehrmann, & Exo, 2013), although predation on *M. gigas* by birds is generally low (Troost, 2010). Oystercatchers were observed prising open smaller *M. gigas* on the oyster reef at Brightlingsea, which is possibly the first reported observation of its kind on wild *M. gigas* in the UK. Yet oystercatchers have learned to feed on *M. gigas* in the Wadden Sea (Cadée, 2008b; Scheiffarth, Ens, & Schmidt, 2007) and

Oosterschelde Estuary (Baptist, 2005). Markert et al. (2013) found that colonization of mussel beds by *M. gigas* had a positive impact on the feeding rates of oystercatcher and curlew and concluded that successful oyster recruitment will enhance the suitability of the feeding ground. Optimal foraging and feeding were observed in the "carpet reefs," where densities of live *M. gigas* are 680 m^{-2} (>25 mm shell length) as opposed to "dense reefs" characterized by a live oysters density of 884 m^{-2}. Densities of live oysters on the reef at Brightlingsea are considerably lower (200 m^{-2}), and most are too large for feeding oystercatchers, which prefer shell lengths between 20 and 60 mm (Markert et al., 2013). It is possible that because densities of Pacific oysters are relatively low and require more handling time, most oystercatchers at Brightlingsea continue to feed on larger polychaete worms and crabs, which are more abundant amongst the oysters.

Both black-tailed and bar-tailed godwits appeared to avoid feeding on both the oyster reef and cleared reef. Unlike oystercatchers and curlew, both species forage by "touch and smell" and, therefore, keep their bills in the mud for longer periods in search of prey. Although polychaetes of suitable size for godwits were found within the oyster reef and cleared reef, clumps of oysters may present significant obstacles to their mode of feeding and birds may risk damage to bills, which are relatively slender. It was not possible to survey benthic assemblages or bird feeding behavior prior to the formation of the oyster reef, so preferences for one area compared with another must be considered with caution. Interspecific interactions between birds may also have an influence on distribution, and this was taken into account in the model. Yet more specific interactions, such as that observed by gulls that appeared to associate with curlew and oystercatcher and steal larger prey such as crabs and clams, were not included in the model.

The control of non-native species in open marine systems is one of the most challenging aspects of environmental management (Bax et al., 2001). However, as some birds avoided the reef, it might be possible in some situations to clear areas in an attempt to encourage a wider range of species, depending on the conservation objectives of the site. Recovery of benthic invertebrate assemblages from dredging disturbances varies according to local environmental conditions, gear type, and substrate (Ferns et al., 2000; Hall & Harding, 1997) and the feeding quality of cleared areas is likely to change over time. Following mechanical dredging on intertidal mudflats, a significant recovery of non-target species abundance is highly variable and could be up to 500 days, and a significant recovery of species biomass could exceed this time period (Clarke et al., 2017). After 6 months, the higher benthic macroinvertebrate biomass measured in the cleared area in comparison with the undisturbed mudflats could suggest that the removal of the oysters did not significantly disturb the benthos that had become established beneath. Alternatively, oyster clearance could have stimulated species settlement and growth in this area, or that the biomass prior to oyster settlement in this region was greater than other parts of the mudflat. This particular clearance scenario might simulate disturbance from recurrent interventions should it be appropriate to remove Pacific oyster reefs from mudflat areas if wild settlement increases. Clearly, a longer period of observations in each area to monitor changes throughout the recovery phase would be very beneficial. If some clearance was considered desirable by management authorities—for example, if wild settlement increased—then it may be practical to rotate clearances depending on the location of reefs and usage by birds. Once cleared by dredge, it may be possible to partially contain settlement by hand-picking to minimize disturbance to the benthos.

Currently, the area of Pacific oyster reef in the Colne Estuary is relatively small, albeit significantly different to proximate intertidal areas that have been designated for protection. However, with rising temperatures, spawning and settlement of Pacific oysters is predicted to increase, and it is possible that more reefs will become established in the region. The impact of such a small area of oyster reef on shorebirds is difficult to establish; however, it appears it could represent a valuable supplementary feeding area compared with adjacent, less productive mudflats. Simulations of feeding behaviour using the computer model MORPH showed the reef was utilized by a variety of bird species over the winter, demonstrating preference for this area over other adjacent habitats, including the adjacent mudflat, which had relatively low amounts of prey. As regional impacts of Pacific oyster reefs are still unknown (Herbert et al., 2016), it would be useful to increase the scale of the model and investigate the effects of changing the initial quality of the habitats, which should include a better characterization of the value of other nearby feeding areas, including terrestrial sources. Modeling the impacts of larger scale dredging on benthic prey resources and bird survival would help to understand the likely benefits of these measures on species of conservation concern.

As wild Pacific oysters are regarded by policy-makers as an invasive species, the value of reefs as supplementary feeding areas for some shorebirds of conservation concern creates a management conundrum. The macrobenthic diversity was much greater on the reef than in nearby mudflats, yet the assemblage included several other non-native species, including the invasive crab *Hemigrapsus takanoi* (Wood et al., 2015). Had a native mussel reef (*M. edulis*) become established instead of Pacific oysters, then both curlew and particularly oystercatcher might also have benefited, and possibly other bird species (Goss-Custard, 1996; Goss-Custard et al., 2006; Scheiffarth et al., 2007). However, it is important to consider the environmental context, as there is considerable regional variation in the abundance of food in estuary mudflats. In comparison to Poole Harbour and the Exe Estuary on the south coast of England (Caldow et al., 2005), the density and diversity of larger macroinvertebrates in the mudflats of the Colne Estuary at Brightlingsea are low. In terms of available biomass, that measured for the mudflat of Colne is ~2 g AFDM m^{-2} (Figure 4), whereas the mean intertidal biomass for the Severn Estuary is 3.45 g AFDM m^{-2}, for Poole Harbour it is ~16 g AFDM m^{-2}, and for the Exe Estuary it is over 63 g AFDM m^{-2} (Bowgen, 2016). Yet in relative terms, the locally available biomass within the Pacific oyster reef is significantly greater than in the surrounding mudflats. Therefore, the use and conservation value of Pacific oyster reefs as supplementary feeding areas for different birds could be variable and dependent on the local availability of food resources. Additionally, the usage of the reefs might also be affected by the proximity of other disturbances, such as intertidal fisheries and recreation. Clearly, the study would benefit from replication in a wider range of contexts within and between systems.

5 | CONCLUSIONS

The combined field and modelling approach helped to understand the impact and value of non-native Pacific oyster reefs as supplementary feeding areas on intertidal mudflats. In this context, the biomass of food in surrounding mudflats was relatively low, and the oyster reefs provided valuable food resources to some species, including curlew and oystercatcher. However, as other birds appeared to avoid the oyster reefs, it may be desirable to make some clearances to ensure a mosaic of habitats is available to a greater variety of birds. In any case, the trade-off between the disturbance caused by dredging or hand-harvesting and the value of an oyster reef needs to be established. Any apparent beneficial use of non-native species can create a conundrum for environmental agencies, and those species' management needs to be considered carefully amongst a broad range of stakeholder groups, which might include fisheries and harbour authorities. Should wild settlement of Pacific oysters increase as predicted, then decisions concerning the maintenance of reefs as supplementary feeding areas in estuaries would benefit from local and regional observations of their use and bird feeding behaviour.

ACKNOWLEDGEMENTS

The study was funded by Natural England. We are very grateful for the assistance and practical support of Brightlingsea Harbour Master and staff and to the Essex and Kent Inshore Fisheries and Conservation Authority. Oysterman Richard Howard was also extremely helpful and supportive. We also acknowledge help from Ross Wheeler, Wayne O'Brien, and Mareike Vilbrandt. The taxonomic analysis of the oyster washings was carried out by MESL Ltd, Bath. The map (Figure 1) was produced by Harry Manley. We are also grateful to the reviewers who improved the manuscript.

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REFERENCES

Baptist, H. (2005). *Habitattoets proef weghalen oesterbanken in de Oosterschelde. Report no. 2005/19*. Kruisland, Netherlands: Ecologisch Adviesbureau Henk Baptist.

Bax, N., Carlton, J. T., Mathews-Amos, A., Haedrich, R. L., Howarth, F. G., Purcell, J. E., … Gray, A. (2001). The control of biological invasions in the world's oceans. *Conservation Biology*, *15*, 1234–1246.

Bowgen, K. M. (2016). Predicting the effect of environmental change on wading birds: Insights from individual-based models (PhD thesis). Bournemouth University. In *UK*.

Bowgen, K. M., Stillman, R. A. S., & Herbert, R. J. H. (2015). Predicting the effect of invertebrate regime shifts on wading birds: Insights from Poole Harbour, UK. *Biological Conservation*, *186*, 60–68.

Cadée, G. C. (2008a). Herring gulls feeding again on Pacific oysters *Crassostrea gigas* in the Dutch Wadden Sea near Texel. *Basteria*, *72*, 33–36.

Cadée, G. C. (2008b). Oystercatchers *Haematopus ostralegus* catching Pacific oysters *Crassostrea gigas*. *Basteria*, *72*, 25–31.

Caldow, R., McGrorty, S., West, A., le V dit Durell, S. E. A., Stillman, R., & Anderson, S, (2005). Macro-invertebrate fauna in the intertidal mudflats. In J. Humphreys & V. May (Eds), *The ecology of Poole Harbour* (pp. 91–108). Proceedings in Marine Science, vol. 7. Amsterdam, Netherlands: Elsevier.

Clarke, K. R., & Gorley, R. N. (2006). *PRIMER v6: User manual/tutorial*. Plymouth, UK: PRIMER-E.

Clarke, L. J., Hughes, K., Herbert, R. J. H., Esteves, L., & Stillman, R. A. S. (2017). Intertidal invertebrate harvesting: a meta-analysis of impacts and recovery in an important waterbird prey resource. *Marine Ecology Progress Series*, *584*, 229–244.

Escapa, M., Isacch, J. P., Daleo, P., Alberti, J., Iribarne, O., Borges, M., … Lasta, M. (2004). The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in northern Patagonia. *Journal of Shellfish Research*, *23*, 765–772.

FAO. (2016a). FAO year book. Fishery and aquaculture statistics. 2014. Rome, Italy: Food and Agriculture Organization of the United Nations. Retrieved from http://www.fao.org/3/a-i5716t.pdf

FAO. (2016b). Species fact sheets: *Crassostrea gigas* (Thunberg, 1793). Rome, Italy: Food and Agriculture Organization of the United Nations. Retrieved from http://www.fao.org/fishery/species/3514/en

Ferns, P. N., Rostron, D. M., & Sima, H. Y. (2000). Effects of mechanical cockle harvesting on intertidal communities. *Journal of Applied Ecology*, *37*, 464–474.

Fey, F., Dankers, N., Steenbergen, J., & Goudswaard, K. (2010). Development and distribution of the non-indigenous Pacific oyster (*Crassostrea gigas*) in the Dutch Wadden Sea. *Aquaculture International*, *18*, 45–59.

Goss-Custard, J. D. (Ed.) (1996). *The oystercatcher. From individuals to populations*. Oxford, UK: Oxford University Press.

Goss-Custard, J. D., Burton, N. H. K., Clark, N. A., Ferns, P. N., McGrorty, S., Reading, C. J., … Worrall, D. H. (2006). Test of a behavior-based individual-based model: Response of shorebird mortality to habitat loss. *Ecological Applications*, *16*, 2215–2222.

Goss-Custard, J. D., Warwick, R. M., Kirby, R., McGrorty, S., Clarke, R. T., Pearson, B., … Rose, R. J. (1991). Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. *Journal of Applied Ecology*, *28*, 1004–1026.

Goss-Custard, J. D., West, A. D., Yates, M., Caldow, R. W. G., Stillman, R. A., Bardsley, L., … Pettifor, R. A. (2006). Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biological Reviews*, *81*, 501–529.

Guy, C., & Roberts, D. (2010). Can the spread of non-native oysters (*Crassostrea gigas*) at the early stages of population expansion be managed? *Marine Pollution Bulletin*, *60*, 1059–1064.

Hall, S. J., & Harding, M. J. C. (1997). Physical disturbance and marine benthic communities: The effects of mechanical harvesting of cockles on non-target benthic infauna. *Journal of Applied Ecology*, *34*, 497–517.

Herbert, R. J. H., Humphreys, J., Davies, C. J., Roberts, C., Fletcher, S., & Crowe, T. P. (2016). Ecological impacts of non-native Pacific oysters (*Crassostrea gigas*) and management measures for protected areas in Europe. *Biodiversity and Conservation*, *25*, 2835–2865.

Herbert, R. J. H., Roberts, C., Humphreys, J., & Fletcher, S. (2012). The Pacific oyster (*Crassostrea gigas*) in the UK: Economic, legal and environmental issues associated with its cultivation, wild establishment and exploitation. Report for the Shellfish Association of Great Britain. London, UK: Shelfish Association of Great Britain.

Humphreys, J., Herbert, R. J. H., Roberts, C., & Fletcher, S. (2014). A reappraisal of the history and economics of the Pacific oyster in Britain. *Aquaculture*, *428–429*, 117–124.

IUCN. (2000). IUCN guidelines for the prevention of biodiversity loss caused by alien invasive species. Approved by the 51st Meeting of the IUCN Council, Gland, Switzerland, February 2000. Retrieved from https://portals. iucn.org/library/efiles/documents/Rep-2000-052.pdf

JNCC. (2017). Essex estuaries. http://.defra.gov.uk/protectedsites/sacselection/sac.asp?EUCode=UK0013690

Lejart, M., & Hily, C. (2005). *Proliferation of Crassostrea gigas in the Bay of Brest: First estimations of the stock and its impact on the global functioning of the ecosystem*. Presented at 8th International Conference on Shellfish Restoration. Brest, France.

Lejart, M., & Hily, C. (2011). Differential response of benthic macrofauna to the formation of novel oyster reefs (*Crassostrea gigas*, Thunberg) on soft and rocky substrate in the intertidal of the Bay of Brest, France. *Journal of Sea Research*, *65*, 84–93.

Markert, A., Esser, W., Frank, D., Wehrmann, A., & Exo, K.-M. (2013). Habitat change by the formation of alien *Crassostrea*-reefs in the Wadden Sea and its role as feeding sites for waterbirds. *Estuarine, Coastal and Shelf Science*, *131*, 41–51.

Markert, A., Wehrmann, A., & Kröncke, I. (2010). Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological Invasions*, *12*, 15–32.

McKnight, W., & Chudleigh, I. J. (2015). Pacific oyster *Crassostrea gigas* control within the inter-tidal zone of the North East Kent Marine Protected Areas, UK. *Conservation Evidence*, *12*, 28–32.

Nehring, S., Reise, K., Dankers, N., & Kristensen, P. S. (2009). Alien species. Thematic report no. 7. In H. Marencic, & J. de Vlas (Eds.), Quality status report 2009. *Wadden Sea ecosystem* no. 25. Wilhelmshaven, Germany: Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group.

Padilla, D. K. (2010). Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster *Crassostrea gigas*. *Integrative and Comparative Biology*, *50*, 213–225.

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J. J., Dekker, R., & Essink, K. (2001). Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *Journal of Applied Ecology*, *38*, 976–990.

Reise, K. (1998). Pacific oysters invade mussel beds in the European Wadden Sea. *Senckenbergiana Maritima*, *28*, 167–175.

Reise, K., Wegener, A., Sea, W., & List, S. (2010). How to deal with alien species in the Wadden Sea? In H. Marencic, K. Eskildsen, H. Farke, & S. Hedtkamp (Eds.), *Science for nature conservation and management: The Wadden Sea ecosystem and EU directives* ()*Wadden Sea Ecosystem, No. 26* (pp. 69–74). Wilhelmshaven, Germany: Common Wadden Sea Secretariat.

Ruesink, J. L., Lenihan, H. S., Trimble, A. C., Heiman, K. W., Micheli, F., Byers, J. E., & Kay, M. C. (2005). Introduction of non-native oysters: Ecosystem effects and restoration implications. *Annual Review of Ecology, Evolution, and Systematics*, *36*, 643–689.

Scheiffarth, G. B., Ens, B., & Schmidt, A. (2007). What will happen to birds when Pacific oysters take over the mussel beds in the Wadden Sea? *Wadden Sea Newsletter*, *33*, 10–14.

Smaal, A. C., Kater, B., & Wijsman, J. (2009). Introduction, establishment and expansion of the Pacific oyster *Crassostrea gigas* in the Oosterschelde (SW Netherlands). *Helgoland Marine Research*, *63*, 75–83.

Spencer, B. E., Kaiser, M. J., & Edwards, D. B. (1998). Intertidal clam harvesting: benthic community change and recovery. *Aquaculture Research*, *29*, 429–437.

Stillman, R. A. (2008). MORPH—an individual-based model to predict the effect of environmental change on foraging animal populations. *Ecological Modelling*, *216*, 265–276.

Stillman, R. A., & Goss-Custard, J. D. (2010). Individual-based ecology of coastal birds. *Biological Reviews*, *85*, 413–434.

Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., & Grimm, V. (2015). Making predictions in a changing world: The benefits of individual-based ecology. *BioScience*, *65*, 140–150.

Stroud, D. A., Davidson, N. C., West, R., Scott, D. A., Haanstra, L., Thorup, O., … Delany, S. (2004). *Status of migratory wader populations in Africa and western Eurasia in the 1990s* ()*International Wader Studies, No. 15*. Thetford, UK: International Wader Study Group.

Thomas, N. S., Caldow, R. W. G., McGrorty, S., le V dit Durell, S. E. A., West, A. D., & Stillman, R. A. (2004). *Poole Harbour bird invertebrate prey availability*. Report no. 04/J/1/03/0454/0412. Poole, UK: Poole Harbour Study Group.

Thomas, R. J., Szekely, T., Powells, R. F., & Cuthills, I. C. (2006). Eye size, foraging methods and the timing of foraging in shorebirds. *Functional Ecology*, *20*, 157–165.

Troost, K. (2010). Causes and effects of a highly successful marine invasion: Case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *Journal of Sea Research*, *64*, 145–165.

Utting, S. D., & Spencer, B. E. (1992). Introductions of marine bivalve molluscs into the United Kingdom for commercial culture—case histories. *ICES Marine Science Symposium*, *194*, 84–91.

Walles, B., Mann, R., Ysebaert, T., Troost, K., Herman, P. H. J., & Smaal, A. C. (2015). Demography of the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef persistence. *Estuarine and Coastal Shelf Science*, *154*, 224–233.

Wonham, M. J., & Lewis, M. A. (2009). Modelling marine invasions: current and future approaches. In G. Rilov, & J. A. Crooks (Eds.), *Biological invasions in marine ecosystems* (pp. 71–105). Berlin, Germany: Springer.

Wood, C. A., Bishop, J. D. D., Davies, C. J., Delduca, E. L., Hatton, J. C., Herbert, R. J. H., & Clarke, P. F. (2015). *Hemigrapsus takanoi* Asakura and Watanabe, 2005 (Crustacea: Decapoda: Brachyura: Grapsoidea): first records of the brush-clawed shore crab from Great Britain. *Bioinvasions Records*, *4*, 109–113.

Zwarts, L., & Wanink, J. H. (1993). How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research*, *31*, 441–476.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Herbert RJH, Davies CJ, Bowgen KM, Hatton J, Stillman RA. The importance of nonnative Pacific oyster reefs as supplementary feeding areas for coastal birds on estuary mudflats. *Aquatic Conserv: Mar Freshw Ecosyst*. 2018;1–14. https://doi.org/10.1002/aqc.2938