<u>Distribution, abundance and temporal variation of the Pacific oyster, *Crassostrea gigas* in Poole Harbour</u>

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Contents

Executive Summary

The Pacific oyster, *Crassostrea gigas*, is a successful aquaculture species. During 2009 1356 t were produced in the UK with an estimated first sale value of £2.4 million; however C.gigas has established naturalised populations in the UK leading to this species being described as an invasive, as well as 'alien' species in the UK. Consequently there is tension between their continued production in UK waters and the perceived risk to native biodiversity associated with developing wild populations. The degree to which wild populations have established varies from substantial reefs in the absence of oyster aquaculture, to apparent absence despite suitable habitat and cultivation proximity. Othniel Oysters Ltd., situated in Poole Harbour, on the South coast of England, produce 300-400 tonnes of Pacific oysters a year, making it one of the largest Pacific oyster aquaculture production sites in the UK; but wild settlement in the Harbour appears sparse and irregular. This project investigates the likelihood that the current distribution of naturalised wild Pacific oysters does not represent the maximum potential settlement in Poole Harbour. To assess this assertion it is necessary to understand the extent of current naturalisation, area of suitable habitat and how much settlement occurs and survives to maturity.

Outside of the oyster culture plots, settlement is sparse within the Harbour; however there is a small aggregation of oysters reaching densities of 10 oysters per m^2 within a sheltered embayment (Blue Lagoon). Histological analysis previously carried out at the University of Southampton showed Pacific oysters in Poole Harbour to be undergoing gametogenesis and subsequently spawning[1,2] in the summer months, consequently in this study settlement plates were located at increasing distances from the aquaculture plot to determine potential total spatfall. Native oysters settled on the plates however no Pacific oysters were found. The pioneering, colonising community on the plates, with which Pacific oysters would have to compete for settlement sites, was analysed. Colonisation was most prolific during mid-August and declined thereafter. Subtidal sites were dominated by ascidians and contained significantly greater species richness than the intertidal site, which was principally colonised by barnacles.

Common shore crabs are abundant in the Harbour and are suspected to be predators of juvenile wild oysters. Shore crabs were used in laboratory experiments to evaluate the predation pressure potentially exerted on recently settled oysters. Large crabs were capable of ingesting up to 22 spat over a 3 day period, spat being up to 7 g in wet weight. Unlike the smaller crabs, that selectively predated small spat, large crabs showed no preference for spat size.

Consideration of historic water temperature data suggests that Poole Harbour only infrequently experiences the 'correct' regime of prolonged raised water temperature that the literature suggests is required for successful settlement. This is consistent

with size frequency data collected from the naturalised population in Poole Harbour and suggests that the last successful naturalised recruitment happened in the summer of 2006.

The work carried out so far highlights Poole Harbour as being an anomaly in the apparent steady progressive development of Pacific oyster populations around the coast, in that there is an obvious source of larvae but little successful settlement. The mechanisms which are 'dampening down' expected settlement appear to include at least one physical factor but it is likely that this is moderated by biological factors such as competition for settlement space and predation. Further work is required to establish which biological factors may be modifying recruitment success and whether recruitment is moderated during the larval stage or post metamorphosis. if the dominant controlling factor(s) act before oyster settlement it is most likely water temperature that controls the naturalised population, however top-down control by predators could be significant if oysters are surviving metamorphosis.

Introduction

The Pacific oyster, *Crassostrea gigas,* is cultured throughout the UK. The greatest production of farmed Pacific oysters comes out of England, with the highest concentration of aquaculture beds occurring in the South East and the South West[3]. Since the 1960s hatchery produced oyster seed has been used to artificially maintain populations on seabed designated for aquaculture. The Pacific oyster requires a different annual temperature regime than had previously occurred in the UK in order to spawn. It was because local environmental conditions inhibited natural reproduction, that this species was allowed to be introduced in to the UK, broadening the base of shellfish industry[4]. However since the 1990s, increasing water temperatures, attributed to global climate change, have exceeded reproductive thermolimits allowing for unregulated populations to establish[5]. Wild Pacific oysters are classified as an established ('invasive), non-native ('alien') species in the UK[6]. This status is a consequence of their ecosystem engineering through the production of reefs by wild populations, so altering the substrate and hydrodynamics of an area, which has possible ecosystem consequences. The degree to which wild Pacific oysters have established in England varies from dense reefs (River Yealm and River Colne), where over 1000 oysters can be counted during a 30 minute period[7], to apparent absence despite cultivation in that area (Portland Harbour and the Fleet)[7].

The extent of naturalisation is expanding throughout Europe. Where settlement was initially found only in close proximity to culture plots[4], there are now populations forming where the only possible larval input are other wild settlements[7,8]. This signifies the progression of wild populations sustained by larvae from cultivated plots to self-sustaining populations, which increases the potential area for larval recruitment. Furthermore the northern boundary where Pacific oysters are recorded has expanded as far as 60°N in Swedish waters[9].

Wild settlement of Pacific oysters may elicit a range of responses. The greatest concerns are for deterioration of habitats listed under Annex 1 of the EU Habitats directive and the exclusion of native biota[5,10,11]. Critically, unregulated proliferation can also have economic impacts through disrupting established aquaculture[12], fisheries[13,14] (although in West Mersea, Essex, Pacifics are now the mainstay of the oyster fishery) and tourism trade[15], and the increased biofouling of ship hulls and industrial cooling systems[16]. The degree of ecological alteration seen in an area will ultimately depend on the progress of the colonisation. The establishment of Pacific oyster populations seems to follow a typical pattern of initial inoculation, where individuals can remain undetected for years, followed by a small established group successfully reproducing. This will lead to continued recruitment and expansion during which the effects on the ecological character of the area will increase from weak to moderate to strong. It is likely that the additional competition for resources by the oyster and the attraction of further conspecific recruits will continue to alter biomass and abundance of native species. Thresholds are reached and finally the abundance of native species present before the introduction of Pacific oysters may decline during a period of adjustment[17]. Larval supply is an important variable for success and rate of population growth. Culture plots contain 1000s of sexually mature oysters, if environmental conditions allow for spawning, each female could release up to 50, 000 oocytes into the water column[18]. Consequently the larval supply is potentially very high in an area surrounding culture plots. In France wild spatfall has been sufficient to supply aquaculture demand since 1976. Farming sites can now comprise up to 75% wild stock and wild oysters colonising farm equipment represent the principle trophic competitor of cultivated oysters[12]. In the Wadden sea, Pacific oysters heavily foul beds of blue mussels (*Mytilus edulis*) and the fishery has suffered a decline[13,14]. This population of Pacific oysters is thought not to have reached co-physiological limits, and increasing reproductive performance may result in further expansion[19].

Invasive species, including Pacific oysters, may be displacing native species[20-22], however, there is no evidence that an invasion of any species has ever resulted in an extinction[23,24]. Further to this, evidence of displacement is often circumstantial with correlation of events too often assumed to imply causation[24]. The reduction in mussels in the Wadden Sea is an example of this, as it is thought now that it was not oysters out-competing mussels for food and space but rather a climatic shift which benefited oyster recruitment but hampered the success of the mussels[25,26]. It is important to remember that having invasive species status is a human appreciation of a species' biogeographic distribution potential at a given point in time. In ecological terms the introduction of alien species often enhances the species richness and biomass of an area[26-28]. Not all non-native species become invasive, but when they do they have the capability to transform habitats. The habitat of both native oysters and mussels are defined as beds when the density of individuals is equal to or exceeds 5 per m^2 [29], the same definition will be used when referring to Pacific oyster habitats throughout this report. Reefs of Pacific oysters form as beds become so dense that recruits are forced to settle on conspecifics and often results in the vertical orientation of individual oysters. The cementation of oysters to one another means that the reef has a consolidated biogenic framework that persists after the oysters die. Reefs transform the ecosystem and have the potential of excluding native species. However alien predators and pathogens have been predicted as far more likely to cause extinctions of native species than exotic competitors for food and space[30]. The effects of bed establishment and subsequent reef building by oysters varies between environments, generally increasing the species richness and biomass of associated fauna on colonised mud flats and littoral rocky shore[27], but leading to deterioration of intertidal biogenic reefs of other species[31].

When studying the colonisation of a non-native species it is important to understand the larval supply and the phase of the colonisation process. Investigations should ideally focus during the initial phases of the colonisation allowing limiting factors to be identified and so aid in predictions[17] of the potential effects on the recipient biota and the extent to which the population of non-native species may proliferate. The variation in Pacific oyster colonisation witnessed across the UK so far illustrates that a case-by-case approach is most appropriate to decipher which parameters regulate the progress and level of colonisation of a non-native species.

Aims and Objectives

This project aimed to determine:

1. The abundance of naturalised Pacific oysters in Poole Harbour and their relationship to settlement surface type, exposure by tides and distance from the oyster farm
2. The potential total spatfall of Pacific oysters
3. The predatory effectiveness of shore crabs, *Carcinus maenas*, and other predators on small, post settlement oysters
4. The mortality of larvae caused by filter feeders, in particular; peacock worms, bivalves and ascidians.

The study address the question, ‘does the existing distribution of naturalised Pacific oysters represent the maximum possible settlement in Poole Harbour.

The objectives of the project were as follows:

1. Beach surveys were carried out, on foot, during spring low tide to quantify population density and size frequency of Pacific oysters naturalised in the intertidal zone. A hand held GPS unit was used to plot the location of oysters against altitude, substrate type and distance from the oyster cultivation plot using the software ArcGIS
2. Settlement plates were placed at different depths along transects radiating from Pacific oyster cultivation plots. New plate (layers) were subsequently added on a weekly basis to monitor recruitment over the reproductive period
3. Top down control was estimated using laboratory based feeding experiments that determined the predatory effectiveness of shore crabs, *Carcinus maenas*, on small, post settlement Pacific oysters. Complementary field experiments made up of predator exclusion zones were set up in the intertidal zone during the reproductive period
4. Larviphagy of *C.gigas* was to be estimated by laboratory based feeding experiments that would have determined the filtration capacity of a selection of filter feeders that are abundant in Poole Harbour. Unfortunately a hoped for supply of oyster larvae wasn’t available during the study

Methods

Beach Surveys

Pacific oyster distribution

Poole harbour has in excess of 100 km of highly indented shoreline with a range of substrates including; clay, mud, sand, shingle and urbanised areas of concrete and wooden structures. Substrate type was the dominant prioritising factor for survey planning as oyster larvae require a hard substrate for attachment during metamorphosis. Identification of priority areas for survey was achieved using Google Earth, Channel Coastal Observatory aerial photography, and the knowledge of colleagues who are familiar with the area.

Surveys were shore based, and carried out within an hour either side of low water on a tide with a range greater than 1.6 m, which indicates a spring tide[32]. For the majority of surveys transects were not necessary due to the low abundance of oysters. Along steeper sections of shore where less than 3 m of substrate were exposed, 2 surveyors walked parallel to the shore approximately a metre apart for as far as the tide/ shoreline permitted. When the intertidal zone exceeded 3 m in width a pathway that traversed the area was taken. In both cases when an oyster was located, the position was recorded using a hand held GPS unit and the length of the oyster shell from umbone to the furthest peripheral was recorded to the nearest mm using Vernier calipers (Figure 1).

Figure 1 Measuring a Pacific oyster using vernier calipers

There was an aggregation of wild Pacific oysters in a sheltered lagoon (Figure 3: Blue Lagoon) area of Poole Harbour, where it was necessary to carry out detailed belt transects to account for the density. Transects were laid the full length of the aggregation and teams of 3 counted and measured all Pacific oysters present in each adjacent area of 5 x 1 m. This process was carried out on both sides of the transect, and repeated for a second transect which was carried out parallel to, and 5 m apart from the first.

Habitat suitability

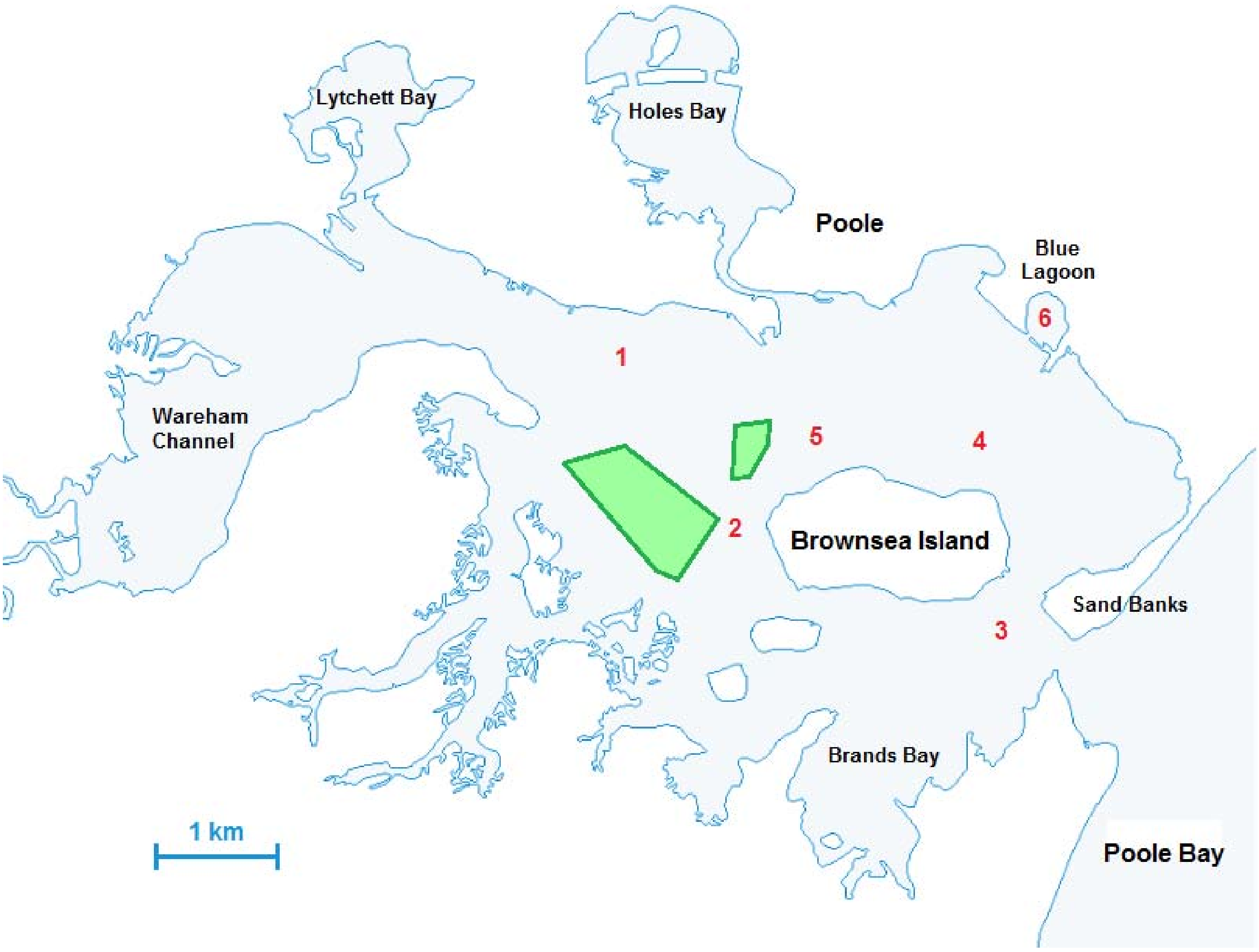
Surface substrate type was described and photographed during surveys for comparisons between areas where naturalisation was both present and absent. Further to this the ArcGIS software was used to map oyster location against altitude data provided by the Channel Coastal Observatory[33], allowing tidal exposure of the Pacific oysters to be approximated.

Settlement plates

Potential spatfall and community structure

Settlement plates were placed in 6 locations within Poole Harbour in July 2012 (Figure 2). Settlement plates were constructed from sections of plastic half-pipe guttering, with an area of approximately 540 cm^2, and attached to a weighted base. Additional layers of plates were added on a weekly basis over a 2 month period allowing a temporal evaluation of variation in settlement. Settlement plates were placed on the seabed and tied onto channel markers to maintain their position.

On removal from Poole Harbour settlement plates were disassembled and a detailed evaluation of fauna was carried out. Sessile epifauna was identified to the lowest practical level of taxonomic detail, and quantified as the percentage of the settlement plate colonised. Each plate was divided into 4 sections for photography, 2 on the underside and 2 on the topside. A grid was applied to an unused piece of guttering and divided into the same 4 sections for photographing. Using these photographs the gridded settlement plate was over-laid onto the sampled settlement plate using the software CorelDRAW X5, and used to calculate percentage cover (Figure 3). The area by which an organism was attached to the settlement plate was estimated using the grid and recorded. On occasion when organisms were overgrowing each other, both were recorded.



Settlement plate key		Coordinates		Depth CD
1	West Transit	50.706283	-2.008050	-0_6
2	South Shellfish Plot	50.690033	-1.993100	-0_4
3	Stone Island	50.683867	-1.959083	-1_1
4	Wych Channel	50.699067	-1.961667	-3_1
5	Will's Cut	50.698833	-1.985283	-0_3
6	Blue Lagoon	50.708200	-1.952700	1_8

Figure 2. Map of settlement plate locations within Poole Harbour. The green blocks show the location of commercial Pacific oyster plots

Figure 3. An example of quantifying colonisation using photographic overlaying

Top-down control

Shore crab population estimate

Mark, Release and Recapture (MRR) using baited pots was carried out to estimate the population size of common shore crabs, *Carcinus maenas,* inhabiting Poole Harbour. MRR was carried out at 2 locations, the Town Quay Marina, a 4 hectare semi-enclosed body of water, and on the Pacific oyster culture plot in the harbours main body of water. At both locations 2 traps were laid approximately 150 m apart, for the duration of 4 consecutive nights, centred on a spring tide.

Figure 2 An example of the parlour trap used during the MMR experiment, shown closed with bait bag ready for deployment

Standard steel framed parlour traps 0.55 m in length were used, with 10 mm mesh, selective grill on the bottom and 2 x 80 mm fixed diameter, side entrances (Figure 4). Half of a recently defrosted mackerel was hung in a net bag immediately prior to the trap being sealed and placed *in-situ*. The traps were laid for 12 hours from 19:00 until 07:00. The carapace width (CW), a measurement from between the 4^{th} and 5^{th} anterolateral teeth, was taken using vernier calipers. Sex, colour and missing appendages were noted and one of the anterolateral spines of the carapace was clipped off to mark the animal before the animals were released. The spine correlated to both the location and the haul number for that location. To increase the chance of recapturing individuals inhabiting the Pacific oyster culture plot, an area which far exceeded the attraction capacity of just two pots[34,35], crabs were collected using the Othniel oyster harvester and marked before the pots were set.

Predation by shore crabs on juvenile Pacific oysters

Shore crabs representing 4 size classes for both males and females were collected from Poole Harbour during January 2013. Size was a measurement of carapace width, and size classes increased by increments of 10 mm starting from 30 mm cw. This represented the size frequency of the animals inhabiting the oyster plot during winter. The crabs were then transported to aquarium facilities at the National Oceanography Centre, Southampton where they were held for 2 weeks to acclimatise. The tank had filtered sea water flowing through it, and temperatures were kept at $13\ ^{+}/_{-}\ 2$ °C. The diet was regulated and consisted primarily of slipper limpets, *Crepidula fornicata.* One slipper limpet was fed to each crab daily, additionally 1-2 dead fish (mackerel/sardines) were fed to the crabs once a week.

The experimental period lasted for 6 days. Crabs were separated into individual testing tanks 20 cm x 30 cm with 2.5 L of filtered sea water flowing through. Each crab was fed a single slipper limpet and then starved for 72 hours, to standardise hunger. A total of 9 juvenile Pacific oysters were then introduced. The juvenile oysters were weighed and allocated to 3 size classes: ≤ 2.00 g, 2.01 – 3.50 g, 3.51 - 5.00 g wet weight. Each crab was presented with 3 oysters from each size class, and left for a further 72 hours. To avoid prey density affecting predation, the shells of ingested oysters were removed at 3 hourly intervals throughout the day, and replaced with a live oyster from the same size class.

Results

Beach Surveys

Pacific oyster distribution

At least 25 km of shore was considered unsuitable for settlement, most of which was mudflat fringed by reeds but also includes 2.5 km of sandflat. Settlement was sparse or absent along the 9 km of shoreline where walking surveys took place. However it was necessary to carry out detailed belt transects in Blue Lagoon because of the high density of settlement (Table 1). Oyster shell length ranged from 57 mm to 232 mm with the smallest animals being found attached to anthropogenic structures such as the sea defence groynes along Hamworthy shore. Settlement density was the most variable factor ranging from an individual oyster being found during a 1.2 km long survey at Cleavel point to densities averaging 301 oysters per 100 m^2 and reaching 10 oysters per m^2 in Blue Lagoon.

There was a unimodal size frequency with 90% of the measured oysters having a shell length of between 110 and 190 mm (Figure 5).

Table 1 A summary of survey locations and findings

Survey name	Coordinates		Survey area m^2	Pacific oyster abundance		Shell length mm
	Start	Finish		Total	Per 100 m^2	
Rockley Point	50°43'7.56"N 2°2'24.02"W	50°43'3.41"N 2°2'30.36"W	480	4	0.833	135 – 155
Hamworthy West	50°42'48.77"N 2°1'30.37"W	50°43'6.5"N 2°2'21.9"W	4800	0	0	
Moriconian Quay	50°42'48.51"N 2°1'29.73"W	50°42'46.45"N 2°1'21.39"W	700	0	0	
Lake Drive	50°42'40.55"N 2°1'1.01"W	50°42'42.56"N 2°1'7.97"W	600	4	0.667	70 – 110
Hamworthy East	50°42'37.73"N 2°0'37.98"W	50°42'38.39"N 1°59'58.18"W	1700	6	0.353	57 – 140
Holes Bay W	50°43'4.07"N 2°0'15.99"W	50°43'15.55"N 2°0'21.99"W	800	0	0	
Holes Bay E	50°43'21.75"N 1°59'29.32"W	50°43'18.49"N 1°59'12.26"W	720	0	0	
Blue Lagoon	50°42'1.75"N 1°59'29.32"W	50°42'30.60"N 1°57'8.27"W	180	541	301	95 – 232
Sand Banks	50°42'3.40"N 1°56'26.44"W	50°41'2.00"N 1°56'25.71"W	4000	0	0	
Cleavel Point	50°40'28.17"N 1°59'55.20"W	50°40'22.05"N 2°0'1.45"W	1200	1	0.083	135
Arne (RSPB)	50°41'31.86"N 2°1'34.09"W	50°41'44.12"N 2°1'29.17"W	850	0	0	

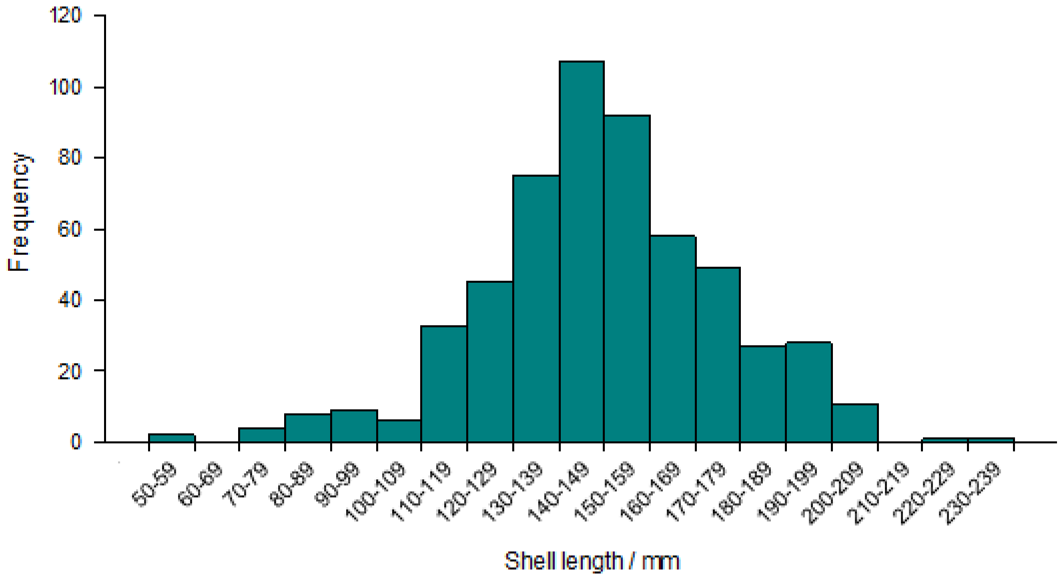


Figure 3 Size frequency distribution of Pacific oysters

The distribution of Pacific oysters was mapped using ArcGIS software. This enabled the position of the oysters with respect to height above Chart Datum to be shown using Lidar data provided by the Channel Coastal Observatory (Figure 6 & Figure 7). Ninety percent of oysters occurred between 0.9 and 1.07 m above Chart Datum. Despite oysters found at elevated positions on the sea defence groynes being noticeably smaller than those found on natural substrate, there was no significant relationship between the shell length of Pacific oysters and their position on the shore (Figure 8).

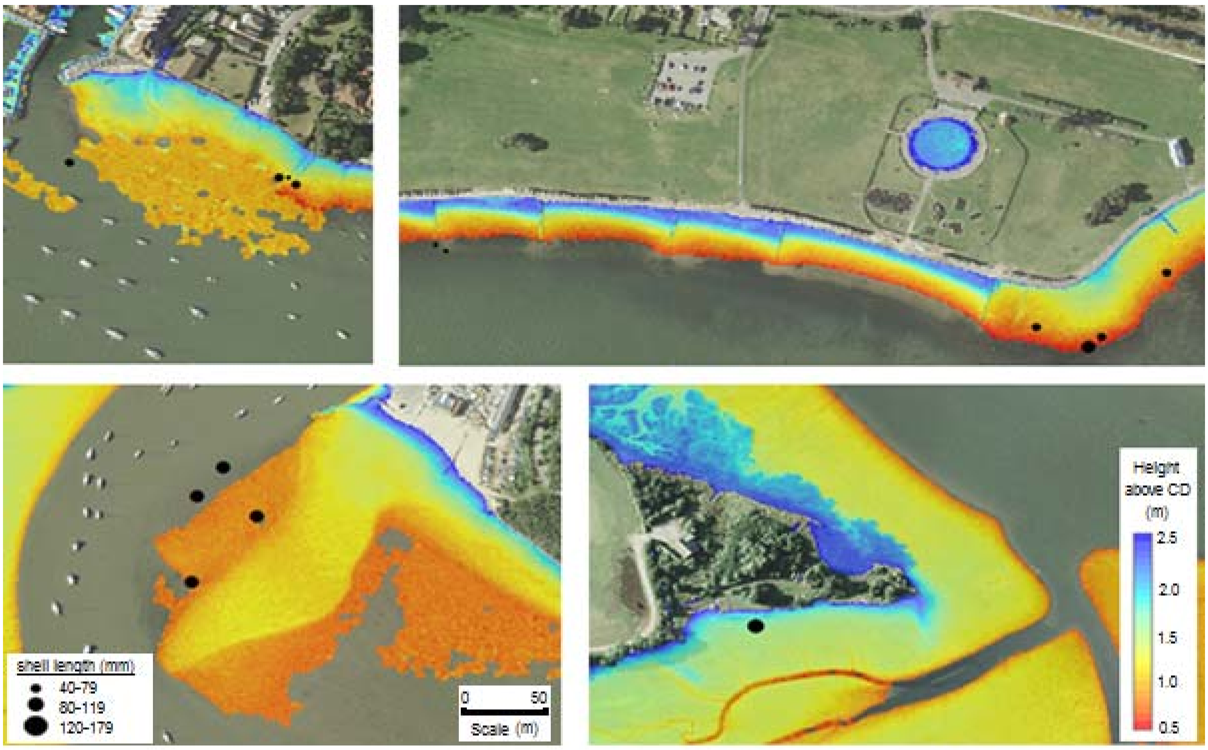


Figure 4 Pacific oyster size and distribution on the shore. Clockwise from top left: Lake Drive, Hamworthy east, Cleavel Point, Rockley Point

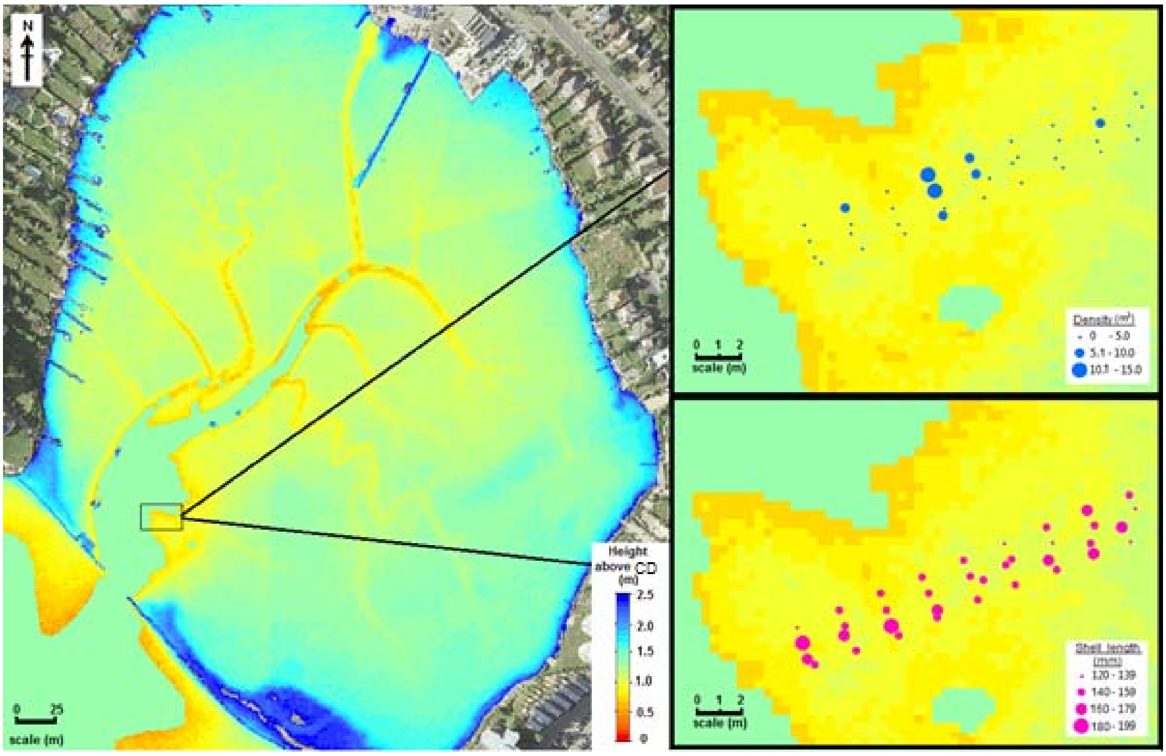


Figure 5 Pacific oyster size and distribution on the shore of Blue Lagoon

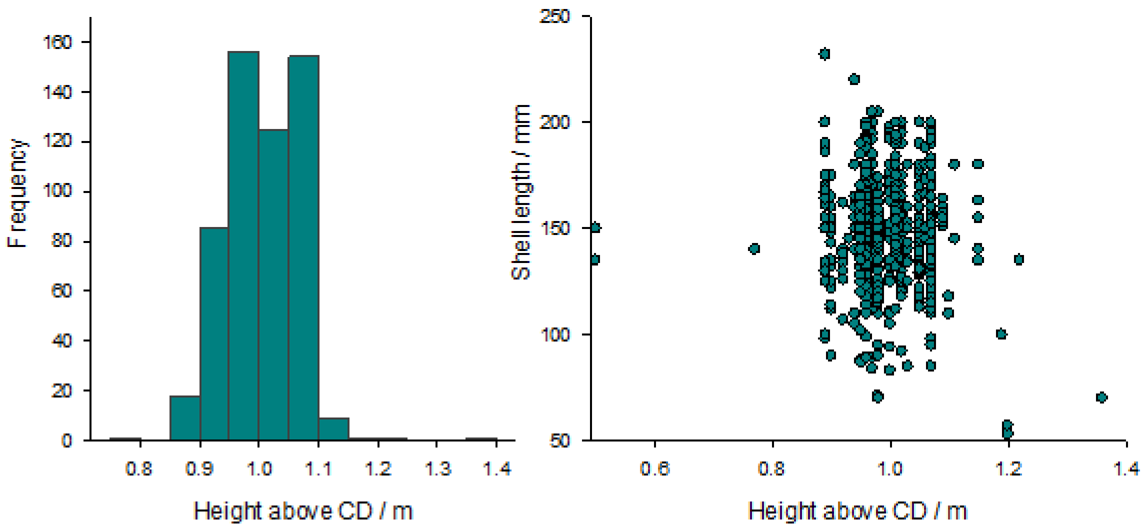


Figure 6 The relationship of shell length and distribution on the shore in relation to tidal height

Water temperatures may have influenced the years in which recruitment has occurred and so data logged from 1 m below the surface just north of Brownsea Island since 2006 was used to identify the most likely years for successful recruitment (Figure 9). During most years summer water temperatures fluctuated considerably. Pacific oyster recruitment requires waters in excess of 19°C for durations of over 3 weeks[36]. However conditions in Poole Harbour rarely maintain warm and stable conditions for more than 16 consecutive days. On average between 2006 and 2012 temperatures remained above 19°C for 10 day periods. During 2006 and 2010 however, water temperatures were more stable and remained above 19°C for 43 and 21 consecutive days respectively (Figure 6).

In 2006 water temperatures increased rapidly throughout June and remained high enough to support larval development for 43 consecutive days. Temperatures cooled gradually to the mildest winter recorded in this data set. The coldest daily average temperature was 5.2°C and the average temperature over the winter months of December, January and February was 8.4°C, nearly 2°C warmer than the winter average temperature of 6.7°C when considering data from the years 2006 to 2012.

Water temperatures during 2010 remained low until March and then increased steadily until July. For 21 consecutive days in July, water temperatures remained sufficiently high enough to support larval development. Temperatures dropped off gradually until mid-October when a decrease of 12°C was experienced over just 2 months. Winter temperatures were below average at 5.6°C and a low of 2.3°C was recorded during December.

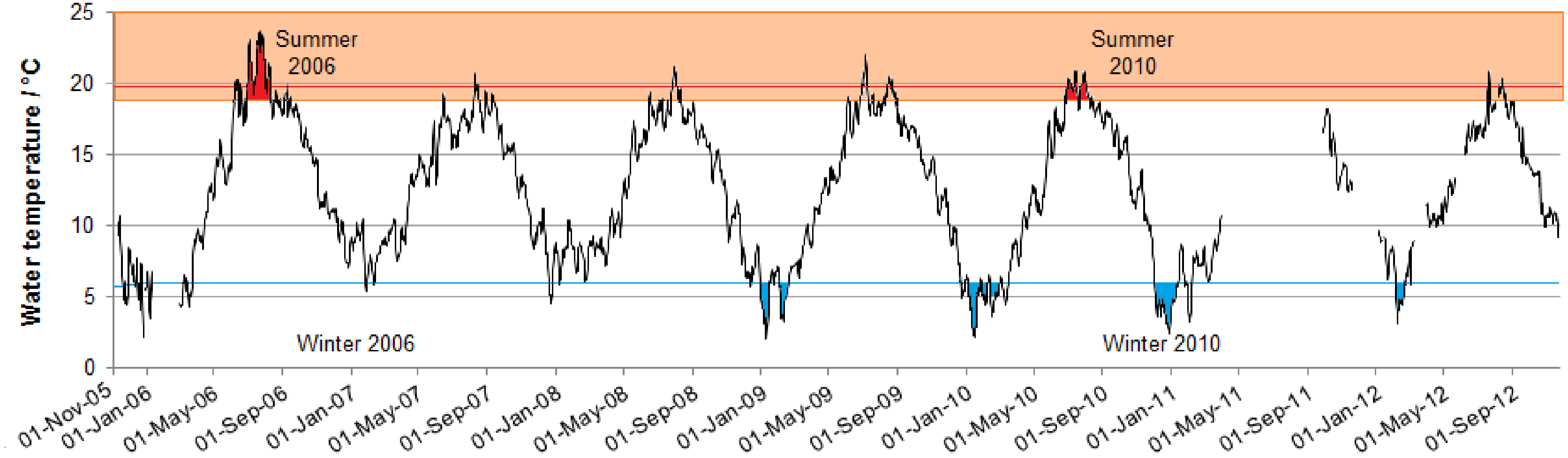


Figure 7 Water temperatures taken from 1 m below the sea surface just north of Brownsea Island in Poole Harbour. Red line: Spawning requirement 19.7°C[2]. Orange block: Larvae require >19°C to develop[37], durations in excess of 3 weeks are required in UK waters[36] (indicated by red blocks). Blue line: Spat mortality is increased notably below 6°C particularly if prolonged over 3 weeks or more[38] (Indicated by blue blocks).

Habitat suitability

All of the Pacific oysters found during the surveys were located on shores with a shallow gradient and so relatively expansive intertidal area. Out of 556 oysters, 1 was found on a mudflat, 3 were found on anthropogenic structures, and the remaining 552 were found on mixed substrate containing mud, shingle and shell (Figure 10).

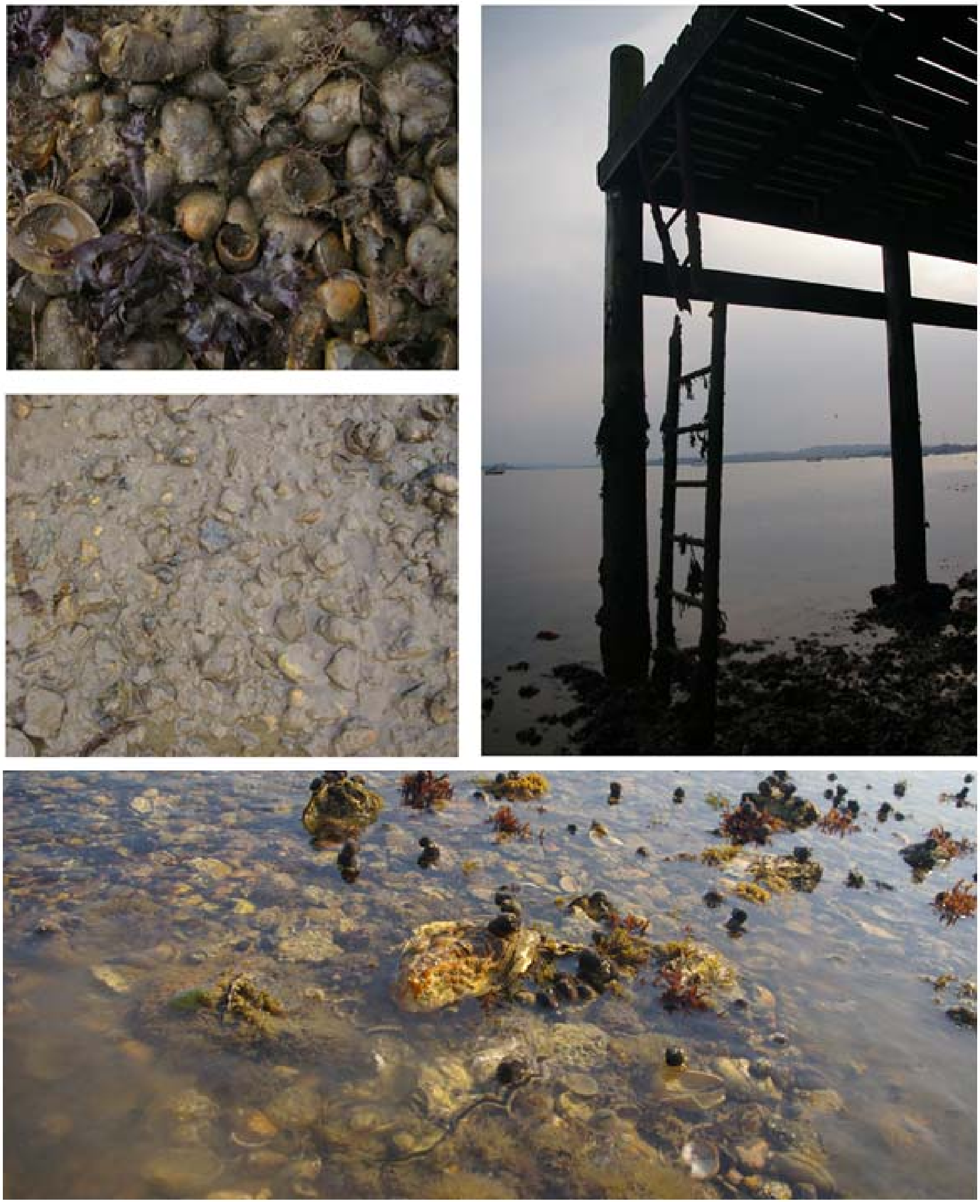


Figure 8 Substrate types where Pacific oysters were found. Hamworthy shore (top left & right) Blue Lagoon (bottom)

Pacific oysters were absent from sandflats, areas where there was strong competition with flora, intertidal areas that were relatively steep in gradient and also from urbanised areas where anthropogenic interference acted to alter habitats (Figure 11).

Figure 9 Substrate types where Pacific oysters were absent. Holes Bay (top left & right). Hamworthy shore (Bottom left). Sandbanks (Bottom right)

Settlement plates

Potential spatfall

No settlement of Pacific oysters was recorded on settlement plates *in-situ* between July and September 2012, however the native oyster *Ostrea edulis* settled on plates located at sites 1, 3 and 4 that were *in-situ* from 27 July 2012 and 11 August 2012.

The seawater temperature threshold for spawning was reached twice during the summer of 2012 (Figure 12). The first potential spawning period at the end of July (22.07.12 – 29.07.12) was followed by 10 days where the average daily temperature dropped below 19°C (the threshold for larval development[36,37]). The second potential spawning period occurred mid-August (14.08.12 - 15.08.12) with water temperatures remaining above the threshold for larval development for a further 10 days. Complete larval development would be expected after 3 to 4 weeks in the UK, although temperatures decreased below 19°C after 6 days the lower threshold for successful metamorphosis was not reached for a month after likely spawning[37].

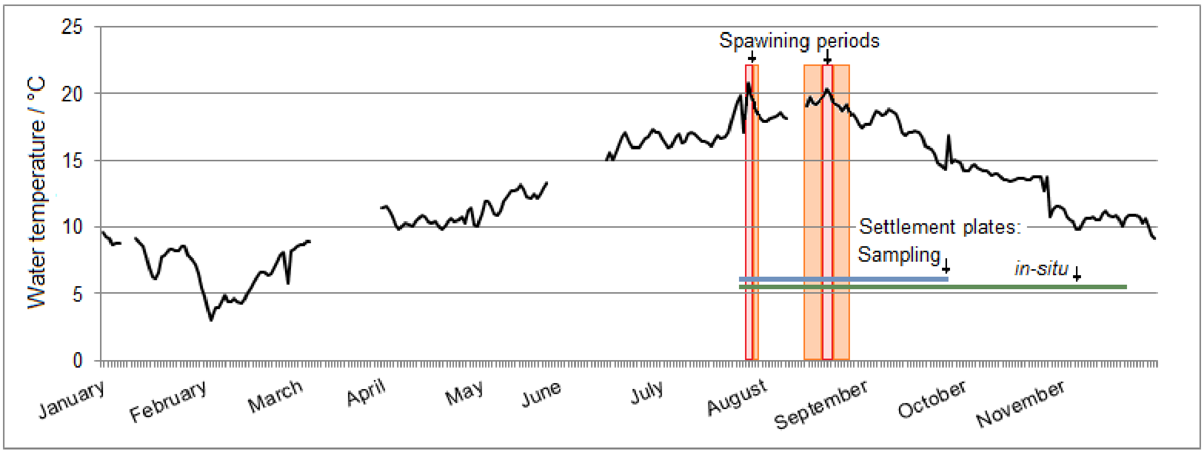


Figure 10 Water temperatures in 2012 taken 1 m above the sea bed over the shellfish beds in Poole Harbour and provided by Poole Harbour Commissioners. Red block: Potential Pacific oyster spawning. Orange block: Potential larval development. Blue line: Settlement plate stacks increasing weekly. Green line: Settlement plates *in-situ.*

Community structure

Within the communities colonising the settlement plates, 13 species were identified and a further 4 genera. Included within these were 5 species not native to the UK (Table 2). All identified species were found on subtidal settlement plates, and only two species, *Elminius modestus and Botrylloides diegense,* were found at the intertidal site. Ninety percent of species covered less than 18% of a single settlement plate; those species that occupied more than 18% of a single settlement plate at least once during the experiment were considered dominant colonising species (Table 2 & Figure 13). The total area of settlement plate colonised varied greatly from <3% after 66 days *in situ* to most sites reaching a maximum between 40-97% after 102-109 days *in situ.*

Of the dominant colonisers, solitary ascidians were present at all subtidal sites throughout the experimental period. *Ascidiella aspersa* dominated site 1 and site 5 from July through to the beginning of September with the greatest settlement occurring mid-august. *Corella eumyota* settlement peaked at the beginning of August colonising up to 37% of the settlement plates at site 1. *C. eumyota* was found alongside *A. aspersa* often at the edges of a plate surrounding clumps of *A. aspersa,* however *C. eumyota* was present at fewer sites than *A. aspersa* and in less abundance.

Botryllus schlosseri settled consistently throughout the experimental period at all subtidal sites. The largest area colonised by this species was at site 1 during late August and early September. Degenerating colonies were abundant on the settlement plates set in July and early September. Although it is most likely these colonies were also *B. schlosseri* it was not possible to identify them to species level and so have not been included in the quantitative analysis.

Cryptosula pallasiana settled at sites 1 to 4 throughout the experimental period however the largest area colonised was recorded on plates set during July and August. The area colonised was highly variable, even between replicate settlement plates, for example at site 4 after 109 days *in-situ, C. pallasiana* had colonised 83% of one settlement plate and 0% of the other.

E. modestus only settled in significant abundance at the intertidal site where it was the only species present on all but one plate and reached highest abundance on plates set during the middle of August. *E. modestus* was present, in very small numbers, at all subtidal sites throughout July and early August.

Table 2 Sessile epifauna colonising settlement plates in Poole Harbour 2012 (*Dominant subtidal organism **Dominant intertidal organism 'non-native' species)

	Species	Sub/ inter- tidal	Found	
			From	Until
Ascidiacea	*Ascidiella aspersa**	Subtidal	27.07.12	13.09.12
	Ascidia conchilega	Subtidal	27.07.12	31.08.12
	Ciona intestinalis	Subtidal	03.08.12	26.08.12
	Molgula sp.	Subtidal	27.07.12	31.08.12
	*Corella eumyota**	Subtidal	27.07.12	13.09.12
	*Botryllus schlosseri**	Subtidal	27.07.12	22.09.12
	Botrylloides diegense	Subtidal & Intertidal	27.07.12	31.08.12
Bryozoan and hydroid turf including:				
	Scrupocellaria scruposa	Subtidal	27.07.12	22.09.12
	Tricellaria inopinata			
Encrusting bryozoan including:		Subtidal	27.07.12	22.09.12
	Cryptosula pallasiana *			
	Tubularia sp.*	Subtidal	11.08.12	13.09.12
Polychaeta	*Pomatoceros* sp.	Subtidal	27.07.12	13.09.12
Crustacea	*Elminius modestus***	Subtidal & Intertidal	27.07.12	22.09.12
	Semibalanus sp.	Subtidal	27.07.12	26.08.12
Bivalvia	*Ostrea edulis*	Subtidal	27.07.12	11.08.12
	Mytilus edulis	Subtidal	27.07.12	27.07.12
Gastropoda	*Crepidula fornicata*	Subtidal	27.07.12	31.08.12

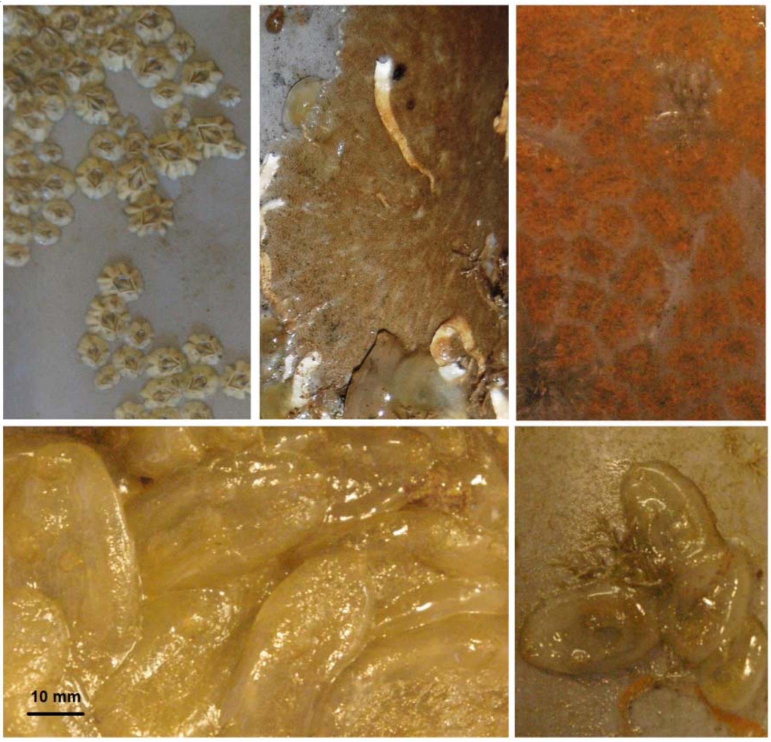


Figure 11 Pioneering colonisers occupying more than 18% space of at least one settlement plate. Top from left: *Elminius modestus*, *Cryptosula pallasiana* & *Botryllus schlosseri*. Bottom from left: *Ascidiella aspersa* & *Corella eumyota*

One-way analysis of variance was used to test for differences between the total areas of colonisation, and the number of species present at each site over time. Prior to statistical analysis the data set for colonised area was transformed using arcsine√(proportion), the data set for species richness however was not subject to any transformation as the data set was normally distributed with equal variance.

Both variables increased over time with resulting significance (colonised area: df=8, f=9.07, P=0.000, species richness: df=8, f=4.43, P=0.000), consequently Fisher's LSD post hoc analysis was used to identify groups of similarity (Figure 14). The colonised area of settlement plates increased with increasing time spent *in-situ* peaking around 109 days and then decreasing. Those settlement plates deployed in July were *in-situ* for 124 days and had a similar area colonised to those deployed 3 weeks earlier. Site 2 was the exception to this pattern as the area colonised was consistently high for the first 3 weeks, decreased throughout August and then experienced a second increase in settlement at the beginning of September. Unlike other subtidal sites there was no consistency to the relative abundance of species over time, instead each time interval was characterised by a different species. Space was never a limiting factor during this experiment.

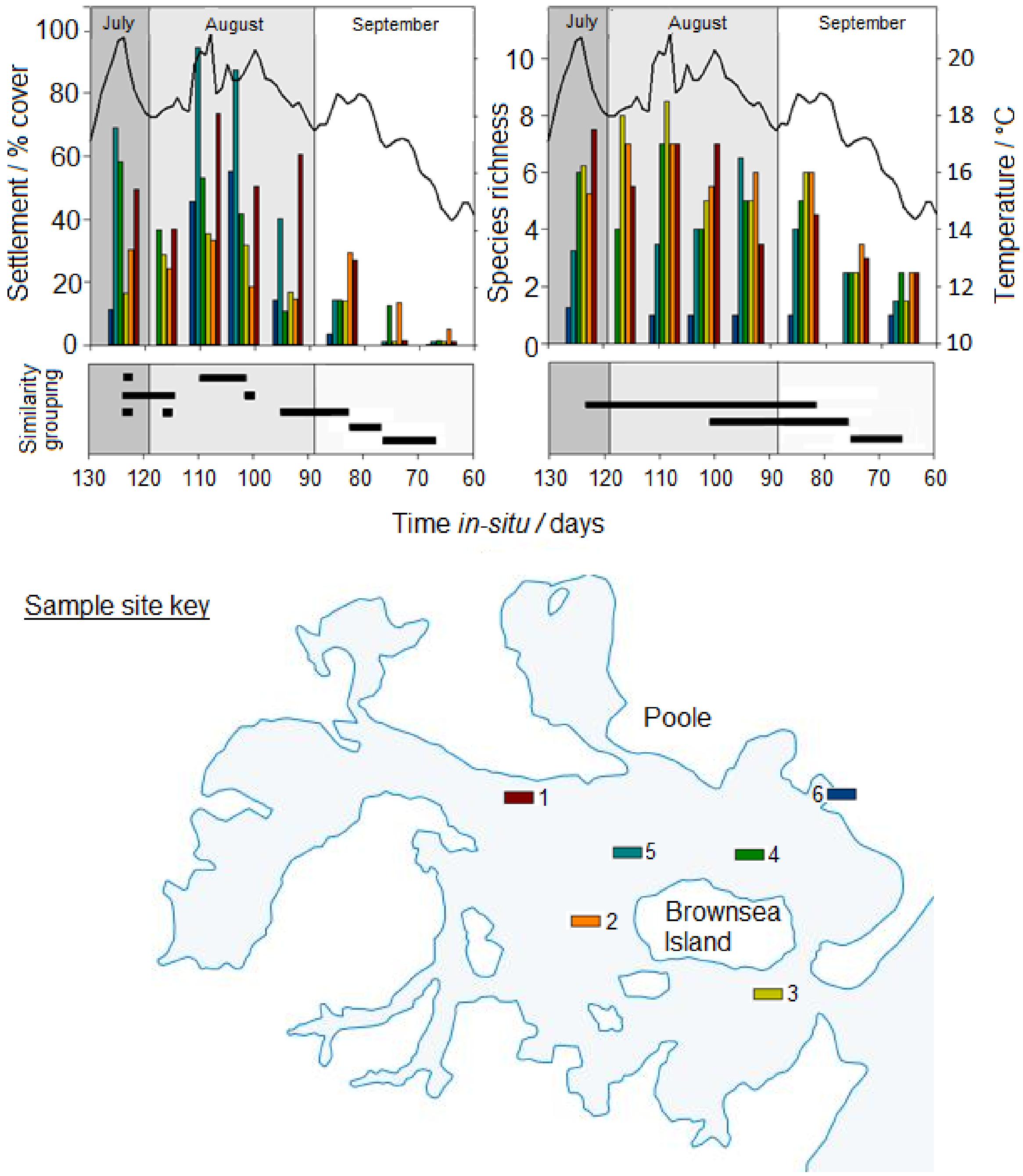


Figure 12 Percentage of the settlement plate colonised (left) and number of species present (right) over time (line graph: water temperature*).

*Poole Harbour Commissioners provided the 2013 ambient water temperature data set. Temperature was logged every 10 minutes from a site 30 cm off the sea bed in the proximity of the shellfish beds

Species richness data showed a similar pattern, however there was greater similarity within the data set; settlement plates deployed throughout July, August and early September had a similar quantity of species present, and fewer organisms recruited later in the year. No single plate held more than 9 species, however in total 18 species were identified throughout the experiment.

The variation in colonisation between sites was only tested for significance where complete data sets existed. The area of a settlement plate colonised varied significantly at all durations that were tested (Table 3), with colonisation at sites 2 & 3 generally covering a smaller area than at sites 5 & 6. Species richness did not differ significantly amongst subtidal sites, however it was significantly less at the intertidal site after 102 days *in situ.* Recruitment closely followed daily average temperatures, with the greatest recruitment being seen during periods of rapidly increasing temperatures. Species richness also reflected fluctuations in temperature but with less sensitivity (Figure 14).

Table 3. One way ANOVA results for significance between sites considering both species richness and colonisation

Month deployed	Species Richness				Percentage Cover			
	Days *in-situ*	DF	F	P	Days *in-situ*	DF	F	P
July	**124**	5	20.77	0.000	**124**	5	4.58	0.007
August	**117**	-	-	-	**117**	-	-	-
	109	5	10.62	0.006	**109**	5	2.07	0.201
	102	5	7.46	0.015	**102**	5	6.69	0.019
	96	5	3.69	0.071	**96**	5	4.59	0.045
September	**84**	5	3.30	0.089	**84**	5	9.49	0.008
	75	-	-	-	**75**	-	-	-
	66	5	0.82	0.579	**66**	5	4.27	0.053

There was a weak linear relationship between the area of a settlement plate colonised and the number of species present on that plate (Figure 15). The strongest correlation was seen during the initial few weeks after deployment however as the settlement plates are *in-situ* for prolonged periods the correlation became weaker due to a single dominant species occupying some of the sites.

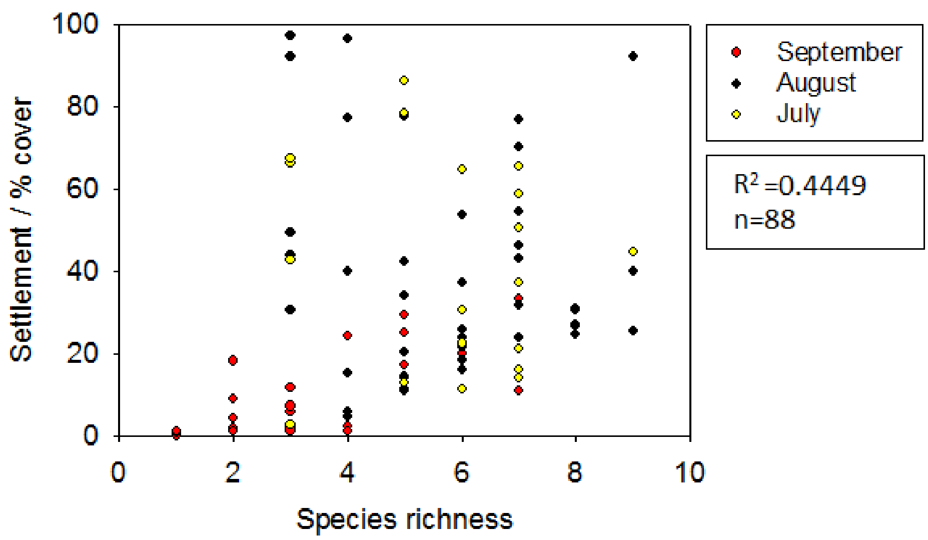


Figure 13 Relationship between the percentage area of the settlement plate colonised and the number of species present

The importance of hydrodynamics on larval distribution, settlement and continued productivity of epibenthos often defines which species exist in an area[39,40]. The sites where settlement was monitored can be collated into 3 groups according to the flow rate they experienced. A bar across the estuary mouth funnels the tidal flow into the Harbour with fast currents that are deflected either side of Brownsea Island. Sites 4 and 5 were close to the Harbour entrance and experienced the highest flow rates reaching in excess of 0.8 m/s during peak spring tides[41], both sites were characterised predominantly by colonial ascidian *B. schlosseri* which was in particularly high abundance throughout August. Site 1 and 5 experience flow rates of between 0.3 – 0.6 m/s during peak spring tides[41] and were both initially characterised by concentrated colonies of solitary ascidians (site 1: *A. aspersa* and *C. eumyota* and site 5: *A. aspersa*) with *B. schlosseri* becoming the dominant coloniser from the middle of August until early September. Site 2 was a subtidal site protected by Brownsea Island which experienced flow rates similar to the intertidal site where flow rates always remain below 0.3 m/s[41]. As previously mentioned the intertidal site was characterised by *E. modestus* however Site 2 was not characterised by any species other than the presence of 2 large colonies of encrusting bryozoan *C. pallasiana.*

Top-down control

Predator population size

A total of 234 individual crabs were caught using baited pots in Poole Quay Boat Haven. Of the animals sampled; 74% were female, 18% were male and 8% were parasitized by *Sacculina carcini* and so gender was indistinguishable. The median size for both males and females was 40-45 mm carapace width (Figure 16). A population density estimate of 1.11 crabs per m^2 was calculated from the Jolly & Seber method [42,43] (Table 4)

Table 4 Jolly-Seber calculations for the estimated population size of shore crabs at Town Quay Boat Haven

Sample	$\widehat{M}_t$	$\hat{\alpha}_t$	Population estimate (crabs per hectare)
1	19.05	0.13	**146**
2	41.56	0.08	**1186**
3	185.56	0.13	**1781**
4	456.25	0.28	**1600**
5	686.00	0.29	**2429**
6	447.75	0.38	**1608**

On the Pacific oyster culture plot within the main body of Poole Harbour, 541 crabs were collected (using the oyster harvester during a 45 minute period) marked and released. A further 161 crabs were trapped over the following 4 nights using baited pots, however only 1 of these animals was a recapture. Consequently the data set did not fit the requirements for the Jolly & Seber model and no estimate could be made. An estimate was made using the sample collected using the oyster harvester however it should be noted that the capture efficiency of this technique has not been established (Table 5).

Table 5 Population density estimate of *Carcinus maenas* inhabiting the Pacific oyster culture plots of Poole Harbour

Harvesting swath	Speed	Duration	Crabs collected	Population density estimate
1 m	1.5 knots	45 minutes	541	260 crabs per hectare

The crabs collected from the oyster plot had a positively skewed size frequency with both males and females having a median size of 30-35 mm cw. This sample also contained a greater relative proportion of males (30%) to females (52%) in comparison to those collected from Poole Quay Boat Haven (Figure 16).

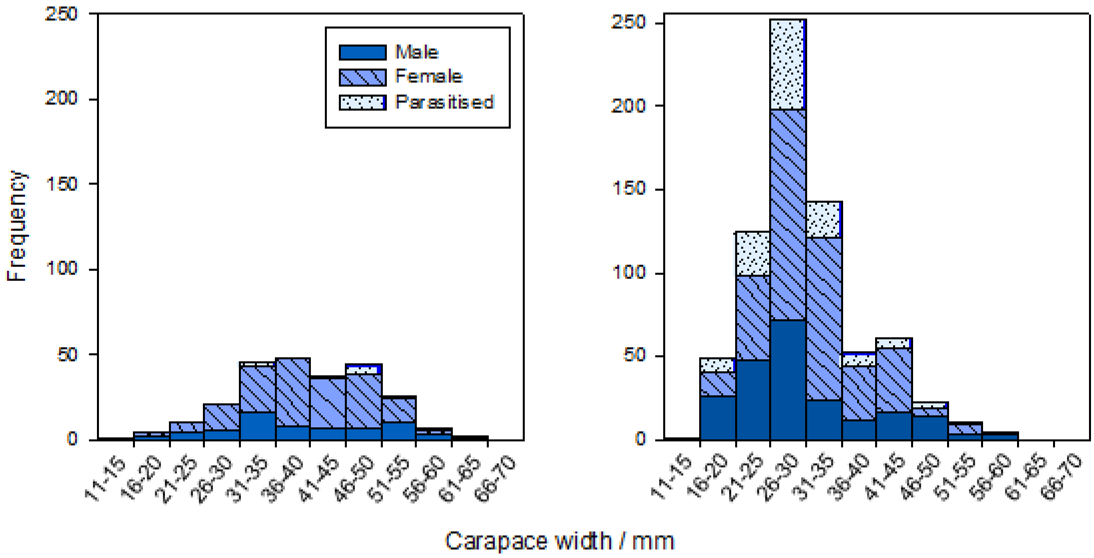


Figure 14 Size frequency of *Carcinus maenas* caught during the MRR experiments at Poole Quay Boat Haven (left) and the Othneil Shellfish oyster plot (right)

Predatory effectiveness

There was no predation by females throughout the duration of the experiment. Further to this, males below 40 mm cw also did not predate any oyster spat. The percentage of experiments resulting in predation increased with increasing crab size (Figure 15). Non-parametric statistical analysis was used to test for significant preferences to spat size by each size class of crab. Only data generated by animals that predated spat during the experiment were used, and found that the largest crabs do not select their prey based on size unlike the smaller crabs which chose smaller prey (Figure 15). Kruskal-Wallis one-way analysis of variance by ranks, found significant differences in the numbers of different sized oyster spat eaten only by crabs with CW 41-50 mm ($H=6.59$, $df=2$, $P=0.037$) and 51-60 mm ($H=6.13$, $df=2$, $P=0.047$). These differences were analysed further using the Mann-Whitney *U* test and it was found that crabs 41-50 mm CW predated significantly more spat from both the < 2.00 g (W=44, df=2, P=0.0331) and the 2.01-3.50 g (W=47, df=2, P=0.0105) classes than the 3.51-5.00 g. Crabs 51-60 mm CW predated significantly more spat < 2.00 g than both larger weight classes (2.01-3.50 g (W=79, df=2, P=0.0409), 3.51-5.00 g (W=34, df=2, P=0.0199)).

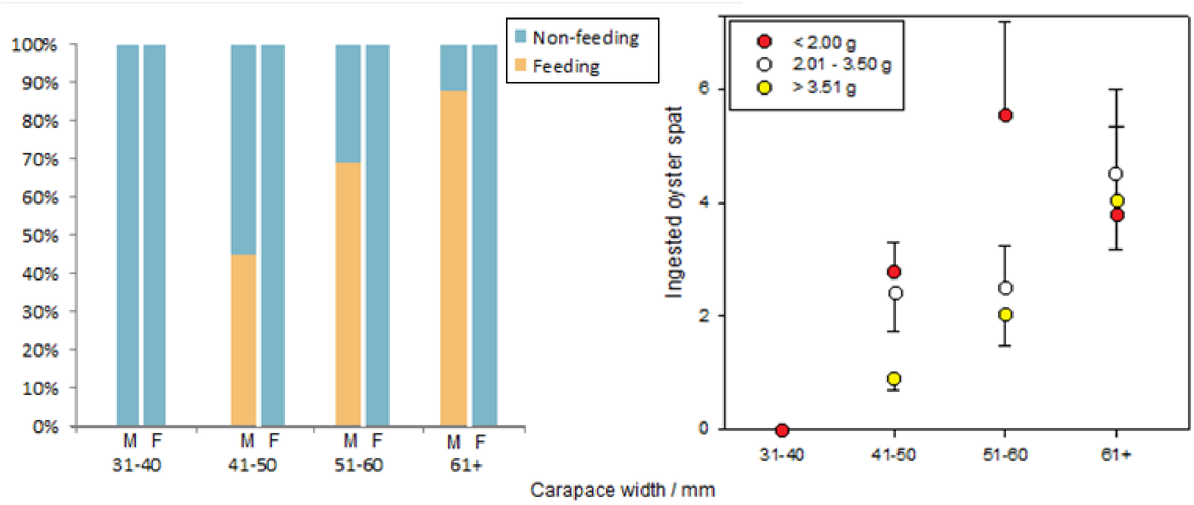


Figure 15 Left: The percentage of feeding experiments that resulted in oyster spat being predated. Right: Feeding preferences of *Carcinus maenas* on different sized oyster spat

Larviphagy

There are plans to initiate laboratory investigations into larviphagy, however there have been delays due to unforeseen circumstances restricting our supply of larvae. Once established the indirect clearance method will be used to quantify Pacific oyster larvae ingested by a range of filter feeders abundant in Poole Harbour.

Discussion

The current distribution of naturalised wild Pacific oysters does not represent the maximum possible settlement in Poole Harbour. It is most likely that water temperature has defined the years in which spawning has occurred and had notable influence on the survival of the larval life stage. Limited space in the subtidal region and potentially heavy predation by shore crabs in both the subtidal and intertidal regions have likely dampened the abundance of settlement during the year/s that it occurred.

Recruitment is known to be affected by abiotic factors including temperature[37,44,45], salinity[46], pollution[47-49], and biotic interactions such as pre/post settlement predation[50,51] and other ecosystem resistances such as competition[5,52]. In particular water temperature has a profound effect on reproductive success, and thermotolerances of Pacific oyster reproduction are well documented (Table 6). Temperature loggers have been recording water temperatures at the shellfish beds in Poole Harbour since October 2006 and analysing this data set has allowed speculation as to the reasons for limited recruitment, notably unstable, fluctuating summer temperatures and harsh winters. Bivalves living in coastal environments typically exert type r- reproductive strategies including high fecundity and a short reproductive period. However the reproductive period of the Pacific oyster shows more variable characteristics, including dependence on seasonal phytoplankton blooms and a minimum specific temperature for gamete release[53]. Rates of gametogenic development are correlated to temperature however initiation of gametogenesis and spawning occur at different temperatures in different regions of the world[13,54,55]. Minimum temperatures required for various stages throughout the reproductive cycle have been recorded for Pacific oysters in Europe (Table 6) and all are low in comparison to the requirements of Pacific oysters in their native waters around Japan, where gonadal developments occurs at water temperatures above 23°C and spawning occurs at temperatures above 27-28°C[56].

Table 6 Temperature thresholds for processes within the reproductive cycle of *Crassostreas gigas*

Reproductive cycle stage		**Temperature (°C)**		**Source**
Gametogenesis	Initiation	10.8	*In situ*: Monthly average April	Pastor (2010) [2]
	Ripe gametes	17.6	*In situ:* Monthly average June	Pastor (2010) [2]
Spawning		19.7	*In situ:* Monthly average July	Pastor (2010) [2]
Fertilisation		>15	Laboratory	Rico-Villa *et al.* (2009) [37]
Larval development		19-32	Laboratory	Rico-Villa *et al.* (2009)[37] Li & Hedgecock (1998)[36] His *et al.* (1989)[46]

Metamorphosis	>15	Laboratory	Rico-Villa *et al.* (2009)[37]
Spat (overwintering)	>3-6	Laboratory	Child & Laing (1998)[38]

The duration of the planktonic larval stage is inversely related to water temperature with the minimum temperature for adequate larval development being 19°C and generally good development being observed above 20°C[36]. Larvae occurring naturally in UK waters can be expected to metamorphose after at least 3 weeks. At some point Poole Harbour daily average temperatures have exceeded 19.7°C every year since 2006 (with the exception of 2007) indicating the potential for spawning and fertilisation. However, for most years, these temperatures have been sustained for between 11 and 16 days only, which is not long enough for the larvae to develop through to metamorphosis. Larvae have the most restricted temperature thresholds that have to be sustained throughout their planktonic life. The thermotolerance is thought to increase with development of the shell permitting pediveliger stages to withstand slightly lower temperatures[37]. Therefore as Pacific oysters are likely spawning in Poole Harbour it is a possibility that fluctuating temperatures are causing retardation of larval development and mortality before metamorphosis can occur.

Assuming the above requirements and that water temperature is the controlling factor on Pacific populations, recruitment in Poole Harbour has only been possible during 2 years since 2006. However this considers only summer temperatures when winter temperatures are important too[13,57]. Throughout Europe, a cold winter is often associated with the mortality of intertidal bivalve recruits[58,59]. Cold temperatures reduce metabolism and result in a higher preserve of carbohydrates[58]. Carbohydrates are the main respiratory substrate during gametogenesis[60] and so greater stores built up over cold winters allowing for more eggs in the early spring[19]. Gametogenesis in Pacific oysters ceases below 10.5°C[61] which is typically experienced in the UK during November, with average winter temperatures over oyster sites being between 5 and 7°C[62]. However juvenile oysters are vulnerable to temperatures below 6°C, with a minimum threshold of 3°C for survival[38]. This considered, any spat that may have recruited during 2010 most likely perished during the harsh winter that followed. Therefore successful recruitment was only likely to have occurred during 2006.

Histological analysis of Pacific oyster gonad was carried out by The University of Southampton for oysters inhabiting Poole Harbour[1,2] during 2010 and 2011. Both cultured and wild Pacific oysters were sampled and found to initiate gametogenesis early in the spring as the water temperatures increased. Peak gonadal maturation was reached during June 2011, when the average monthly water temperature was 17.6°C. In conjunction with the gonad histology, shore based surveys were carried out in Poole Harbour. The unimodal size frequency of wild aggregations in Poole Harbour reported[1] is consistent with this study's findings and support the theory that only a single successful settlement has occurred since 2006[13]. The mean shell size of Pacific oysters inhabiting Blue Lagoon in 2011 was 127 mm giving an average growth of 22 mm between 2011 and 2013 (Figure 16).

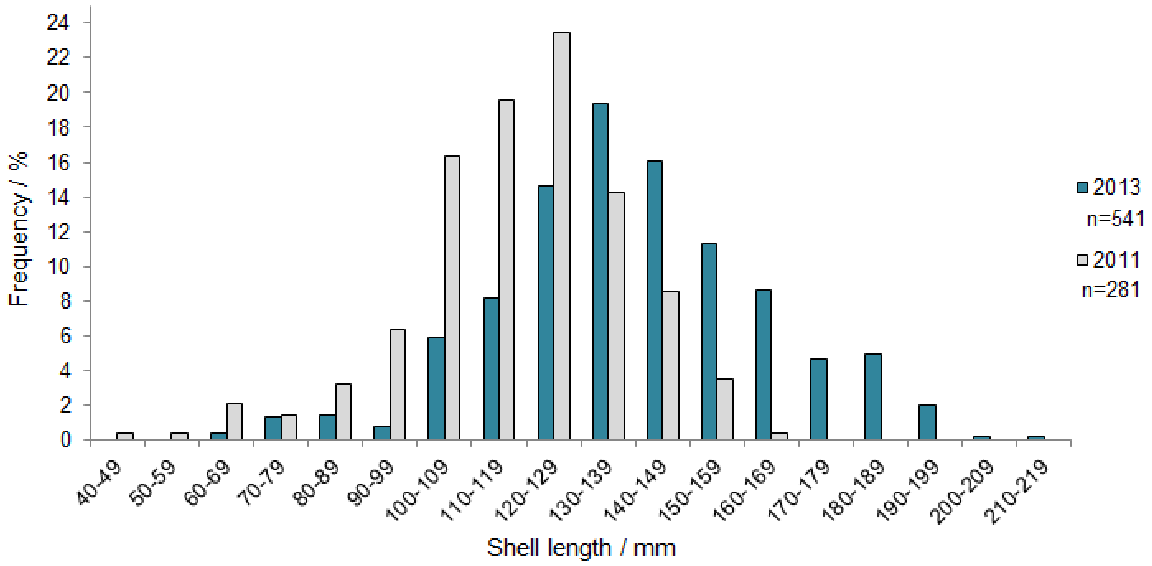


Figure 16 Growth of Pacific oysters at Blue Lagoon, Poole Harbour, using unpublished data from a University of Southampton project from 2011[1] and the current study

Pacific oyster larvae require a hard substrate to settle on in order to metamorphose into their adult form. However the most successful and abundant invasions of Pacific oysters have occurred on mudflats[12,13]. The presence of biogenic and anthropogenic substrate has often allowed aggregations to establish, after which intraspecific colonisation has resulted in the development of oyster beds and then the spread of oyster reefs. Mudflats are often expansive, providing room for reefs to extend with infaunal inhabitants presenting minimal competition for food. Blue Lagoon is located on the north shore of Poole Harbour and contained the greatest aggregation of Pacific oysters in Poole Harbour. The lagoon is almost entirely a shallow intertidal mudflat, ranging from 1.2 m to 1.8 m above Chart Datum and is exposed on every low tide throughout the monthly tidal cycle. A small patch of shell and shingle has accumulated on the inside of a meander where the water channel enters the lagoon and it is here that the densest aggregation of Pacific oysters has been found within Poole Harbour. Outside of Blue Lagoon oysters were found on a mixed substrate of mud, gravel and shell on intertidal reaches with a shallow gradient, which resulted in large, almost flat expanses uniform in substrate type. Otherwise they were attached to anthropogenic structures. Further to this oysters appeared to be aggregated where the shoreline protruded into the main body of water, often at the ends of a long straight section of beach (Figure 6).

The range of 175 mm in shell length is most likely attributed to the varying ambient conditions[63], natural variation in growth rates[64,65], and disturbances caused by predation[66] or fishing activities[12]. This assumption is fortified by the fact that all of the animals found with a shell length less than 80 mm were attached to sea defence groynes or piers, or on a couple of occasions larger oysters. Oysters cemented to anthropogenic structures were at a higher elevation than their counterparts occurring on the adjacent seabed, the prolonged tidal exposure reducing feeding potential and thus energy available for growth. Structures were heavily fouled by fucoid algae which did not occur on the adjacent seabed and fucoid cover has been shown to both negatively impact bivalve shell growth through increased sedimentation[67], and to promote increased shell growth[68]. It is uncommon to find Pacific oysters settling amongst dense fucoid growth[13,14,69] and in the literature where increased shell growth was recorded those oysters were artificially placed for experimental purposes and suffered a slight decrease in condition[68]. The most apparent physical disturbances were caused by the fishing related activity of bait digging. Bait digging is common along most muddy public shores in Poole Harbour, with many people visiting the exposed intertidal shore on a low tide to dig up ragworm and lugworm. The disturbance caused by bait digging is generally considered to have a negative effect on filter-feeders located within the immediate vicinity[70-72]. It is also not known whether Pacific oysters have ever settled along these areas of shoreline or if they once did, and subsequently have been physically displaced during digging or smothered by disturbed substrate. It is evident however, that bait digging occurs on substrate types suitable for Pacific oysters, and that none are present. Further still small Pacific oysters are growing on the groynes and peripheral substrate surrounding areas of bait digging.

Settlement plates provided a passive and convenient way of sampling fouling biota of intertidal and subtidal habitats. Although settlement plates are considered to give a good representation of the epibenthic fauna there are often considerable differences between communities colonising anthropogenic substrate and the surrounding natural substrate[73,74]. This is thought to be the result of chemical cues associated with different substrates[75,76] and altering sediment and water column dynamics[77]. The resulting environment is one that local fauna has not had time to adapt to over evolutionary time and consequently is often exploited predominantly by introduced species[73] and frequently used as a stepping stone to establishing in the surrounding natural habitat.

Pioneering species established within the first week of the experiment. Bryozoans and both solitary and colonial ascidians spread quickly creating mats that remained almost completely free of epizooites through the experimental period. The ability to remain free of fouling can benefit the organisms growth, reproductive output and potentially survival[78]. Several defence mechanisms against epizootic fouling have been recorded: including the production of mucus, sloughing of the epithelium, and the production of secondary metabolites[79-81]. Typically, species which are not indigenous to an area initially establish in small numbers which can remain low for years until conditions are favourable. Generally an increase in abundance will occur following a reduction in abundance of one or more species in the community and so the appearance of primary space[82]. Acceleration is promoted by the invading species being freed from both predators[83] and parasites[84]. Multiple non-native species have been present in the fouling community for over a decade in Poole Harbour but remain in low abundances, perhaps indicating a lack of primary space and strong competition for it when available. However competition for space is less of a problem for species which are able to tolerate the highly fluctuating environmental conditions of the intertidal zone. Species composition differs markedly between intertidal and subtidal communities with only species adapted to periods of aerial exposure, able to survive in the intertidal zone. Typically benthic epifauna have calcareous outer surfaces that can seal shut to protect their soft tissues when the tide retreats. Unlike ascidian tunics larvae are able to settle and colonise these hard surfaces, so that even in intertidal areas that are heavily populated recruitment is still feasible. However the proliferation of fouling not only effects potential settlement sites, it also hampers recruitment through the increasing the abundance of filter feeders which can lead to greater larval mortality. Those filter feeding species that cannot digest larvae as large as Pacific oyster veligers also contribute to mortality as larvae rarely survive passing through the gut, or the process of being expelled as pseudofaeces[85].

Post metamorphosis juvenile oysters remain vulnerable to being eaten until they reach a size refuge from predators such as crabs, shrimp and bottom feeding fish[18,86]. Shore crabs are highly abundant in Poole Harbour and are well known influential predators of many bivalves. Stomach content analysis has revealed the majority of prey to be molluscs, specifically gastropods and bivalves[87-89]. Shore crabs predate with great dexterity, exerting significant pressure on different species of bivalves depending on location and often negatively impacting lucrative commercial fisheries[90-94]. Most previous literature has focused on the effects of shore crabs predating commercially important bivalves such as *Argopecten irradians, Crassostrea virginica, M. edulis, Katelysia scalarina,* and *M. arenaria* as an invasive predator in a foreign ecosystem[90,94-96]*.* One reason for the proliferation of invasive species is their release from predation pressure that controls numbers. This does not mean that animals capable of predating the invading species are absent, rather that there is already an established food web and the alien species is not recognised by its potential predators as prey. Pacific oyster spat are recognised by at least shore crabs as prey and it was evident how notable the predation pressure could be (13 spat were consumed by a single crab during just 1 hour of the experiment).

Shore crabs are believed to select prey on the basis of its size in order to optimise the net energy gained[97-103]. In coastal environments where crab abundance is high, the size selective predation strategy of shore crabs, has been shown to be powerful enough to affect benthic community structure and dynamics. Size frequency distribution of sessile fauna is disrupted by the focus of crab predation on optimal sized prey. This is often apparent where mussel beds coincide with dense crab populations[97,100,102,103].

The design of decapod chelae is important to consider when analysing its feeding behaviour as it can influence the predators success with prey[104]. Shore crabs are generalist feeder, predating a wide range of prey items. The chelae of generalist predators tend to be weaker than those that specialise in feeding on molluscs. The lower pressure forces applied by the chelae of generalist feeders often result in prolonged handling times and very specific size selectivity of the prey that can be opened. Shore crabs have a general feeding strategy that appears consistent for all hard-shelled prey. The shell of small prey (relative to crab size) can be crushed outright by the master chelae; however larger prey involves further work. Bivalves are usually parted by the insertion of the cutter chelae between the valves or compressive force is applied by the crusher chelae is to a focussed point where the shell is weakest[101].

Shore crabs generally handle mollusc prey using a variety of limited techniques. These feeding techniques were first categorised for shore crabs feeding on blue mussels[105] and have been confirmed for an extended selection of gastropods and bivalves[106-108], including now, Pacific oysters. As previously defined small spat, shells were crushed outright with large amounts of shell often being ingested along with the flesh. However not once were the valves of large spat parted to access the flesh, instead a seemingly novel technique of chipping a small hole near the umbone region of the cupped valve was consistently used by multiple crabs (Figure 19).

Figure 17 Damage to oyster spat valves caused by shore crabs

The positioning of the hole requires the chelae to be at an obtuse angle and so exerting the smallest crushing force and is located away from the abductor muscle, meaning that on multiple occasions the shell was penetrated however the oyster did not die and the valves remained closed, on these occasions the flesh was not excavated. The size of the spat had a more profound effect on smaller crabs, with smaller crabs selecting smaller sized prey. This is explained by the chelae size being proportionate to its strength, and dictating strongly the upper size boundary of prey predated by generalist feeders such as shore crabs. Large crabs however showed no preferences between prey of various sizes. This may be a result of continuing dimorphism throughout moults resulting in the non-proportional increase in the size and strength of the master chelae when compared to the carapace. Female crabs do not exhibit dimorphism in chelae growth however the lack of female predation was more likely to be an effect of season. Males have been found to reduce feeding during the summer months and females to reduce feeding during the winter[109]. Although males reach a greater size, females may grow large enough to predate small bivalves and could notably influence juvenile oyster success immediately after they settle until the water temperatures cool sufficiently to reduce feeding.

Conclusions

This project concludes that the current distribution of naturalised wild Pacific oysters does not represent the maximum possible wild settlement in Poole Harbour. If water temperatures are maintained above 19°C throughout the summer further settlement can be expected on the large expanses of intertidal shore where shingle and shell are mixed within the mud, such like Blue Lagoon and Rockley Point. Further to this if suitable conditions prevail, anthropogenic structures such as the beach groynes, marinas and even boat hulls have the potential to become fouled, and although predation seems sufficient to dampen the number of juvenile oysters reaching adulthood, they are less likely to predate oysters colonising anthropogenic structures through reduced accessibility.

More specifically this report concludes the following:

1. Recruitment of Pacific oysters in Poole Harbour is not hampered by space as there is an abundance of uncolonised suitable substrate. There is great reproductive potential in the cultivated oyster population in the Harbour, however recruitment is minimal and colonisation is still in the initial stages, showing no evidence of progression into a self-sustaining population. Unimodal size frequency distribution and supporting water temperature profiles suggest that only one settlement of wild Pacific oysters has occurred in Poole Harbour, most likely from larval output from oysters cultivated within the harbour. This provides a rare and great opportunity for the further study of the progressing invasion.

2. A healthy and rich subtidal epibiotic community exists which provides substantial resistance to non-indigenous species establishing in the subtidal zone. In contrast the intertidal bay of Blue Lagoon has a low biodiversity and provides a suitable habitat for the Pacific oyster to colonise. Here, the conditions at low tide result in desiccation of most soft-bodied animals reducing settlement competition to other calcareous animals and minimising resilience to colonisation. The only species significantly colonising primary space was the Australasian barnacle which reproduces all year round with a peak in recruitment between May and October[110]. Although this overlaps with oysters recruitment the two species are often found co-inhabiting with no detrimental repercussions[111].

3. The European shore crab is a highly abundant predator inhabiting Poole Harbour that has the capability to predate Pacific oyster spat. Shore crabs exhibit size selective predation on the spat. The degree of selectivity seems to be determined by the relative size of the crab and its prey. A unique feeding technique was consistently used on larger spat. Such behaviour warrants further investigation as it points to not only an undocumented feeding technique but also a potential weakness in the spat shell.

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