Urban Seals/Wild Seals: Behavioural Shifts and Impacts of Habituation

by

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Abstract

The ongoing expansion of human activity into coastal regions has influenced grey seal (Halichoerus grypus) behaviour, resulting in a divergence between seals inhabiting urbanized environments and their counterparts in undisturbed habitats. This discussion paper examines the behavioural adaptations and ecological consequences faced by 'urban seals' compared to 'wild seals,' focusing on resting, foraging, breeding, and social behaviours. Observations highlight the adverse effects of human disturbance, including altered vigilance patterns, increased stress levels, and disruption of critical life-cycle stages.

Grey seals in urban settings demonstrate a notable capacity for behavioural plasticity, often utilizing human-fabricated structures and modifying their natural behaviours to navigate anthropogenic pressures. However, these adaptations come at a cost, including diminished health, reduced reproductive success, and erosion of ecological roles, such as their function as apex predators. Conversely, wild seals exhibit behaviours optimized for survival in undisturbed environments, emphasizing the necessity of conserving remote habitats to maintain biodiversity and species resilience.

By contrasting the ecological dynamics of urban and wild seal populations, this paper underscores the urgent need for targeted conservation strategies. Managing human-wildlife interactions in coastal areas is essential to mitigating conflict, preserving marine ecosystems, and ensuring the long-term survival of grey seal populations in an increasingly urbanised world.

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Introduction

The grey seal (Halichoerus grypus), is a prominent pinniped species of the North Atlantic, distinguished by its robust physiques and distinctive morphological characteristics. It's typical to observe grey seals resting on secluded coastlines and rocky islets, or foraging in cold coastal waters, where their behaviours are a product of extensive evolutionary adaptation to their natural environment. Historically, the grey seal has thrived in undisturbed, remote habitats; however, in recent years, with increased human activity taking place across coastal regions, we have seen a growing presence of the grey seal in more urbanised and anthropogenically influenced environments.

To the casual observer, their presence in human-occupied areas might appear harmless or suggestive of their ability to adapt to modern environments. However, this behavioural shift from wild habitats to urban settings carries significant consequences for their well-being. Seals residing in close proximity to humans face challenges that are seldom encountered by their wild counterparts, resulting in marked behavioural and ecological changes. These alterations not only affect the seals' daily routines but also have long-term implications for their survival, reproductive success, and overall health.

In their natural habitat, wild grey seals adhere to established patterns, seeking secluded areas to rest, breed, moult and forage with minimal disturbance. Seals in urbanised habitats are often subjected to elevated levels of human disturbance, pollution, and stress, which can disrupt their natural behaviours and gradually lead to a deterioration in health. Habituation to human presence can lead to maladaptive behaviours, such as scavenging or a diminished fear of predators and human activities, further compromising their chances of survival in the long term.

In anthrozoology, the term ‘urban species’ refers to animals and plants that have adapted to live in urban or suburban environments, often thriving in close proximity to human populations (Francis and Hoggart, 2009). Unlike their wild counterparts, these species are capable of exploiting urban resources, such as food waste, artificial shelter, and altered landscapes (McDonnell and Hahs, 2015).

Over time, some urban species have evolved distinct behaviours or physical adaptations to survive and even flourish in city ecosystems (Bateman and Fleming, 2012). The term 'urban species' is used in this document in comparison to the term 'wild species'. Wild species exist with little to no dependence on human-modified environments (McKinney, 2006) and are typically found in wilderness areas, national parks, and other natural ecosystems. They have not adapted to live alongside human populations in urban settings (Miller and Hobbs, 2002).

The behavioural and ecological differences between wild and urban grey seals reveal the complex and often detrimental effects of human encroachment on native wildlife. Understanding these differences is critical for effective conservation efforts, as human impact continues to shape the future of these iconic marine mammals.

Note: In this report, the terms urban and wild species are used to describe behavioural and character variances observed within a species, rather than suggesting distinct species or subspecies classifications. Individual grey seals may inhabit both urban and wild environments throughout their lifetime, displaying significant flexibility in their behaviours depending on the habitat they occupy. Some grey seals navigate between these two settings, adjusting their foraging, resting, and reproductive behaviours accordingly. Others may predominantly reside in urbanised coastal areas, exhibiting a distinct set of behavioural traits that reflect adaptations to these human-altered environments. This adaptability highlights the species' behavioural plasticity in response to varying levels of human presence and environmental change.

This report evaluates grey seal behaviour in one urban and one wild location, which constrains the applicability of findings to other regions. Different locations may exhibit unique environmental and anthropogenic pressures, potentially leading to variations in seal behaviour not captured here. This limitation could affect the interpretation of results and their applicability to broader conservation strategies. Future research should expand the geographic scope, incorporating multiple urban and wild sites to provide a more comprehensive understanding of grey seal behavioural adaptations and their ecological impacts.

Wild Grey Seals: Natural Behaviour in the Absence of Humans

In habitats free from human disturbance, grey seals follow instinctive patterns of movement, foraging, breeding, and social interaction, shaped by ecological factors such as prey availability, seasonal rhythms, and threat avoidance. Their behaviours, from long-distance migrations to specific site fidelity for pupping, demonstrate a deep connection to the marine ecosystems they inhabit. Studying grey seals in these undisturbed settings provides critical insights into their life cycles, ecological roles, and the importance of preserving wild habitats for the health of seal populations.

Wild grey seals are highly transient, covering substantial distances to access prey and breeding sites. Their migratory behaviours reflect the species' adaptability, ensuring survival through ecological flexibility (Bonner, 1999). This mobility is integral to their life cycle, with seals often traversing between shallow coastal waters and deeper offshore areas in pursuit of prey (Thompson et al., 1996).

Once the breeding season concludes, grey seals disperse over wide ranges in search of optimal foraging areas. These post-breeding migrations are essential for replenishing energy reserves lost during the energetically demanding breeding period. In addition to breeding-related movements, grey seals' foraging behaviour is highly mobile and opportunistic. They travel extensive distances to exploit prey availability, with their foraging grounds often varying in response to seasonal shifts in fish populations, oceanographic conditions, and other environmental factors. This mobility enables grey seals to exploit a range of habitats, from shallow coastal waters to deeper offshore environments, ensuring access to diverse prey species.

The annual movement patterns of grey seals are therefore complex and multifaceted, driven by a combination of biological imperatives, such as breeding and moulting, and ecological variables such as prey distribution. Understanding these patterns is crucial for conservation efforts, as disruptions to key habitats, whether breeding sites or foraging grounds, can have a significant impact on population dynamics and overall species resilience.

Over a period of 15+ years, Manx Wildlife Trust on the Isle of Man, have conducted detailed annual surveys of the Calf of Man, a small island off the southwest coast contained within the Calf of Man & Wart Bank Marine Nature Reserve, to observe the natural breeding behaviours of grey seals in undisturbed conditions, specifically focussed on site fidelity of returning breeding females and pup mortality.

Site fidelity is a crucial aspect of grey seal reproduction. Studies show that female seals frequently return to the same breeding location each year (Twiss et al., 2002), often pupping in the exact spot within their haul-out site. Such behaviours are particularly pronounced in undisturbed environments (Manx Wildlife Trust, 2018). However, human disturbance can weaken this fidelity, leading to abandoned pups and higher mortality rates.

A seal pup will largely remain on land for the first three weeks of its life, reliant on suckling from the mother to build up the strength needed to fend for itself and venture into the ocean as an independent seal once its mother has departed. During these weeks, the pup goes through 5 distinct stages of growth. With minimal human interference, the breeding females (cows) can fully focus on maternal care, ensuring the best chances of survival for their offspring. Disruption to feeds can dramatically increase pup mortality during this period.

Male grey seals (bulls) in these colonies engage in regular territorial challenges, vying for dominance and the opportunity to maintain control over a breeding site. The successful dominant male then has the first opportunity to mate with breeding females post weaning. These contests, though fierce, are part of the natural order and ensure that the fittest males pass on their genes. In the absence of human disturbance, these behaviours are carried out with minimal stress to the animals, allowing them to maintain the complex social dynamics that are essential for healthy reproduction.

In their natural habitats, grey seals are also highly attuned to environmental cues. They are quick to respond to potential threats, such as predators or harsh weather, by fleeing into the safety of the water. This heightened alertness is critical for their survival. In undisturbed settings, seals can rest

for extended periods, which is essential for maintaining their energy levels and overall health. Sensitivity and vigilance to disturbance is high in areas of low human activity.

In wild settings, grey seals maintain their role as apex predators, hunting independently for fish and other marine species. Where human interference is minimal, seals can spend hours foraging in the open ocean, returning to their haul-out sites to rest between trips. This sustainable hunting behaviour is a key aspect of their ecological role as apex predators in marine ecosystems.

Wild grey seals thrive in environments where human impact is minimal, displaying behaviours that have evolved to maximise their survival, reproductive success, and role within their natural ecosystem. Surveys conducted by Manx Wildlife Trust on remote grey seal pupping sites, provides a valuable glimpse into the lives of wild seals, highlighting the importance of preserving undisturbed habitats for the continued health and stability of grey seal populations.

Urban Seals: Behavioural Changes in Human-Populated Areas

Seals that inhabit human-populated areas such as harbours or marinas, exhibit a markedly different set of behaviours. These 'urban seals' often become habituated to human presence, resulting in the loss of natural wariness that characterises their wild counterparts. Habituation in grey seals can lead to a range of negative impacts on their overall well-being.

One of the most significant consequences of habituation is an increased risk of mortality. Urban environments expose seals to numerous risks, including boat strikes, entanglement in fishing gear, and pollution from industrial activities (Womble & Gende, 2013). Additionally, seals scavenging on human refuse or discarded fish are more prone to poor nutrition and malnutrition (Beck et al., 2003). Any reliance on humans for food, whether through direct feeding or scavenging, can lead to dietary imbalances. Seals accustomed to scavenging are less likely to engage in natural foraging behaviours, leading to a decline in hunting skills over time. This not only affects their ability to thrive independently but also increases the likelihood of stress.

Constant human presence in urban areas disrupts seals' resting and breeding cycles. Frequent disturbances from boat traffic, noise pollution, and close human interactions lead to chronic stress, which has been shown to impair immune function and reproductive success in seals (Paterson et al., 2012). Disturbances during the breeding season can be significantly detrimental. When seals are disrupted during critical periods of nursing, it can lead to premature weaning or abandonment of pups, lowering pup survival rates.

The cumulative impact of increased disturbance, stress, and poor nutrition in urban settings negatively affects grey seals' reproductive success. Stress caused by human/seal interaction has been shown to interfere with both seal mating and pup-rearing behaviours. Female seals may be less likely to nurse their young effectively, while males may face greater competition and disruption during the breeding season, affecting the birth rate and overall reproductive fitness of urban populations.

Additionally, seals living in close proximity to humans may experience a decline in overall quality of life. Their natural behaviour is altered as they become more reliant on humans for food or protection, leading to a breakdown in their ecological role as apex predators and important players in marine ecosystems. The resulting imbalance can have ripple effects on local fish populations and marine biodiversity.

This loss in natural behaviours is one of the most concerning aspects of urban seal adaptation. Seals that become tolerant of human activity are more likely to suffer injury or mortality. This habituation diminishes their ecological role, as their predatory instincts become impaired (Kovacs et al., 2016). Adapted tolerance to disturbance is commonly observed in seals who breed in wild secluded sites but then migrate into human-populated territories. When at the wild remote haul-out sites, they remain highly vigilant, yet at sites where there is a regular increase in human activity, the same individual seal presents a greater tolerance to disturbance.

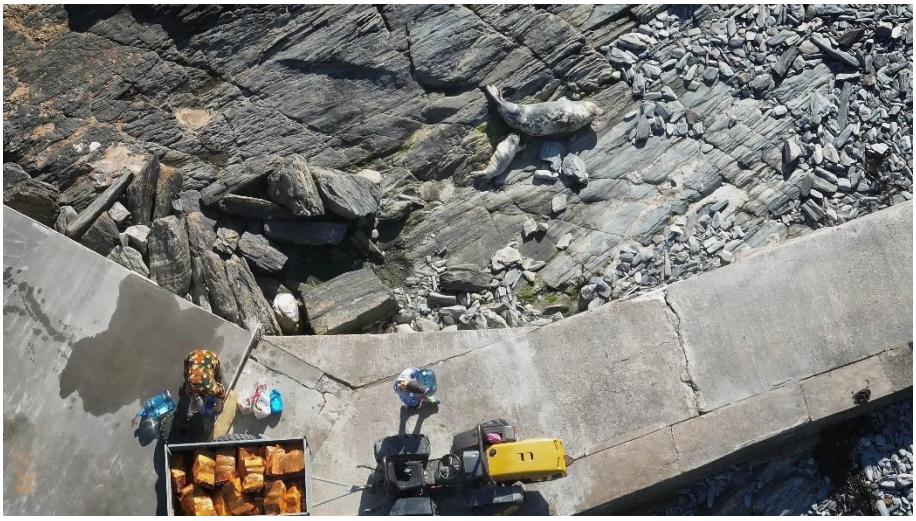
During the 2023 and 2024 surveys on the Calf of Man, experienced grey seal mothers using the South Harbour (SH) pupping site were observed to be significantly more tolerant of human disturbance than those at neighbouring pupping sites, such as the Puddle (PU). The SH site is a small dock where the island's supply boat delivers food and equipment to wardens once a week throughout the pupping season. In addition, the supply boat operates commercially and brings day visitors to the island, often resulting in prolonged period mooring at the SH jetty during grey seal pupping season. During the 2024 season, the supply boat was observed docking at SH in close proximity (≤5 metres) to the grey seal mothers and pups that use the adjacent beach and rock ledges, remaining at the dock for approximately 30 minutes on a supply run, or in excess of 2 hours when transiting day visitors. In contrast, two boats were observed entering the PU area during the same season, not anchoring/mooring and maintaining a distance more than 100 metres from the pupping beaches and drifting for less than five minutes before departing. Despite this, both boats observed at PU triggered stress responses (shuffling and flushing) in resting grey seals. In addition, one commercial tour boat operator manoeuvred within 5 metres of the prominent pupping beach

at the puddle which triggered a stress response in a suckling mother, resulting in temporary abandonment of the pup disrupting a critical feed.

At the SH dock, regular observations were made of wardens and volunteers conducting tasks of unloading and loading the supply boat in close proximity to the seal mothers and pups. Despite frequent human presence and activity, these seal mothers, particularly those who had used the site for multiple seasons, displayed a remarkable tolerance to this disturbance. They would typically raise their heads to assess the situation, remaining in a vigilant but calm state. Importantly, these mothers did not exhibit behaviours commonly associated with heightened stress, such as abrupt movements, vocalisations, or attempts to leave the site. Instead, they often continued their regular resting routines and were recorded suckling their pups within ≤5 metres of the dock activity.

One specific seal, identified by her field catalogue number 015, was particularly noteworthy. This individual first pupped on the island in 2010, and by 2024, had given birth to her eighth pup (Fig 1 P17) on the island and her fourth pup at the SH site. Despite frequent human activity at SH, she exhibited minimal signs of distress, continuing her usual maternal behaviours, such as socialising with, suckling her pup and resting in close proximity to human activity on a regular basis.

Figure 1. Adult female grey seal 015, hauled out at SH suckling her pup P17 in close proximity to human activity. Manx Wildlife Trust/Duncan Kenny. 2024.



The greater tolerance to disturbance exhibited by seal 015 and other experienced mothers at SH can be explained by several factors. Firstly, seals, like many non-human animal species, can habituate to non-threatening, consistent human activity over time (Andersen et al., 2016). Seal 015, having used SH as a pupping site for multiple seasons, may have learned that the presence of humans in the area poses no immediate threat to her or her pup, allowing her to remain calm. This contrasts with less experienced or younger mothers at PU, who may not have been exposed to regular human activity and thus displayed more heightened stress behaviours, such as flushing and potential abandonment of their pup, in response to even minimal disturbances.

Additionally, more experienced mothers tend to exhibit greater maternal confidence and behavioural stability. This could be due to physiological adaptations, as well as learned experience in dealing with environmental and anthropogenic factors (Twiss et al., 2002). Younger, less experienced mothers may not yet have developed these skills, leading to increased anxiety and defensive behaviours when faced with even minor disturbances (Beck et al., 2003). Seal 015's extensive experience as a mother and her repeated use of a site where human presence is predictable and non-invasive, likely contribute to her calm demeanour, demonstrating that experience and habituation play crucial roles in how individual seals respond to potential threats (Sih, Ferrari, and Harris, 2011). Seals that do not flee from approaching boats are more likely to be struck or entangled in fishing nets. Additionally, seals that have lost their natural fear of humans may venture into more dangerous areas, such as commercial/industrial zones, where they are exposed to pollution, poor water quality, or physical harm.

This habituation also reduces the effectiveness of wildlife management strategies. In wild populations, efforts to conserve seals through creating protected areas and limiting human access are crucial to minimising disturbance. However, urban seals, accustomed to human presence, are less likely to respond to these conservation efforts, making them more vulnerable to human-related threats.

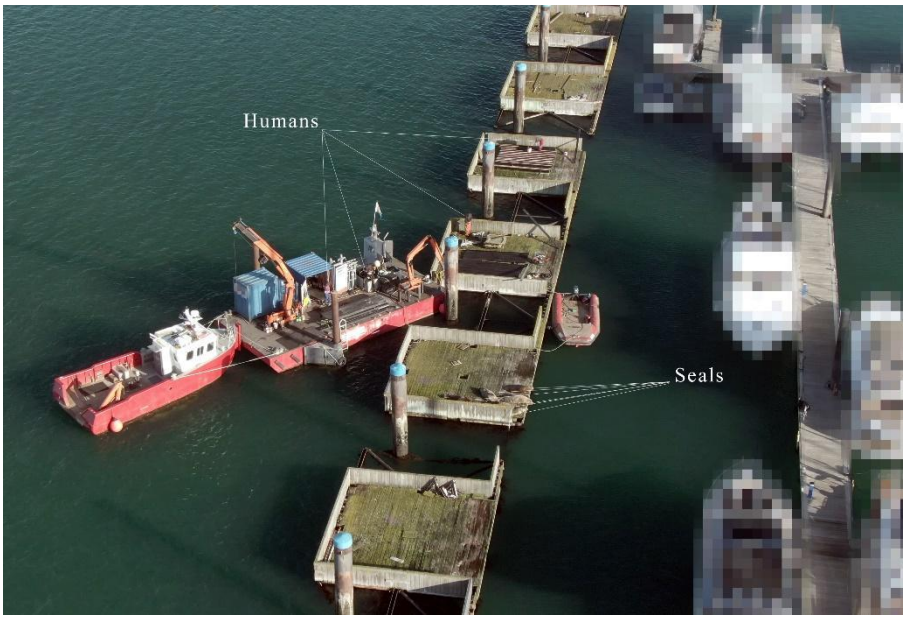
Figure 2. Supply boat and staff (a) at SH dock after loading the vehicles. 5x greys seals presenting high tolerance to disturbance: Pup P17 with mother 015 suckling (b), and pup P24 (c) resting whilst mother 502 (d) fends off an unknown bull seal in the shallows. Manx Wildlife Trust/Duncan Kenny. 2024.

Generalised guidance around ensuring humans maintain set distances away from wildlife is positive, however as wild and urban wildlife behaviours vary, so must the need to adapt guidelines around varying habitats. For example, if risk of disturbance is high at remote haul-out sites and access can be managed at a safe distance, then this is reflected in the guideline distance set (example 100/200m). However, if urban habitats such as busy commercial and recreational harbours have regular seal haul-outs, to set the same distance restriction could be perceived as unrealistic and may create conflict with regular commercial and recreational water users. In addition to this, urban seals are prone to approach kayaks, SUPS, wild swimmers and divers as they go about their daily activities. These encounters may be on the seal's terms, but they are a product of desensitisation to human activity in an urbanised habitat.

Grey seals rely on haul-out sites to rest, digest, moult, and engage in social interactions. Traditionally, these haul-out sites include remote beaches and coves that are inaccessible to human interference. However, in areas where seals and humans overlap, an increase in human coastal activity is affecting the availability of these natural sites, forcing seals to adapt to new environments. The behavioural patterns of grey seals using natural haul-out sites on the Calf of Man and comparably using the human-fabricated platforms at Brixham Marina in Devon, present observable

variants. Anthropogenic structures, such as tidal platforms can alter the grey seal's natural behaviour and can have potential implications for human-seal conflict, tourism, and conservation.

Figure 3. Commercial repair operations to Brixham Marina wave barrier, showing humans working in close proximity to hauled out grey seals. Duncan Kenny. 2022.



In natural environments, grey seals exhibit a clear pattern of behaviour that aligns with tidal cycles. During low tide, seals rest and sleep, traditionally on beaches and rocks, taking advantage of the exposed intertidal zone. As the tide rises, natural haul-outs reduce in size, prompting seals to return to the water, either to hunt or swim until the next low tide (Cronin et al., 2018). This behaviour allows the seals to synchronise their resting and foraging activities with environmental cues, further conserving energy and avoiding potential threats.

However, as human activity increases on these natural sites, such as dog walking, kayaking, stand-up paddleboarding, and other recreational pursuits, seals are increasingly disturbed. Seals can be forced to vacate their haul-out sites prematurely, causing unnecessary energy expenditure and stress, which may impact their health and reproductive success (Andersen et al., 2016).

Brixham Marina's protective wave barrier is made up of 22 tidal platforms, each approximately 5 metres square. These platforms present an opportune environment for seals, offering them a

consistent resting place that moves with the tide cycles. This structure allows seals to avoid returning to the water at high tide, providing uninterrupted resting periods. However, the platforms can alter a seals' natural rhythm. Typically, more active during high tide when hunting is more efficient, a seal on these platforms may remain sedentary for longer periods than they would in a natural environment (Harding et al., 2017).

Whilst these platforms provide a refuge from human disturbance on busy beaches, they introduce new challenges. Seals sharing space in close proximity with commercial and recreational human fishing operations pose potential conflicts, particularly as seals are perceived to raid fish stocks, leading to tension between the two groups (Smith & Harwood, 2021). In addition, these platforms have become a point of interest for tourist boats, increasing human-seal proximity and risking further disturbances or increased risk to habituation.

There are several comparative behavioural observations to note. On the Calf of Man, seals hauled out on beaches during low tide, are able to maintain a predictable resting behaviour pattern as the incoming tide pushes the seal into the water due to a lack of available dry substrate. In contrast, Brixham seals rest for considerably longer periods, as their resting platform raises and lowers with the tide meaning they are not impacted by a reduction in space.

In response to human presence and recreational activities that take place on the beach and rocks, natural haul-outs are increasingly disturbed, which commonly leads to stress and flushing of seals into the water, increasing risk of injury. The wave barrier platforms in Brixham provide a relatively undisturbed area as they are only accessible to humans by boat or restricted Marina foot access. However, the rise in eco-tourism and human activity around Brixham Harbour introduces a new form of human presence, often leading to behavioural changes such as increased alertness or premature re-entry into the water. However, unlike the shallow rocky foreshore of the natural haul-out sites, the wave barrier platforms allow the seals immediate and direct access into deep water with no obstacles, thus reducing risk of injury.

Grey seals in Brixham exhibit an increased reliance on artificial haul-outs because of diminishing natural options. This adaptation highlights the growing competition between seals and humans for coastal space and resources (Smith & Harwood, 2021). The adaptation of grey seals to human-fabricated platforms in Brixham reflects a broader trend of wildlife modifying their behaviour in response to shrinking natural habitats. Whilst these platforms offer a temporary solution to overcrowding and human disturbance, they come with their own set of challenges. A seal's altered resting pattern could have long-term effects on its energy budget, reproduction, and overall health, and secondly, an increased overlap between seal habitats and commercial fishing and tourism industries presents a growing challenge in managing human-wildlife interactions (Duck & Morris, 2020).

As human activity continues to rise along the UK coastline, an increase in the numbers of seals using human-fabricated structures as regular haul-out sites is likely. This shift will require robust management strategies to mitigate conflict between seals, fisheries, and tourism (Smith & Harwood, 2021). Collaborative conservation efforts are essential for balancing the specific needs of both seals and humans, whilst also ensuring the long-term survival of grey seal populations within the region.

Although the platforms in Brixham offer an alternative to increasingly disturbed natural haul-out sites, they do raise important questions about the long-term impact on seal behaviour and welfare. As the UK coastline becomes busier, further research is required to develop strategies that protect both seal and human interests to help foster a positive coexistence between marine wildlife and the expanding human presence.

Whilst wild seals continue to thrive in relatively undisturbed environments, urban seals face a host of challenges that threaten their long-term survival. Increased mortality rates due to entanglements, collisions, and pollution, combined with poor nutrition and higher stress levels, contribute to reduced reproductive success and overall decline in population health.

The habituation of urban seals to human presence and activity exacerbates these problems. Seals lose their natural instincts for evasion and hunting and as a result, their ecological role is diminished, creating an unhealthy dynamic for both the seals and their ecosystems.

Whilst grey seals may appear well-adapted to urban environments, the negative impacts of human disturbance, habituation, and altered behaviours far outweigh the perceived benefits. Long-term conservation strategies should aim to reduce human-seal interactions in these environments, ensuring that grey seals can maintain their natural behaviours, thrive in their wild habitats, and contribute to the balance of marine ecosystems. Only by minimising human interference can we hope to preserve the health and resilience of these remarkable marine mammals.

Function of Resting Behaviours

Grey seals exhibit distinct body positions while resting at natural haul-out sites. These positions serve multiple purposes, including thermoregulation, social interaction, and predator vigilance. Body posture also varies depending on several factors, such as environmental conditions, individual health, and social hierarchy.

One of the most common positions observed in the grey seal is the "banana" position, where the seal can be seen to arch its body and raise its head and tail off the ground (Bonner, 1999). This posture minimises heat loss by reducing the surface area to substrate ratio, which is particularly useful in colder environments where the substrate is cooler (Twiss et al., 2002). A raised head and tail also allows the seal to remain vigilant to potential predators or disturbances without needing to frequently move.

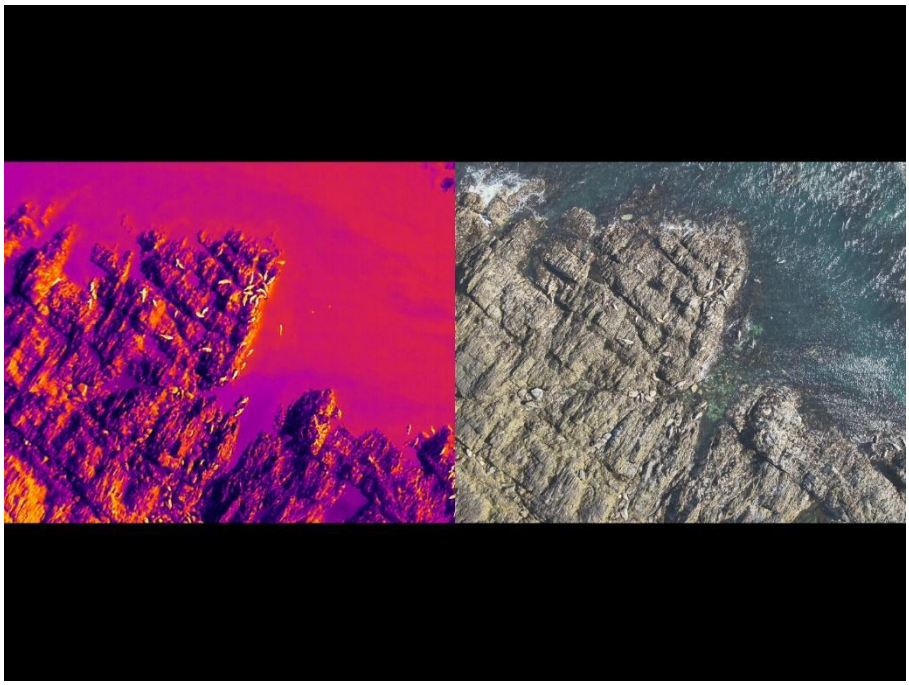
Grey seals often rest on their sides with one flipper extended. This is referred to as lateral resting. This position enables the seal to remain stable on uneven terrain, such as rocky shorelines, whilst maintaining thermoregulation by exposing or shielding parts of their body to the sun or wind (Beck et al., 2003). Lateral resting can also indicate a relaxed state when the seal is not under stress from other seals or external threats.

Another common posture is sternal resting. In this position the seal lies on its belly with both flippers tucked beneath the body. This position offers greater stability and allows the seal to quickly rise if threatened (Bonner, 1999). Sternal resting is typically observed in situations where seals are more cautious, such as during busy haul-out periods when there are high levels of social interaction or environmental disturbance (Thompson et al., 1996).

When resting at natural haul-out sites, it's common for grey seals to occupy a wide area of the intertidal zone, where they often exhibit multi-directional body positions. This behaviour is influenced by a variety of factors including tidal changes, substrate type, and social dynamics. This

spatial variation in positioning is important for helping seals adapt to the dynamic nature of their haul-out environment, particularly in areas with strong tidal influences.

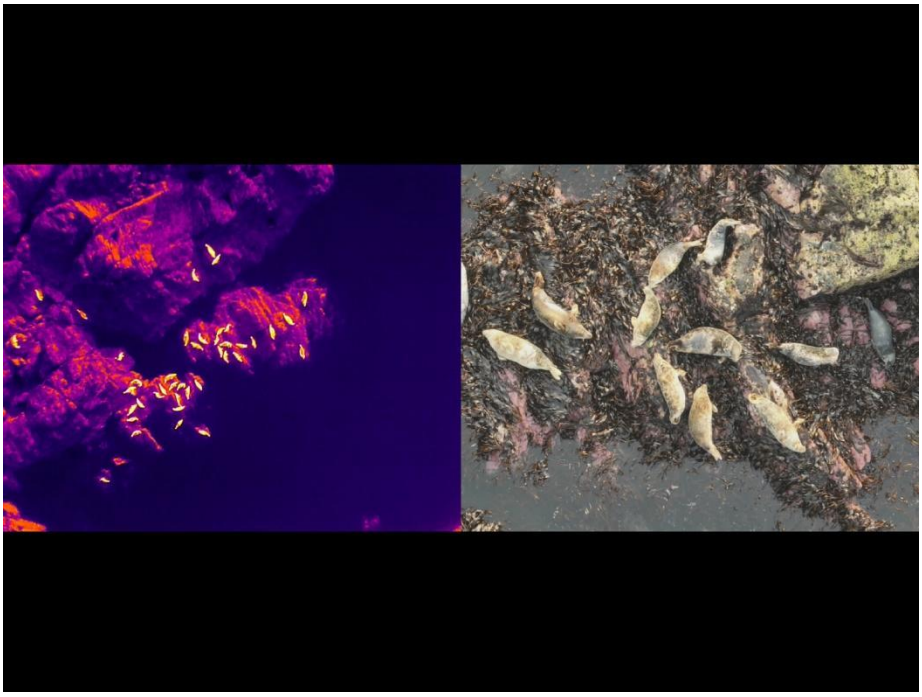
Figure 4. Simultaneous thermal and standard drone images of grey seals hauled out on the Calf of Man illustrating wide area dispersal at low tide. Manx Wildlife Trust/Duncan Kenny. 2024.



Multi-directional body positioning is thought to serve several key functions. Firstly, varying body orientations enable seals to better regulate their temperature. By adjusting the angle of their body relative to the sun or wind, seals can either expose more surface area to cool down, or shield themselves to conserve warmth (Beck et al., 2003). This is particularly important during periods of prolonged exposure on land, where temperature regulation becomes more difficult than in water. The spacing of seals within the intertidal zone also reflects the social dynamics within the group.

While grey seals are not considered highly social, they do exhibit some degree of social structure during haul-outs. Dominant individuals often occupy the prime resting spots, such as those closer to the water's edge or on higher ground, while subordinate seals are forced to take less favourable positions (Twiss et al., 2002).

Figure 5. Simultaneous thermal and standard drone images of grey seals hauled out on the Calf of Man illustrating multi-directional resting body positions. Manx Wildlife Trust/Duncan Kenny. 2024.



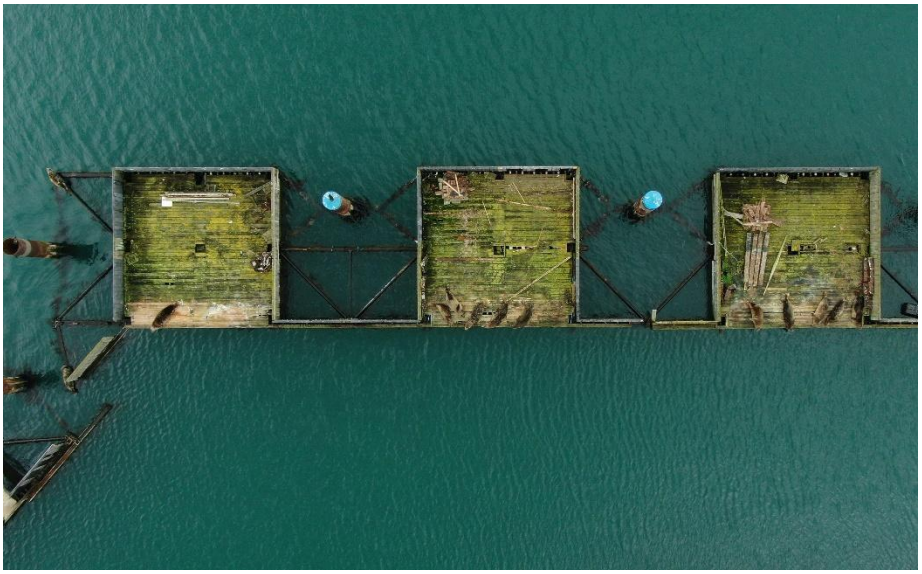
When resting, grey seals typically maintain a good distance from one another, particularly in less dense haul-out sites. This spacing likely reduces aggression by allowing individuals to establish their own space for thermoregulation and easier access to the sea (Thompson et al., 1996). However, in more densely populated areas or during peak haul-out periods, this distance decreases, resulting in increased social interactions, such as vocalisations and posturing, which may help to establish social order and reinforce dominance hierarchies (Twiss et al., 2002).

On artificial or human fabricated haul-out sites, grey seals exhibit behaviours that suggest heightened stress and a greater need for situational awareness. Uniform body positions, with heads aligned towards perceived threats or escape routes, suggest a collective response to the unpredictability of human presence. This posture facilitates a quicker reaction to potential threats by minimising the time required to re-enter the water if disturbed (Paterson et al., 2012).

Unlike natural haul-out sites that tend to be more secluded and may have fewer frequent disturbances, human-fabricated sites are often situated in areas with increased human activity, such as harbours, marinas, or near coastal developments. Consequently, seals at these sites must remain

more vigilant, regularly scanning their surroundings to assess the risk of disturbance from nearby boats, people, or even dogs (Smith & Harwood, 2021). This heightened need for awareness raises energy expenditure and this can impact overall health as it reduces the time available for resting, which is a crucial period for thermoregulation and recuperation (Andersen et al., 2016).

Figure 6. Grey seals hauled out on human fabricated structures in Brixham, Devon, illustrating unidirectional resting body positions, heads facing exit passage. Duncan Kenny. 2022.



Group vigilance is a key survival strategy for grey seals who inhabit human fabricated haul-out sites. By maintaining similar body positions and facing potential threat directions, grey seals collectively enhance their ability to detect disturbances early. This uniform positioning enables a more efficient response to threats, as individuals are better synchronised in their escape behaviour (Twiss et al., 2002). At these sites, seals are often forced into closer proximity with one another due to the limited space on artificial platforms or docks, further reinforcing the need for coordinated vigilance (Bonner, 1999).

Human disturbances at fabricated haul-out sites can significantly alter the natural behaviour of grey seals. Increased vigilance comes at a cost, as individuals must divert energy that would otherwise be used for resting, foraging, or socialising (Duck & Morris, 2020). Seals disturbed too frequently

may haul-out less often, resulting in reduced time on land for thermoregulation and social interaction, and ultimately a reduction in overall fitness and reproductive success (Beck et al., 2003).

Repeated disturbances can lead to habituation, where seals become less responsive to human presence, or sensitisation, where they become more reactive over time (Paterson et al., 2012). Both outcomes can be detrimental, as habituation increases the risk of human-seal conflict, while sensitisation can lead to seals abandoning preferred haul-out sites altogether, potentially pushing them into less suitable or more dangerous environments (Smith & Harwood, 2021).

Despite the challenges posed by human fabricated haul-out sites, grey seals exhibit remarkable behavioural flexibility. Their ability to adjust resting postures, modify vigilance levels, and adopt synchronised group behaviours demonstrates an adaptive response to increased human presence (Sih et al., 2011). These adaptations allow them to continue utilising these sites, which are often necessary in regions where natural haul-out spaces have been reduced due to coastal development or habitat degradation (Roman et al., 2014).

While grey seals may adapt to these artificial environments, it is essential to consider the long-term impacts of increased disturbance and stress. Continued research into their behaviour at human fabricated sites can inform management strategies aimed at minimising human-seal conflicts and ensure that seals have access to suitable, undisturbed haul-out areas where they can rest and recuperate without excessive disruption (Smith & Harwood, 2021).

Mating Behaviours at Remote and Human-Frequented Sites

Grey seals display a variety of mating behaviours that are influenced by environmental conditions, including the presence of humans. While grey seals are renowned for their exceptional adaptability, the features of their haul-out sites can greatly influence their mating strategies. These sites range from remote coves and beaches to areas heavily frequented by humans. Classic examples are harbours and the busier beaches.

In more secluded environments, such as remote beaches or isolated coves, grey seals typically engage in mating on land or in the shallow waters adjacent to haul-out sites. These areas offer the space needed by males to establish their territory. Dominant males often compete for access to females, displaying aggressive behaviours that include vocalisations, posturing, and physical confrontations (Boness & James, 1979). Females typically choose their mate based on dominance and their success in maintaining territory (Twiss et al., 2007).

During mating season in the UK, which generally occurs between September and December, males patrol the breeding sites, attempting to monopolise access to multiple females. In remote areas, males frequently copulate with females on land, taking advantage of the space and stability offered by sandy or rocky substrates (Anderson & Fedak, 1987). On-land mating, observed primarily at secluded haul-out sites, often results in intense physical contact. Males may bite the females' neck to hold her in place, as he positions himself to achieve copulation (Twiss et al., 1994).

The prolonged presence of seals at these breeding sites facilitates extended courtship. This helps in strengthening social bonds and enables females to choose a high-quality mate. When mating does occur on land, particularly in isolated areas, the male often maintains physical attachment with the female post-copulation. This resting behaviour, wherein the male continues his bite grip and physical dominance, can last anywhere between 20 and 35 minutes and is thought to serve multiple functions. Firstly, it ensures successful insemination by maintaining a prolonged connection during the crucial moments post-ejaculation.

Figure 7. Male grey seal dominating female during the mating process on the Calf of Man. Duncan Kenny. 2023.

Secondly, it may act as a form of mate guarding, preventing rival males from attempting to mate with the female immediately afterward, an action that could reduce the chances of successful fertilisation (Twiss, 1991). These behaviours ensure the male's genetic material is preserved by increasing the likelihood of a successful fertilisation. The bond is broken by the female before they part ways. Post copulation, the male will remain at the pupping site if there are other breeding females present with pups, but the female will leave the site.

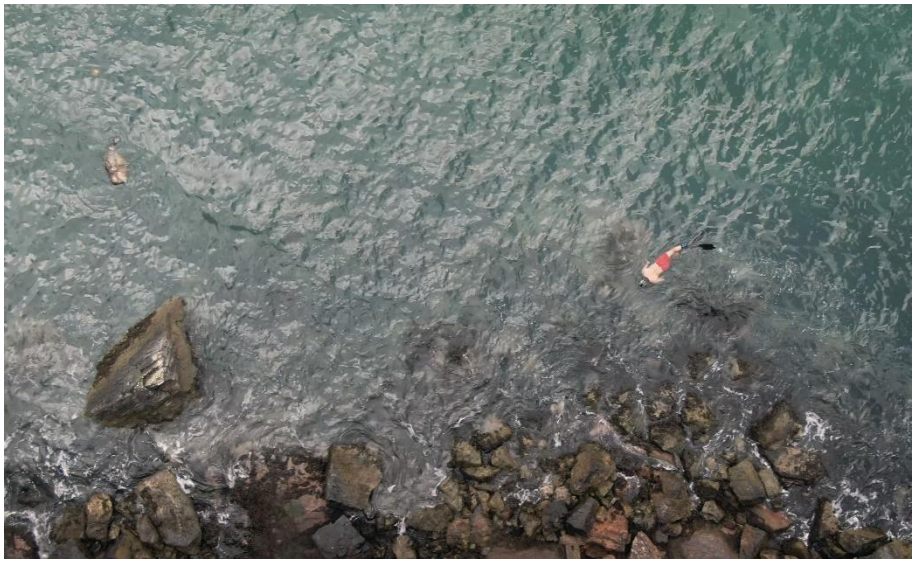
Figure 8. Grey seals in the post copulation 'rest' on the Calf of Man. Duncan Kenny. 2023.

In wild, less-disturbed settings, grey seals may also mate in the shallow waters adjacent to haul-out sites. Shallow waters provide buoyancy, facilitating copulation while still allowing the male to maintain physical control over the female. This type of mating behaviour, commonly observed at remote coves, is far more energy-efficient due to the supportive nature of the water, while still offering protection from other apex predators (Boness et al., 1993).

In contrast to these remote sites, grey seals in areas with higher human activity, such as harbours and busier beaches, demonstrate distinct shifts in their mating behaviour. This change in behaviour is likely a response to the need for increased vigilance in areas where humans are present, as well as a reduction in available land space for undisturbed mating (Hastie et al., 2015).

In harbours or frequently visited coves, mating is often observed on the surface of the water rather than on land or within the shallows. This behaviour may be a direct adaptation to the disturbance posed by human activity. Water-based mating reduces the likelihood of human interaction or interruption during critical mating periods. Unlike the more aggressive land-based copulation, mating in these areas tends to be less physically intense (Boness & James, 1979), and for a shorter duration of around 8-10 minutes.

Figure 9. Grey seals mating on the water surface in close proximity to a human snorkelling. Churston Cove, Brixham. Duncan Kenny. 2022.



In some cases, seals have been observed mating entirely underwater, particularly in regions with increased human activity. This may offer an added level of security and privacy from human onlookers (Hastie et al., 2015). Mating underwater also provides additional buoyancy, reducing the physical strain on both the male and female compared to mating on land or at the surface. This behaviour is especially advantageous in crowded or noisy environments, enabling seals to remain undetected by humans while meeting their reproductive needs.

Human-frequented sites, particularly harbours, often provide limited space for seals to establish any form of territory. Seals are highly sensitive to disturbance during breeding, and human activities can cause females to flee or males to abandon territorial displays (Giese, 1996). As a result, dominant males may have fewer opportunities to monopolise females on land, leading to more frequent mating in water where space is not as constrained. This shift may also contribute to the observed reduction in aggressive male-male competition at these sites (Hastie et al., 2015).

Increases in the Transient Grey Seal Population Observed in Brixham Harbour Since 2015

The transient grey seal population in Brixham Harbour has seen a marked increase over the past decade, highlighting significant shifts in habitat usage among marine mammals adapting to human-modified environments. In 2015, survey data recorded 26 individual seals utilizing the wave barrier at the northern aspect of MDL Brixham Marina as a resting/haul-out site. By December 2024, this number had grown to 67 individuals, indicating an annual increase that may reflect broader ecological trends influenced by urbanization, habitat availability, and human-seal interactions.

The floating platforms integrated into the Brixham Marina wave barrier, a human-fabricated structure, provide grey seals with an artificial but ecologically significant haul-out habitat. These platforms offer a stable resting environment that closely aligns with the species' natural haul-out behaviours, which are essential for thermoregulation, social interactions, and recovery from foraging activities. However, the ecological characteristics of this site differ markedly from those of traditional natural haul-out locations, such as rocky shores and sandbanks.

Natural haul-out sites often require seals to navigate uneven terrain and shallow waters, which can increase their exposure to predation and the risk of injury. By contrast, the wave barrier's design provides immediate access to deep water, enhancing escape efficiency during disturbances. This reduced energy expenditure for safe retreat may influence the seals' habitat selection, favouring the wave barrier as a low risk resting site. This adaptation underscores how anthropogenic structures can alter habitat-use patterns by mitigating ecological constraints typically associated with natural environments.

The transient grey seal population utilising the wave barrier has also exhibited behavioural adaptations that highlight the interplay between ecological and anthropogenic factors. This habituation reflects the predictable nature of the wave barrier environment, where human

presence, while frequent, poses minimal direct threats. Such tolerance may reduce stress-related energy costs and allow seals to exploit the benefits of this artificial habitat more effectively.

Figure 10. The 22 platform that make up the wave barrier at MDL Marina Brixham, South Devon. Duncan Kenny. 2024.

From an ecological perspective, these findings suggest that human-fabricated structures, while initially disruptive, can become integrated into marine ecosystems, providing alternative habitats that support species with adaptable behaviours. However, the long-term ecological consequences, such as potential shifts in local population dynamics or alterations in interspecific interactions, warrant further investigation. Understanding the balance between ecological benefits and the risks associated with anthropogenic habitats is crucial for informed management of human-wildlife interactions in coastal environments.

Long-term observational data highlight distinct seasonal patterns in grey seal usage of the Brixham Marina wave barrier, with peak presence recorded between September and February. This temporal trend aligns with key life-history stages, including post-breeding recovery, moulting, and increased energy demands during colder months. The platforms provide a stable and secure resting environment during these energetically taxing periods, fulfilling a critical ecological function for transient individuals.

The peak in site utilization following the pupping season is particularly noteworthy, as it corresponds to a time when adult seals require extended haul-out periods to replenish energy reserves depleted during reproduction. Additionally, moulting demands elevated resting time to support the physiological processes involved in fur regeneration. The wave barrier's stability and proximity to foraging grounds may reduce the energy costs associated with travel and recovery, further enhancing its ecological value.

Evidence of high site fidelity and increasing seal numbers at the wave barrier underscores its growing importance as a supplementary habitat within an anthropogenically altered landscape. Such trends suggest that the wave barrier plays a compensatory role, mitigating habitat loss or degradation in surrounding areas. However, the reliance on artificial structures raises questions about the long-term implications for local and regional seal populations, particularly in the context of changing environmental conditions and human activities.

These findings emphasize the need for continued monitoring and integrative management strategies to balance human development with the ecological requirements of marine wildlife. Understanding the drivers behind habitat selection and temporal patterns in artificial environments can inform conservation efforts and promote coexistence in shared coastal spaces.

The increasing presence of grey seals at Brixham Harbour has highlighted long-standing tensions between conservation efforts and local fisheries, rooted in the perceived competition for marine resources. Historically, seals have been a source of conflict due to their proximity to fishing activities, with fishers often blaming them for depleting fish stocks or damaging gear. These perceptions have, at times, escalated into direct persecution, undermining both seal welfare and broader conservation goals.

Seals are frequently scapegoated as the cause of reduced fish yields, despite substantial evidence indicating that overfishing, habitat degradation, and climate-driven changes are the primary drivers of fish stock depletion (Smith & Harwood, 2021). While seals do predate on commercially valuable species, their overall impact on fisheries is minor compared to industrial-scale fishing operations.

Misattributing blame to seals obscures the larger ecological and anthropogenic factors contributing to marine resource declines, perpetuating conflict.

Historical records document instances of seal harassment, injury, and entanglement in fishing gear, both accidental and intentional. These incidents contravene wildlife protection laws and exacerbate tensions between conservationists and coastal communities. For example, seal entanglement not only results in physical harm to the animals but also symbolizes the broader challenges of coexistence between humans and marine predators (Duck & Morris, 2020).

The roots of this conflict lie in the economic dependency of coastal communities on fisheries. As fish stocks declined due to overexploitation and environmental degradation, competition for resources intensified, with seals becoming an easy focal point for frustration. This dynamic reflects broader ecological shifts where apex predators are often blamed for issues arising from unsustainable human activities (Hammond & Grellier, 2006). Bridging this divide requires fostering understanding of the ecological roles of seals, including their contributions to healthy marine ecosystems, and promoting sustainable fishing practices. Educational initiatives have shown promise in reframing seals as indicators of ecosystem health rather than as competitors (Madden & McQuinn, 2014).

Eco-tourism has introduced both opportunities and challenges to human-seal interactions at the harbour. The visibility of seals on the wave barrier attracts tourists, providing opportunities to raise awareness and fund conservation efforts. However, unregulated tourism risks disturbing seals during critical resting periods, compounding existing tensions with fishers, who may view such activities as prioritizing conservation and tourism over traditional livelihoods. Effective management strategies, including setting guidelines for wildlife interactions and promoting shared benefits between tourism and fisheries, are essential to fostering coexistence.

This historical and ecological context underscores the importance of collaborative approaches to mitigate human-seal conflict. By addressing the root causes of resource competition and integrating

the needs of both local communities and wildlife, sustainable solutions can be achieved that support marine biodiversity and human livelihoods alike.

The grey seals' observed tolerance to disturbance at the Brixham Marina wave barrier underscores their behavioural flexibility in adapting to human-dominated environments. Unlike natural haul-out sites, where seals often face challenging terrain and limited escape routes, the wave barrier's design provides immediate access to deep water. This proximity enhances escape efficiency during disturbances, reducing stress and injury risks. Consequently, the wave barrier serves as an attractive haul-out location, meeting the seals' needs for rest and recovery while minimizing energetic costs associated with disturbance response.

However, this behavioural adaptation raises important conservation concerns. While human-fabricated structures like the wave barrier can serve as temporary refuges, they lack the complexity and ecological functionality of undisturbed natural habitats. Over reliance on artificial sites may alter natural behaviour patterns and inadvertently increase seals' exposure to anthropogenic risks. For example, habituation to human presence can lead to maladaptive behaviours, such as scavenging near fishing vessels or approaching boats, heightening the potential for entanglement, injury, and conflict with human activities.

Additionally, artificial haul-out sites may not fully support the ecological roles and life-history requirements of seals, such as pup-rearing or social bonding, which are better facilitated in secluded natural habitats. The long-term implications of relying on human-fabricated structures remain uncertain, particularly as these environments may expose seals to chronic disturbances or limit their ability to avoid interactions with humans.

From a conservation perspective, the increasing use of anthropogenic habitats emphasizes the need for a balanced approach that addresses both immediate habitat availability and the preservation of natural ecosystems. Efforts should focus on mitigating human-seal conflicts at artificial sites while safeguarding and restoring natural haul-out habitats to ensure their long-term viability. Public

education, strict wildlife interaction guidelines, and habitat management strategies can reduce the risks associated with habituation and promote coexistence.

While the seals' behavioural flexibility demonstrates their resilience in adapting to human-altered environments, reliance on artificial structures like the wave barrier should not replace conservation priorities centered on protecting natural habitats. Understanding and managing the ecological trade-offs associated with these adaptations are crucial to ensuring the species' long-term survival in an increasingly anthropogenic world.

Effectively managing the increasing transient grey seal population at Brixham Harbour requires a multifaceted approach that balances the ecological needs of the seals with the economic and cultural priorities of the local fishing community. Achieving this balance will depend on the implementation of practical and collaborative strategies, including:

1. Education and Outreach: Raising public awareness about the ecological roles of grey seals and their contributions to marine biodiversity can help foster empathy and support for conservation efforts. Educational campaigns should highlight the importance of seals as apex predators in maintaining healthy marine ecosystems and dispel misconceptions about their impact on fisheries.

2. Regulation of Human Activities: Establishing and enforcing guidelines for vessel operations and recreational activities near the wave barrier during peak seal presence can reduce disturbances. Temporal zoning, speed restrictions, and minimized human activity buffer zones around haul-out sites are effective measures to protect seals from unnecessary stress and disruption.

3. Collaborative Management: Engaging stakeholders—including fishers, conservationists, eco-tourism operators, and local authorities—in co-developing management plans can mitigate conflict and promote coexistence. Solutions could include gear modifications to prevent seal entanglement, shared economic benefits from ecotourism, and transparent dialogue to address community concerns.

4. Research and Monitoring: Long-term studies of the seal population are essential for tracking behavioural adaptations, health trends, and ecological impacts. Monitoring can also identify potential risks associated with increased human-seal interactions and provide data to refine management strategies.

The resilience and adaptability demonstrated by the transient grey seals at Brixham Harbour highlight their capacity to navigate human-altered environments. However, their growing presence also underscores the complexities of managing human-wildlife interactions in shared spaces. As seals increasingly utilize artificial habitats like the wave barrier, it is crucial to address the underlying causes of conflict, such as competition for resources and perceptions of blame for fish stock declines.

By prioritizing education, collaboration, and evidence-based decision-making, it is possible to foster a sustainable coexistence that benefits both seals and the communities that rely on coastal ecosystems. This balanced approach will ensure that conservation efforts align with the social and economic realities of human stakeholders while safeguarding the ecological integrity of shared marine habitats.

Maintaining Biodiversity

The North Atlantic grey seal plays a crucial role as a keystone species within the marine ecosystem. Keystone species are organisms that have disproportionately large impacts on their environment relative to their abundance or biomass, influencing the structure and health of ecosystems (Paine, 1969). The removal or loss of a keystone species often leads to significant changes within the ecosystem, potentially causing the collapse of the entire system. Grey seals, as top predators, have profound impacts on the trophic dynamics of the ecosystems in which they live.

As apex predators, grey seals occupy a high trophic level, primarily feeding on fish such as sand eels and herring (Hammond & Grellier, 2006). Through predation, grey seals help to regulate fish populations, which in turn influences the lower trophic levels. This top-down regulation helps prevent some species, especially mesopredators or prey species, from overpopulating and disrupting the ecosystem's balance. For example, if the grey seal was removed from its ecosystem, fish like the sand eel would experience an unchecked population growth leading to overgrazing on plankton and a subsequent disruption to the base of the marine food web (Estes et al., 2011). By regulating the population size of prey species, grey seals play an indirect role in supporting the health and diversity of marine ecosystems. Their predation pressure prevents competitive exclusion amongst fish species, allowing a greater variety of species to coexist. The "mesopredator release hypothesis" suggests that without apex predators like the grey seal, mid-level predators could proliferate and reduce biodiversity through intensified competition (Prugh et al., 2009).

The grey seal also contributes to nutrient cycling within the marine ecosystem. Their predation facilitates nutrient redistribution, as prey consumed and digested in one location is then excreted within a different location. This movement of nutrients between habitats, known as nutrient subsidies, can enhance productivity in various parts of the marine ecosystem (Bouchard & Bjorndal, 2000). In particular, the excretion of nitrogen-rich waste can boost primary productivity, benefiting lower trophic levels like phytoplankton and supporting the broader food web. (Roman et al., 2014).

In addition, the grey seal can influence the physical environment and community structure of their haul-out and breeding sites. For example, seals in coastal areas can alter substrate composition through their physical movements as well as the buildup of organic matter from their waste. This, in turn, can influence invertebrate communities and seabird populations, highlighting the broad-reaching impact seals have on their ecosystem. (Bowen, 2011).

Disruptions to seal populations, whether through human activities such as overfishing, pollution, or habitat loss, can create imbalances across trophic levels, triggering cascading effects throughout the ecosystem. This can be highly consequential, as these are effects that could ultimately lead to the destruction of the entire habitat., (Hammond & Grellier, 2006).

Humans: Shaping Behaviour, Shaping the Future

Human activities, particularly urbanisation, have had unprecedented impacts on wildlife, altering ecosystems and shaping animal behaviours. The consequences of this human-induced rapid environmental change (HIREC) are evident in the behavioural shifts seen in species like the urban seal, who have adapted to environments vastly different from those it evolved in (Sih et al., 2011).

The expansion of coastal cities has fragmented marine habitats and increased the frequency of wildlife-human encounters. Seals in urban areas face much higher risks due to pollution, habitat fragmentation, and human persecution. Public perceptions of wildlife, shaped by societal and cultural attitudes, often resist conservation efforts for species perceived as invasive or problematic, such as gulls and seals (Madden & McQuinn, 2014).

Figure 11. A grey seal hauled out on human fabricated structure surrounded by surface pollution. Brixham, South Devon. Duncan Kenny. 2022.

Artificial lighting in urbanised coastal areas can interfere with the natural cycles of nocturnal animals, disorienting birds, bats, and other wildlife. Additionally, the introduction of pollutants such as oil, heavy metals, sewage, and plastics can degrade water quality, forcing marine organisms to alter their foraging habits as they search for clean, nutrient-rich areas. Such disruptions can

ultimately diminish biodiversity and compromise ecosystem resilience, making it more challenging for wildlife to thrive in these altered environments.

In the past, ecosystems have evolved through a series of natural checks and balances, with different species occupying ecological niches to maintain biodiversity. For example, the complex food webs of the African Savannah or the South American rainforest rely heavily on a vast array of species interactions to sustain stability. However, in modern times, humans have reshaped these environments on a massive scale, leading to habitat destruction, species extinctions, and climatic changes, all of which have altered the natural cycles nature needs to maintain balance.

Unlike smaller-scale ecosystems where species dominance often leads to ecosystem collapse, such as in the case of the invasive species, the cane toad *(Rhinella marina)* in Australia, or the European rabbit (*Oryctolagus cuniculus*) in New Zealand, human dominance operates on a global scale. These invasive species, introduced into ecosystems with few natural predators or competitors, have caused widespread ecological damage, driving native species to extinction and destabilising the environment. Similarly, human overpopulation and industrialisation have led to deforestation, pollution, and ocean acidification, all of which threaten the stability of the global ecosystem.

This human-driven imbalance raises concerns about the long-term sustainability of many species. The consumption of finite resources, from fossil fuels to arable land, mirrors the destabilisation observed in smaller ecosystems, where dominant species exhaust resources and precipitate collapse. The consequences of this unsustainable trajectory may lead to environmental degradation that undermines the very systems humans depend upon for survival, from food production to climate regulation.

The dominance of humans within the global ecosystem is not only without precedent, but also deeply unsustainable. As history and smaller-scale ecological examples demonstrate, unchecked species dominance often leads to ecosystem collapse. Given the global scale of human influence, this situation presents a pressing challenge for both conservation efforts and the future of human society itself. Without meaningful changes in human behaviour concerning consumption patterns,

population growth, and environmental stewardship, the Earth's capacity to support its diverse life forms, including humanity, could be severely compromised.

Human urbanisation has caused substantial behavioural changes in grey seals, creating challenges both for their survival and the health of marine ecosystems. Whilst it may appear that the grey seal has adapted to the human environment, the long-term impact of this adaptation may threaten their very welfare and reproductive success. Moving forward, conservation efforts must address the unique challenges posed by urbanisation on wildlife behaviour, whilst also promoting public empathy for those species who share our habitats to influence and encourage lasting positive changes in human behaviour.

References

Anderson, S.S. and Fedak, M.A., 1987. Grey seal males: Energetic and behavioural links between size and reproductive success. *Animal Behaviour*, 35(2), pp.794-805.

Andersen, S.M., Teilmann, J., Dietz, R., Schmidt, N.M. and Miller, L.A., 2016. Disturbance effects on the behaviour and energetics of harbour seals and grey seals in Denmark. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26(5), pp.789-803.

Arnould, J.P.Y. and Hindell, M.A., 2001. Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*) and their inter-relationships. *Canadian Journal of Zoology*, 79(1), pp.35-48.

Bateman, P.W. and Fleming, P.A., 2012. Big city life: Carnivores in urban environments. *Journal of Zoology*, 287(1), pp.1-23. https://doi.org/10.1111/j.1469-7998.2011.00887.

Beck, C.A., Bowen, W.D. and Iverson, S.J., 2003. Seasonal changes in buoyancy and diving behaviour of adult grey seals. *Journal of Experimental Biology*, 206(15), pp.2517-2528.

Boness, D.J. and James, H., 1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Mammalogy*, 60(3), pp.504-519.

Boness, D.J., Bowen, W.D. and Iverson, S.J., 1993. Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? *Behavioral Ecology and Sociobiology*, 32(1), pp.19-30.

Bonner, W.N., 1999. *Seals and man: A study of interactions between seal populations and human activity*. Oxford: Oxford University Press.

Bouchard, S.S. and Bjorndal, K.A., 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology*, 81(8), pp.2305-2313.

Bowen, W.D., 2011. Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series*, 423, pp.281-293.

Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M. and Marshall, G.J., 2003. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series*, 244, pp.235-245.

Cronin, M.A., Jessopp, M., Houle, J., MacLeod, R. and Reid, D., 2018. Effect of tidal state on haul-out behaviour and disturbance responses of harbour seals (*Phoca vitulina*) at a dynamic haul-out site. *Marine Mammal Science*, 34(4), pp.955-972.

Duck, C.D. and Morris, C.D., 2020. *Grey seal population dynamics: Isle of Man and UK coasts*. Aberdeen: SMRU Marine Mammal Research Unit.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. et al., 2011. Trophic downgrading of planet Earth. *Science*, 333(6040), pp.301-306.

Francis, R.A. and Hoggart, S.P.G., 2009. *Urban ecosystems: Understanding the human-environment relationship*. London: Routledge.

Giese, M., 1996. Effects of human activity on Adelie penguin breeding success. *Biological Conservation*, 75(2), pp.157-164.

Hammond, P.S. and Grellier, K., 2006. Grey seal diet composition and prey population impacts. *Journal of Applied Ecology*, 43(4), pp.749-760.

Harding, K.C., Fujiwara, M., Axberg, Y. and Härkönen, T., 2017. Grey seal population recovery and associated population-level effects on marine ecosystems in the Baltic Sea. *Ambio*, 46(2), pp.203-212.

Hastie, G.D., Russell, D.J., McConnell, B., Moss, S. and Thompson, D., 2015. Sound exposure in harbour seals during the installation of an offshore wind farm: predictions of auditory damage. *Journal of Applied Ecology*, 52(3), pp.631-640.

Kovacs, K.M., Aguilar, A., Aurioles, D. et al., 2016. Pinniped conservation – An imbalance of impacts. *Marine Mammal Science*, 32(2), pp.278-292.

Madden, F. and McQuinn, B., 2014. Conservation's blind spot: The case for conflict transformation in wildlife conservation. *Biological Conservation*, 178, pp.97-106.

Manx Wildlife Trust, 2018. *Annual seal survey report*. Isle of Man: Manx Wildlife Trust.

McDonnell, M.J. and Hahs, A.K., 2015. *The ecology of cities and towns: A comparative approach*. Cambridge: Cambridge University Press.

McDonnell, M.J. and Pickett, S.T.A., 1990. Ecosystem structure and function along urban-rural gradients: An unexploited opportunity for ecology. *Ecology*, 71(4), pp.1232-1237. https://doi.org/10.2307/1938309.

McKinney, M.L., 2006. Urbanisation as a major cause of biotic homogenization. *Biological Conservation*, 127(3), pp.247-260. https://doi.org/10.1016/j.biocon.2005.09.005.

Miller, J.R. and Hobbs, R.J., 2002. Conservation where people live and work. *Conservation Biology*, 16(2), pp.330-337. https://doi.org/10.1046/j.1523-1739.2002.00420.x.

Paine, R.T., 1969. A note on trophic complexity and community stability. *The American Naturalist*, 103(929), pp.91-93.

Paterson, W., Sparling, C.E., Thompson, D., Pomeroy, P.P. and Currie, A., 2012. Seals like it hot: Changes in behaviour and metabolic rate in response to warm water. *PLOS ONE*, 7(2), e31897.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. and Brashares, J.S., 2009. The rise of the mesopredator. *BioScience*, 59(9), pp.779-791.

Roman, J., Dunphy-Daly, M.M., Johnston, D.W. and Read, A.J., 2014. The role of marine mammals in the provision of ecosystem services. *Journal of Mammalogy*, 95(3), pp.504-516.

Sih, A., Ferrari, M.C.O. and Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4(2), pp.367-387.

Smith, J. and Harwood, J., 2021. Managing human-seal interactions: A challenge for sustainable fisheries and conservation. *Marine Policy*, 134, p.104-118.

Thompson, D., Duck, C.D., McConnell, B.J. and Garrett, J., 1996. Movements, diving and foraging behaviour of grey seals. *Journal of Zoology*, 239(1), pp.53-67.

Thompson, D., Duck, C.D., Morris, C.D. and Russell, D.J.F., 2019. The status of grey seals in Britain and Ireland in 2018. *NAMMCO Scientific Publications*, 11, pp.53-67.

Twiss, S.D. (1991). Social and reproductive behaviour of grey seals: post-copulatory mate guarding. *Animal Behaviour*, 41(1), pp.29-38.

Twiss, S.D., Pomeroy, P.P. and Anderson, S.S., 2002. The behavioural ecology of lactation in grey seals: Maternal behaviour and pup outcome. *Journal of Zoology*, 256(4), pp.425-432.

Womble, J.N. and Gende, S.M., 2013. Post-breeding season migrations of a top predator, the harbour seal (*Phoca vitulina richardii*), from a marine protected area in Alaska. *PLOS ONE*, 8(2), e55386.