

Assessing wave energy effects on biodiversity: the Wave Hub experience

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Marine renewable energy installations harnessing energy from wind, wave and tidal resources are likely to become a large part of the future energy mix worldwide. The potential to gather energy from waves has recently seen increasing interest, with pilot developments in several nations. Although technology to harness wave energy lags behind that of wind and tidal generation, it has the potential to contribute significantly to energy production. As wave energy technology matures and becomes more widespread, it is likely to result in further transformation of our coastal seas. Such changes are accompanied by uncertainty regarding their impacts on biodiversity. To date, impacts have not been assessed, as wave energy converters have yet to be fully developed. Therefore, there is a pressing need to build a framework of understanding regarding the potential impacts of these technologies, underpinned by methodologies that are transferable and scalable across sites to facilitate formal meta-analysis. We first review the potential positive and negative effects of wave energy generation, and then, with specific reference to our work at the Wave Hub (a wave energy test site in southwest England, UK), we set out the methodological approaches needed to assess possible effects of wave energy on biodiversity. We highlight the need for national and international research clusters to accelerate the implementation of wave energy, within a coherent understanding of potential effects—both positive and negative.

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1. Introduction

The current reliance on fossil fuels for energy production directly impacts marine ecosystems via warming effects and acidification [1], as a result of increasing levels of atmospheric CO₂ [2]. In the marine realm, these impacts have been documented across various species groups, from plankton [3], to fish [4], seabirds [5] and other large vertebrates [6,7]. In order to mediate these impacts, there is a need to harness energy from renewable sources. The oceans hold a vast and largely untapped source of renewable energy in the form of wind, wave and tidal resources, and there has been a recent acceleration in the development and deployment of marine renewable energy installations (MREIs) to harness this potential.

Renewable energy from wind has rapidly increased in capacity [8]. Wind farms located onshore do, however, typically require conflict resolution with regard to aesthetics, environmental impacts and land use [9]. As a result of these conflicts, and accepting that wind resources are superior in offshore areas, the development of offshore wind farms has escalated [10], with some of the world's largest developments proposed for the UK continental shelf. Alongside the development of commercial wind farms, the potential to capture energy from waves has seen increasing interest, with pilot developments in a number of nations [11–14]. Technology for harnessing wave energy lags behind that of wind energy generation, but has the potential to contribute significantly to renewable energy production [15,16].

Coupled with the hopeful outlook for marine renewable energy generation, there have been concerns regarding the potential effects and subsequent impacts that these technologies may have on biodiversity and the physical environment [17–23]. Given that wave, tidal and deep-water offshore wind energy generation are still in their infancy, an opportunity exists to investigate the effects (both positive and negative) of pilot-scale projects so that the effects of future commercial-scale developments might be mitigated (if negative) or embraced (if positive) [20].

Here, we highlight the potential effects of marine renewable installations for biodiversity, with particular emphasis on wave energy and wave energy converters (WECs), and share our methodological approaches in use at the Wave Hub (an offshore wave energy test site in southwest England (UK) in waters of about 58 m depth).

2. Potential effects of wave energy on biodiversity

(a) Possible negative effects

(i) Habitat loss/degradation

MREIs, such as wave farms, are unlikely to cause substantial widespread alteration to benthic habitats, particularly when considered in relation to other human activities, such as commercial trawl fisheries [24]. Inappropriate placement of MREIs in sensitive areas, such as fish spawning habitats or regions with high biodiversity, does however have the potential to negatively impact certain taxa [20]. Anchoring, used to maintain the position of WECs, may include the use

of pile driving, gravity bases or drag anchors, each having different potential effects. The cumulative effects of multiple array-based wave farms is not fully understood. The addition of novel structures to marine habitats also represents the opportunity for colonization and, while there may seem obvious benefits for some species (e.g. crustaceans), new structures may provide substrates for colonization by invasive species or alter dynamics of existing populations.

(ii) *Collision/entanglement/entrapment*

The study of effects on marine biota in offshore environments, such as at MREIs, is particularly challenging and requires novel detection strategies [25–27]. Strike risk between WECs and mobile marine species is likely to differ with device type, and avoidance ability is likely to vary as a function of species and body size [28–30], diel activity pattern [31,32] or age and reproductive stage [33]. WECs are likely to have less above-water vertical structure than wind farms, hence reducing avian collision risk [34]. The impact of WECs on diving birds does, however, require further research, particularly with respect to the potential fish aggregating effects that WECs and their associated structures might have. This response may potentially serve to aggregate prey for diving birds and other species, with a concomitant chance of increased interactions between WECs and mobile species. Subsurface fixed structures such as wind turbine monopiles most probably pose little risk owing to their ease of navigation; however, WEC cables, chains and power lines will be more mobile and so potentially more complex to navigate [35]. Proposed WECs with rotating turbines or sea-water intake have the potential to seriously injure or kill some organisms [20], although this may be more of a concern for tidal stream devices. Continued modelling efforts will, however, help us to further clarify issues regarding the potential effects and subsequent impacts of wave energy for marine birds [36].

(iii) *Noise/disturbance/displacement/redirection*

There is an increasing body of evidence suggesting that anthropogenic underwater noise and vibrations can have adverse effects on a range of marine taxa, including marine mammals, fish and benthic invertebrates [37–39]. For MREIs, disturbance is likely to be most severe during construction [40]; for example, pile driving affects the behaviour of seals [41] and cetaceans [42]. Noise during the operational phase of wave farms is likely to have a less acute effect; however, research is required to determine the potential for chronic, long-term effects, which will depend on the frequency of noise, energy emitted and species' auditory ranges [38]. Current research on noise from wind farms during their operational phase suggests little evidence of impact (when compared with noise during the construction phase) beyond small-scale behavioural avoidance [43]. The impacts of wind farms on bird abundance have received much attention [44], but the behavioural mechanisms and cues used by birds to detect and avoid wind farms remain under-studied, although it has been suggested that the noise from turbines is used to help minimize collisions [31]. Owing to this lack of current knowledge, and the very different operation of WECs compared with wind turbines, noise production and its scale of impact are key areas of interest required from future studies and should thus be a focus of research at the design phase.

(iv) *Electromagnetic fields*

Wave farms and their associated WECs are likely to support a higher relative concentration of cables than wind farms. These cables will produce electromagnetic fields (EMFs), which will be detectable by a range of marine organisms that can be either electro- or magneto-sensitive, such as bony fish, elasmobranchs, marine mammals and marine turtles [45–49]. Furthermore, WECs employing coil and magnet engineering could further emit larger EMFs than anticipated from subsea power cables alone. There is a paucity of current knowledge on the likely effects of anthropogenic EMFs at the population level, with a few studies providing limited insight from experimental systems [18,45,50], and, as such, more focused research is required.

(v) *Impacts on plankton*

Plankton may be affected directly or indirectly during construction and operational phases of MREIs: sediment disturbance may generate phytoplankton blooms through release of extra nutrients, while local reductions in light attenuation due to increased turbidity, particularly during WEC installation, may decrease primary productivity of algae. Extraction of energy is expected to reduce surface water turbulence and may thus cause shifts in phytoplankton species composition from large diatoms to motile dinoflagellates, which may in turn affect zooplankton grazers. A combination of reduced turbulence and decreased grazing pressure may provide favourable conditions for the formation of harmful algal blooms, with implications for higher trophic levels, including fish species. Toxic antifouling chemicals may induce enhanced mortality or reduced fitness of planktonic species, whereas zooplankton may also be directly affected owing to enhanced mortality when passing through moving parts of machinery [51]. In addition, changes in behaviour and/or abundance of predators, such as fish larvae, seabirds and marine mammals, may affect mortality and fitness of their zooplankton prey.

(b) *Possible positive effects*

(i) *Habitat enhancement/artificial reefs*

WECs have the potential to attract mobile organisms and to increase the area of habitat for sessile epibiotic species; hence, they have the potential to act as artificial reefs [52]. There is, however, a fundamental difference from artificial reefs in that habitat enhancement effects are secondary, rather than the sole, potential outcome of construction. The capacity of WECs to provide habitat for marine life could be increased through the addition of novel modifications to enhance the available habitat. In this regard, it may be possible to translate the outcomes of recent work examining habitat enhancement on other structures such as coastal defences [53] (appendix A). The extent to which these ‘artificial reefs’ attract marine life and the nature of the species attracted will largely be shaped by the location of the MREI and the design of its components [20], with structural complexity of exposed surfaces being a key driver of the extent of colonization [54]. The latter will cause conflict if it interferes with equipment performance. A wider consideration is that MREIs may help to restore areas of seabed that have been lost through commercial fishing [55].

(ii) *Fish aggregation devices*

WECs will support extensive mooring systems, which along with the WECs themselves are likely to function as patch reefs, or as fish aggregating devices (FADs) [56,57]. Many species of fish aggregate around floating objects, a phenomenon that fishermen have exploited for centuries [58]. Species richness and assemblage size are positively correlated with FAD size [59]; as such, large WECs may be better at recruiting certain fish species. This effect may also have consequences for the attraction of larger predatory birds, fish and marine mammals that feed on the concentrated prey resources.

(iii) *Marine protected areas*

Owing to the potential for collision between vessels and WECs or fishing gear entanglement, it will not be possible to undertake many forms of commercial fishing within the immediate vicinity of WECs. As a result, wave farms have the potential to act as *de facto* marine protected areas (MPAs). Providing such a refuge from intense fishing pressure has the potential to protect and enhance fish stocks; the implementation of such MPAs will also enrich benthic biota, by locally eliminating the damage caused by fishing gear towed along the seabed [24].

(c) *Synergistic effects*

There is the potential for MREIs to have a significant anthropogenic influence on marine ecosystems, and the positive and negative effects are likely to interact in complex and unpredictable ways. Effects may also be cumulative, both in time, and with the introduction of increasing numbers of MREIs; hence, it is critical that we consider the wider marine ecosystem. Trophic cascades have been shown to affect seabird populations by altering food supplies in complex ways [60,61]. Furthermore, there may be unforeseen community-level changes in trophic interactions, although the magnitude of any effect will determine to what extent these might have consequences at the population level. It is also unclear how the ecosystem will respond to such perturbations, and further work at the farm scale and multiple farm scale, i.e. a few to 100 km², is required to investigate how the main potential positive and negative effects might offset one another.

(d) *Conflicts and solutions*

While data on the potential effects of wind-powered energy generation in the marine realm are growing (although mostly for near-shore shallow-water deployments; less than 50 m depth), uncoordinated experimental designs make comparisons and meta-analysis problematic [62], which most probably limits the inference of findings from wind to wave MREIs. Future developments in all marine energy sectors (wind, tidal and wave) need to incorporate well-designed and replicated monitoring from the initial planning stages through to completion, targeted towards those factors with most uncertainty. Inadequately designed programmes may not detect effects with the potential for delivering misleading results, particularly if natural variability in biological systems is poorly quantified prior to construction. Baseline work should be followed by long-term monitoring of the site in order to look at both immediate and

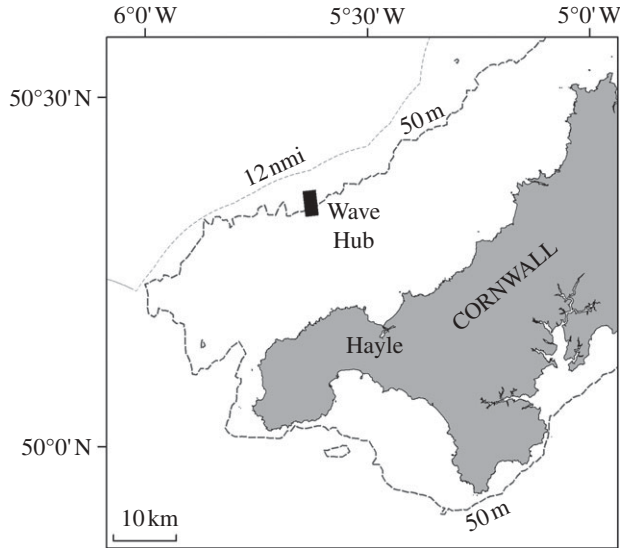


Figure 1. Location of Wave Hub on the north coast of Cornwall (southwest England, UK).

longer-term changes. In combination, this will enable robust examination of change at the individual site level, as well as providing the criteria for multi-development level comparisons. In order to inform the global industry, certain key sites should be chosen for major national, or international, investigation. If MREIs are engineered to enhance biodiversity, particularly in degraded habitats, then we must ensure that these enhancements are not lost during decommissioning [20].

Whether designed to be relatively environmentally benign or to enhance biodiversity, it is critical that a broad range of stakeholders are involved at all stages from design, site selection, pre-construction monitoring/impact assessment, construction, operation and any decommissioning. Furthermore, research should be, as far as is commercially viable, transparent, with results published in scientific journals and peer-reviewed reports, to maintain credibility and promote accessibility to other researchers.

If research and development programmes are targeted at identifying and promoting environmental benefits, then marine renewable energy has the capacity to enhance biodiversity in degraded marine habitats, thus representing an excellent potential example of ‘win-win ecology’ [63]. Consideration should be given to leaving new habitat-forming infrastructure *in situ*, and building this factor into the consenting process.

(e) *Assessing the potential effects of harnessing wave energy at Wave Hub*

We now explore methodologies to examine the potential effects of harnessing wave energy on benthic species, fish, seabirds, marine mammals, fisheries and the water column, with specific reference to our work at the Wave Hub—a test facility for prototype arrays of WECs (figure 1).

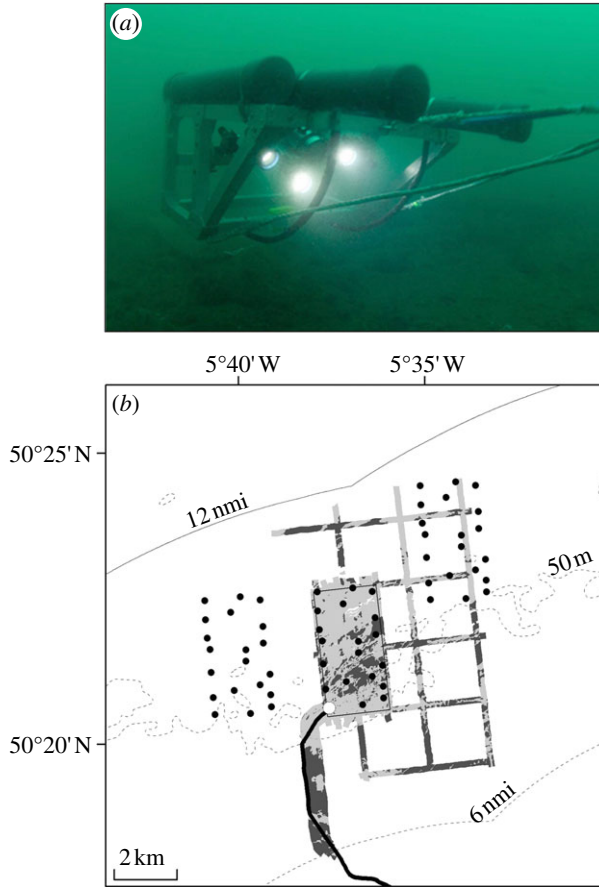


Figure 2. Benthic surveying at Wave Hub. (a) High-definition video camera flying array. (b) Side scan sonar-derived habitat (grey scale polygons: rock and rock with intermittent sediment cover (dark grey) and gravelly sand with gravelly sand and intermittent rock exposure (light grey); South West of England Regional Development Agency, offshore geophysical survey, Wave Hub, 2007) and video camera sampling start locations (filled circles) with extents of Wave Hub development zone (solid line quadrangle), Wave Hub cable route (thick line) and Wave Hub deployment location (white circle).

Wave Hub is situated 10 nautical miles (nmi) (18.5 km) offshore from Hayle on the north coast of Cornwall and comprises a 33 kV subsea power cable that runs from a land-based substation to the offshore WEC development site. At this development site, the cable terminates at the Wave Hub, an electrical junction box (approx. 58 m depth), from where four tails extend for future connection with WECs. The total development area for WECs (8 km²) is within a dynamic seasonally forming frontal system, with annual average significant wave heights of 1.9 m and mean spring and neap peak current speeds (depth averaged) of 0.8 and 0.4 ms⁻¹, respectively [64]. The development site supports four bays (1 × 2 km) that can be leased to wave energy device developers for the deployment of WECs. The development area encompasses a range of seabed habitats, including gravelly sand, rock and rock with intermittent sediment cover (figure 2).

3. Methodological approaches

(a) *Benthos*

It is important to recognize that many seabed habitats on continental shelves, the likely locations of MREIs, have undergone some form of modification due to human activities, e.g. fishing and/or aggregate extraction [65–67]. As such, methodological approaches to assess biodiversity must be able to tease apart changes brought about by MREIs superimposed upon those impacts of other human activities.

Traditional methods for sampling seabed biodiversity have included destructive grabs and trawls [68], but these approaches are not suitable for sites where biodiversity is to be repeatedly measured through time. Remote sensing techniques may, however, offer a potential solution for monitoring deep and/or physically inaccessible regions. For example, digital video cameras have been used to capture data on larger, less abundant, mobile fauna such as fish and crustaceans [69,70], with still cameras being used to obtain high-quality images for species identification, e.g. for abundant sessile fauna such as sponges and corals. Still pictures obtained from frame grabs of traditional video are of limited quality, and, as such, smaller, more cryptic species may not be identified to species level, and larger, less common species may be missed entirely. Previous camera platforms have included sledges with runners, suitable for soft sediment and low-relief habitats [71,72]. In other industries (e.g. offshore oil and gas production), remote-operated vehicles (ROVs) are used in place of divers for many tasks, including biological surveys [73]. ROVs of the class required to operate in offshore habitats can be prohibitively expensive, require significant technical and boat support, and can typically cover only small areas.

Given the limitations of existing sampling approaches, a single high-definition (HD) towed video camera system has been developed to collect high-quality video data of seabed habitats. The HD video camera is mounted upon a towed aluminium frame with a mass of 30 kg in air when all equipment is installed (figure 2*a*); this array was purpose built for use at MREIs [74]. The frame is anchored to the seabed by a length of chain, such that it floats at a pre-determined height in the water column. The system represents a low-impact, cost-effective method of filming large areas of the seabed from medium-sized (10–15 m length) fishing vessels, at depth and over variable habitat types.

The effects of WECs at Wave Hub are being assessed using the towed HD video camera system in a ‘beyond before–after control–impact’ sampling approach [75]. The baseline sampling units comprise 20 × 200 m HD video transects conducted within the Wave Hub development zone and at sites to the east and west of Wave Hub (figure 2*b*). Data from each transect are geo-referenced to facilitate comparison. Randomly selected still images are extracted from the HD video data and can be used to quantify sessile and encrusting organisms by superimposing a quadrat over each image. Analysis of captured HD video data has enabled the identification of 115 species across the study area, including annelid worms, tunicates and cnidarians, molluscan and vertebrate species. The spatial pattern of sampling stations also facilitates a gradient style of analysis where impacts are assessed with respect to distance to WECs along a northeast–southwest axis (constant depth). This approach provides additional insights, given uncertainty

regarding the spatial distribution of potential effects (which applies for many of the receptor groups addressed here—e.g. benthic species, fish, marine birds and marine mammals).

The towed array is appropriate for monitoring control and development sites pre-construction; however, following the deployment of WECs at MREIs, a towed array system will not be appropriate, as access among WECs and their associated matrix of moorings and cables may be impracticable. Video data capture will then be made possible using an ROV equipped with HD video camera technology. Formal comparison of HD video data obtained from the towed array and ROV will be undertaken using 200 m geo-referenced transects surveyed by both technologies. It is expected that an ROV will also be suitable for monitoring biodiversity associated with the man-made structures (see appendix A), which includes the seabed-mounted Wave Hub itself, WECs and the substantial subsurface rock and concrete mattress armouring used to protect the subsea power cable that runs to the mainland.

(b) *Fish*

The knowledge that fish exist/aggregate around or near solid structures deposited in the sea is long-held, and it has been demonstrated that increasing the size, complexity and biofouling of the objects supports greater numbers of increasingly large fish [76] (see appendix A). Although these observations are relevant to predicting the likely effects on fish of WECs, whether these structures merely attract free-swimming biomass from elsewhere or enable greater productivity remains difficult to assess [77,78].

(i) *Monitoring fish movement*

Passive acoustic tracking to assess long-term space use by individual fish has not yet been used with respect to movements around human-made underwater structures, such as MREIs. Several field studies are currently trialling this type of technology, including one off southwest England (figure 3). At the site, 2 m high seabed landers carry data-logging acoustic receivers. Data on detections of fish instrumented with acoustic transmitting tags are uploaded remotely every few months using an underwater acoustic modem aboard a ship positioned over each lander in the array. This type of monitoring allows insights into fish behaviour over the large spatio-temporal scales relevant to issues such as the nature and dynamics of any potential ‘spillover’ effect at MREIs. If sufficient numbers of fish are tagged with acoustic transmitters (hundreds), the departures, arrivals and occupancy times of individual fish, in numbers significant to those present in the region, can be determined. Studies using similar technology but in natural habitats on small shark species have shown behaviours that indicate long residence times in preferred areas [79,80]. Preliminary results from lander-borne acoustic receivers show residence times and visitation patterns for over 150 individuals of commercially important fish species for more than 18 months, and support the concept of site fidelity to preferred habitat among diverse species. These preliminary data indicate that areas around MREIs, if made *de facto* fishing-free zones, could potentially provide important long-term refuges to fish during important stages of the annual cycle. Identifying the spatial dynamics of mobile species whose spatial footprints intersect with MREIs will be essential in

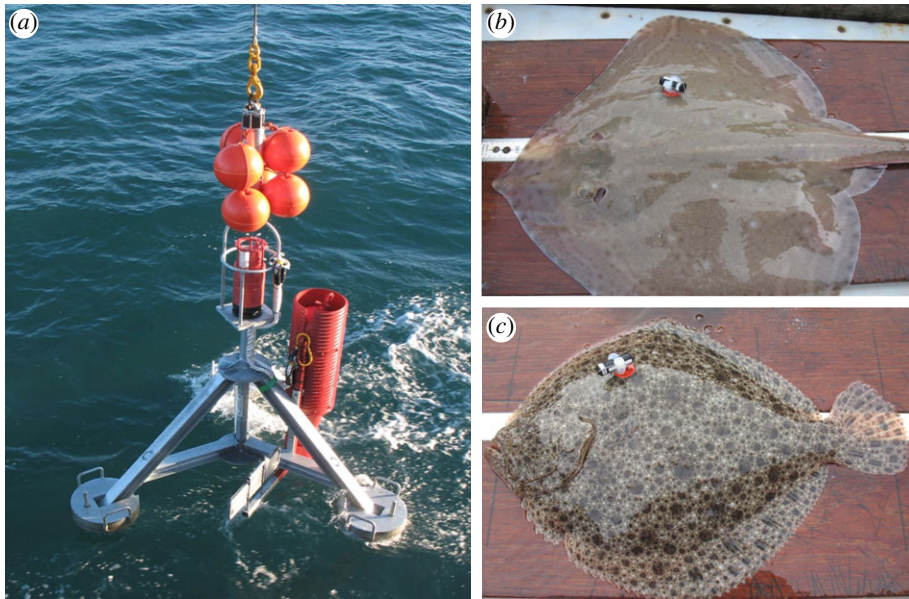


Figure 3. Long-term monitoring of fish movements. (a) Seabed lander equipped with a data-logging acoustic receiver (red cylinder in cage; Vemco VR3) at a test site in Whitsand Bay, Cornwall. Examples of acoustic transmitter-tagged (Vemco V9) fish tracked by the array include (b) a small-eyed ray *Raja microocellata* and (c) a turbot *Scophthalmus maximus*.

the assessment of whether such sites displace fish to other areas, or whether they act as refuges from activities such as fishing, and hence provide fish ‘spillover’ to adjacent areas. Wider-scale movements and activity patterns, outwith the footprint of passive acoustic monitoring, is possible by reconstructing the most probable tracks of demersal fish fitted with data storage tags when these are recovered.

To investigate the potential effects of WECs upon mobile species diversity and abundance, particularly for species that cannot be adequately instrumented with tracking technologies, it is necessary to use alternative approaches. Methods to undertake such censuses are varied (e.g. hydroacoustic assessment, baited traps, standardized trawls); however, all approaches have associated biases [81]. Given that many census techniques for mobile species are destructive, the act of measuring biodiversity using these methods holds the potential to impact future assessments. Baited HD video camera technology provides a possible alternative method with well-defined caveats [81] and has been used in the estimation of deep-water fish abundance [82] and adapted for use in shallow-water environments, typically in tropical ecosystems [69,83]. The approach has been used more recently in near-shore shallow habitats of the North Sea [81]. At Wave Hub, small portable HD wide-angle video cameras housed within bespoke water-tight housings are used to capture video data of mobile species visiting bait positioned forward of the cameras. Cameras are deployed upon the seabed and in the mid-water column within the development zone and at locations extending along a northeast–southwest axis transecting Wave Hub. This spatial layout of sampling

units facilitates an assessment of mobile species diversity and abundance with increasing distance from the development site while maintaining a nearly constant seabed depth across the sampling space. Knowledge of the physical environment at sampling sites is particularly important, given the influence of temperature on species distribution both vertically and horizontally [84,85], and, as such, prior to camera deployment, vertical upcasts of temperature against depth are recorded at each sampling station using a 1 Hz conductivity–temperature–density (CTD) probe.

(c) *Marine birds*

The diversity of WEC technology likely to be deployed at MREIs complicates the selection of suitable monitoring approaches for seabirds. Survey programmes that deliver robust data must be consistent and repeatable in their application, through both time and space. Given this necessity, boat-based strip and line transects commonly used in impact assessment may be inappropriate if the exact positioning of WECs is unknown during the early stages of development or if WEC devices differ across a single MREI, such as at Wave Hub. Aerial surveying using HD video data capture methods [86] were discounted owing to their considerable cost, particularly given the need to collect data over several years both pre- and post-WEC installation. As such, a boat-based point count approach for assessing seabird diversity and abundance was adopted. Bird count sampling stations are positioned within and outside the Wave Hub site, with stations outside the development extending northeast–southwest. Sampling stations are visited on a near-monthly basis by two surveyors and counts are made over an approximately 4 h period. Birds are identified and sightings are categorized as being within or outside a 300 m radius of the sampling location. Abundance estimates of birds counted (by species, foraging guild, etc.) are then derived using standardized methods [87]. This approach, when complemented with count data following WEC installation, will facilitate an assessment of any change in species diversity, distribution and abundance. The pattern of sampling locations for marine birds also facilitates a gradient style analysis to be used, in which bird distribution and abundance can be investigated with respect to distance from the centre of the Wave Hub.

In addition to *in situ* counts of marine birds at development sites, the recent proliferation of miniaturized electronic technology (e.g. satellite transmitters, light-based geolocators and time–depth recorders) allows knowledge to be gained on the fine-scale movements and behaviour of marine birds, and other species, in their natural surroundings [88]. These devices offer the potential not only to study the degree of spatial overlap between marine birds and MREIs, but also to reveal behavioural responses (including diving) to such installations in detail and therefore assess the costs and benefits of these interactions [89]. One important objective is to link the degree of connectivity between breeding colonies and potential or extant MREI. This can be best achieved by satellite tracking or bio-logging technology. As such, bio-logging devices, using several tracking methodologies, have been deployed on species at regional colonies in the southwest of England, including the Isles of Scilly, and Grassholm island (Wales), which host regionally important colonies of northern gannets (*Morus bassanus*) and lesser black-backed gulls (*Larus fuscus*), species that have been frequently identified at

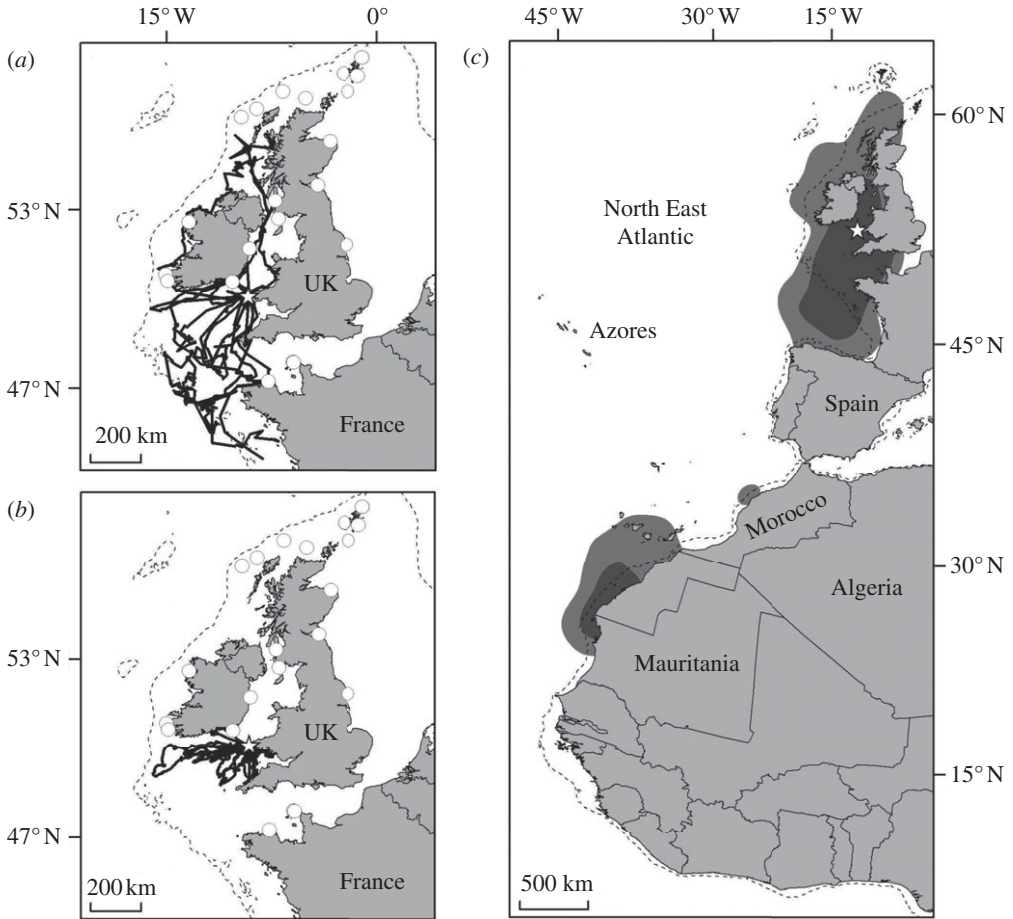


Figure 4. Movements of northern gannets (*Morus bassanus*) caught at Grassholm, Wales. Study colony (empty star); all other gannet colonies in the UK, Ireland and France (empty circles). (a) Movements of immature birds equipped with global positioning system satellite transmitter attached during July and August 2009 [90]. Gannets do not breed until they are at least 4 years old and only visit the colony for short periods in the summer months, so they are not easily recaptured, making satellite transmitters the only realistic way to study them. The data reveal a high degree of itinerancy with potential for overlap with Wave Hub. (b) Movements of incubating and chick-rearing adults gathered using GPS loggers, on a 3 min duty cycle [91]. Constrained to return to the nest, these birds move less than immature individuals. Some individuals overlap with Wave Hub. (c) Bivariate normal kernel smoothed distribution of a single bird during the inter-breeding period recorded using a leg-mounted global location sensing logger. Kernel grid interval = 10 km, smoothing (h) = 150 km, 50 and 75 per cent of all locations (areas circumscribed by dark and mid-grey polygons, respectively). During the wintering period, gannets travel long distances away from the breeding grounds.

Wave Hub from near-monthly boat surveys. Results from these bio-logging efforts have provided considerable insight (figure 4) in terms of at-sea habitat utilization, with clear differences within individuals, age classes and different components of the annual cycle (figure 4).

*(d) Marine mammals**(i) Cetaceans*

Surveying for cetaceans at sites of planned anthropogenic disturbance—e.g. construction of an MREI [92]—or for large spatial scale biological monitoring programmes—e.g. SCANS [93] and SCANS II [94]—has typically been dominated by visual detection methods allied with the use of distance sampling techniques [95]. In offshore environments, surveys using visual detection methods can be impracticable, as prevailing weather conditions in autumn, winter and spring affect species detectability. As an alternative to visual detection methods, there is growing interest in passive acoustic monitoring (PAM). PAM is the practice of detecting marine mammals, typically cetaceans, in a surveyed area by the distinctive sounds they make during communication, foraging and geolocation, such as echolocation clicks and whistles [92,96]. The approach of statically moored PAM has significantly furthered understanding of small cetacean spatial ecology and behaviour in a variety of northeast Atlantic habitats [97–100].

C-Pods (Chelonia, UK) are commercially available PAM echolocation click detectors. After long-term deployment at multiple sites, C-Pods can provide a spatial picture of seasonal changes in levels of echolocation [98], providing a coarse measure of relative abundance of cetaceans and highlighting regions of relative importance. Efforts to use static PAM at MREIs should be focused both at the proposed development site and at a regional scale to provide contextual information. As such, C-Pods have been deployed at Wave Hub, at coastal locations around the southwest UK peninsula and at deep-water control sites (more than 50 m depth). At several of these locations, C-Pods have also been deployed throughout the water column to ascertain vertical patterns of detection.

In addition to the use of C-Pods, at Wave Hub broadband sound recording equipment is being used to collect data on the presence of other marine mammal species that use sound at lower frequencies and hence outside the detection range of C-Pods. These broadband recording units sample sound using flexible duty cycling to investigate specific features of biological sound, but also anthropogenic noise and the ambient sound field over extended periods of time (months). The recording units are housed within custom-fabricated deployment frames, co-mounted with CTD sampling units, automated acoustic emergency relocation equipment and acoustically triggered pop-up buoy retrieval units. Knowledge on the ambient sound field will be important for assessing the impacts of anthropogenic noise on marine species, such as commercially important fish species [38] and marine mammals [18].

(ii) Pinnipeds

Anticipating and potentially mitigating the potential impacts of MREIs on pinniped species is challenging particularly with respect to offshore sites. For pinnipeds at natural haul-out locations (on land), it is possible to use visual census techniques and correlate changes in abundance or behaviour with activities at MREIs [101]. Monitoring at haul-out sites unfortunately cannot provide information on the likelihood of interaction between pinnipeds and offshore MREIs, unless individuals are followed using satellite tracking technologies [102]

or perhaps through the use of sonar remote sensing in the vicinity of MREIs. Wave Hub is located within 12 nmi (20 km) of a regionally important grey seal (*Halichoerus grypus*) haul-out [103]. Grey seals are not sufficiently vocal when subsurface to make routine use of PAM a reliable and informative monitoring strategy and satellite telemetry studies are not fiscally feasible. To build a baseline understanding of seal abundance and distribution in the region prior to installation of WECs, boat-based annual counts of seals along the coastline of Cornwall, including the Isles of Scilly, have been undertaken since 2008 in partnership with local non-governmental organizations. These counts take place during early spring when the maximum number of individuals are thought to be using key haul-out sites, which include a number of offshore rock systems fringing the north coast of Cornwall [103].

(e) *Fisheries*

Large-scale civil engineering projects, such as MREIs, necessitate a coherent spatial and temporal understanding of patterns of human activity, including recreational use, aggregate extraction, commercial vessel traffic and fisheries. Of considerable concern to the fishing industry is the potential for loss of access to important fishing grounds. In addition, from a biodiversity perspective, any resultant displacement of fishing effort needs to be considered, especially if there is transfer of effort from existing fished habitats that will have already undergone some degree of habitat modification to those that have been comparatively less disturbed. Detailed knowledge of the spatial footprint of UK fisheries will aid marine spatial planning activities and facilitate MREI site selection by allowing quantitative assessment of the potential costs and benefits to biodiversity and the fishing industry.

The movements of the larger fishing vessels in the UK fleet (more than 15 m length overall, LOA) are tracked by a mandated vessel monitoring system (VMS; figure 5) [66]. In the UK, satellite tracking data have been collected from 2000 onwards for vessels more than 24 m LOA and from 2005 for all vessels more than 15 m LOA. VMS-enabled fishing vessels transmit their position, instantaneous speed and heading approximately every 2 h. Using VMS data along with a generalized understanding of the speeds of movements for different at-sea behaviours—i.e. steaming versus fishing, linked to different fisheries and associated gear types [65,104,105]—it is possible to identify areas of prominent fisheries activity. Through time, these data can be used to build a detailed understanding of intra- and inter-seasonal patterns in fisheries [66], and help to quantify the relative financial importance of regions and the level of disturbance that the habitats receive. Additionally, these data can also highlight regions that receive little effort and are therefore comparatively undisturbed.

While describing the ‘footprint’ of the larger vessel fleet is made somewhat easier by VMS, creating a spatio-temporal understanding of the coastal fleet is more challenging and requires novel approaches. Initial distribution mapping can be achieved by integrating UK Government statistics on fishing activity at the level of ‘home port’; these data include number of vessels at each port and the number of days active in fishing, summarized by gear types and vessel size. These data can be integrated with generalized behavioural rules on movement, based on

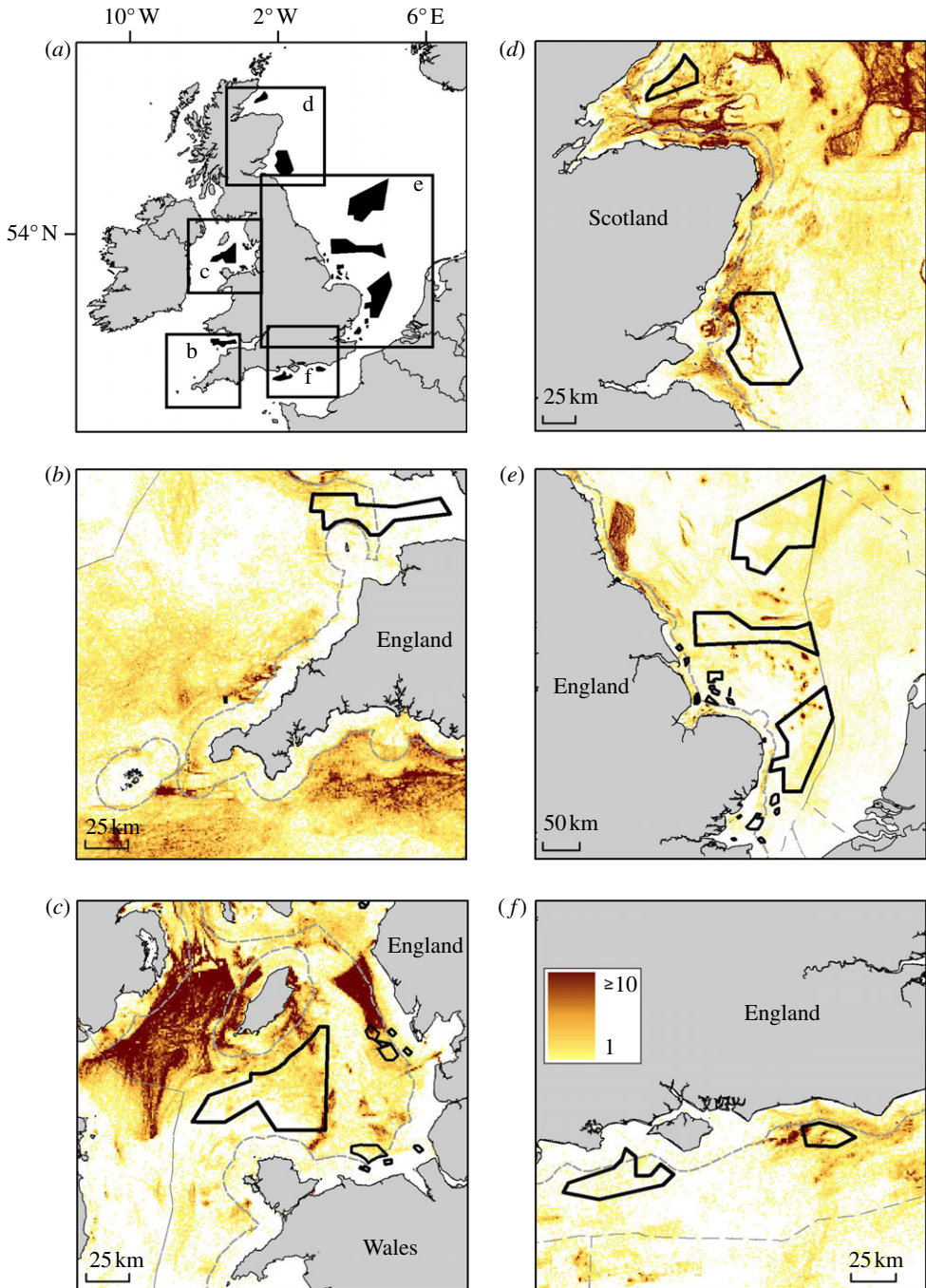


Figure 5. Spatial distribution of potential fishing effort made by vessels tracked by the UK Government vessel monitoring system (VMS, 2005–2007; 1 km² grid resolution). Colour scale represents mean annual number of VMS records received. (a) UK marine wind farm developments, rounds 1, 2 and 3, (b) southwest UK, (c) northern Irish Sea, (d) northern North Sea, (e) southern North Sea and (f) southern England. Black polygons (filled in (a), open in (b–f)) are spatial limits of consented and proposed MREIs.

vessel length. The coastal fleet typically operates to 12 nmi from land; although much effort is focused on areas within 6 nmi, their transit distance from their home port along the coast can be somewhat greater, but has been shown to be somewhat related to vessel length [106]. Using a behavioural rule approach, it becomes possible to circumscribe a zone of influence from each home port for vessels less than 10 m LOA (rule: 10 nmi maximum distance from home port) and vessels more than 10 m and less than 15 m LOA (rule: 15 nmi maximum distance from home port). Coastal seas around the UK are then described by 1 km^2 pixels and each zone of influence and the number of boats and activity days registered to each port are mapped to the pixels coincident to each zone. When this process is repeated for all ports of the UK and for both boat length categories, then summed, it becomes possible to create an inferential picture of the fisheries footprint of the inshore fleet using mobile (e.g. trawling) and static (e.g. potting) gear types (figure 6). This approach provides an initial indication of how MREI site placement might be informed by the potential footprints of coastal fisheries.

(f) *Water column*

The extraction of energy from the marine environment constitutes a potentially significant modification to the dynamic physical and biological oceanographic environment. A key issue is that the energy to be extracted would otherwise be available for ocean mixing, which is essential for a range of processes related to biological productivity, gas uptake and regional circulation.

Assessing the sensitivity of the physical oceanographic environment at Wave Hub to energy extraction consists of three components: identifying the key processes governing the integrity of the dynamic physical environment, monitoring their temporal variability and improving predictive capability. The core component of the study is a series of field-based process studies to provide measurements of turbulent mixing and stratification during the spring bloom, peak summer stratification and its subsequent breakdown. Each process study represents a comparatively short time period, reducing our ability to make broad-scale interpretations. To compensate for this, it is also necessary to monitor key physical oceanographic properties continually over an extended period. These data are provided by a high-frequency, land-based radar that enables the measurement of sea surface currents and spectral properties of the surface wave field coincident to Wave Hub and the wider development region (figure 7). Internal processes in the water column will be monitored for approximately six months with full-depth current and temperature measurements being gathered by a range of deployed equipment. By combining the radar and *in situ* measurements with remote sensing data on sea surface temperature and surface chlorophyll concentration, the extent to which the observed mixing and re-stratification processes govern the structure of the front over long time scales will be evaluated. Any perturbations to the natural system due to localized wave energy extraction may then be identified through comparison of our observations with numerical models developed for the region.

Data from these planned efforts will be contextualized with species occurrence and abundance data on plankton collected at the Wave Hub development site during the past 3 years (i.e. monthly vertical plankton trawls from the seabed to

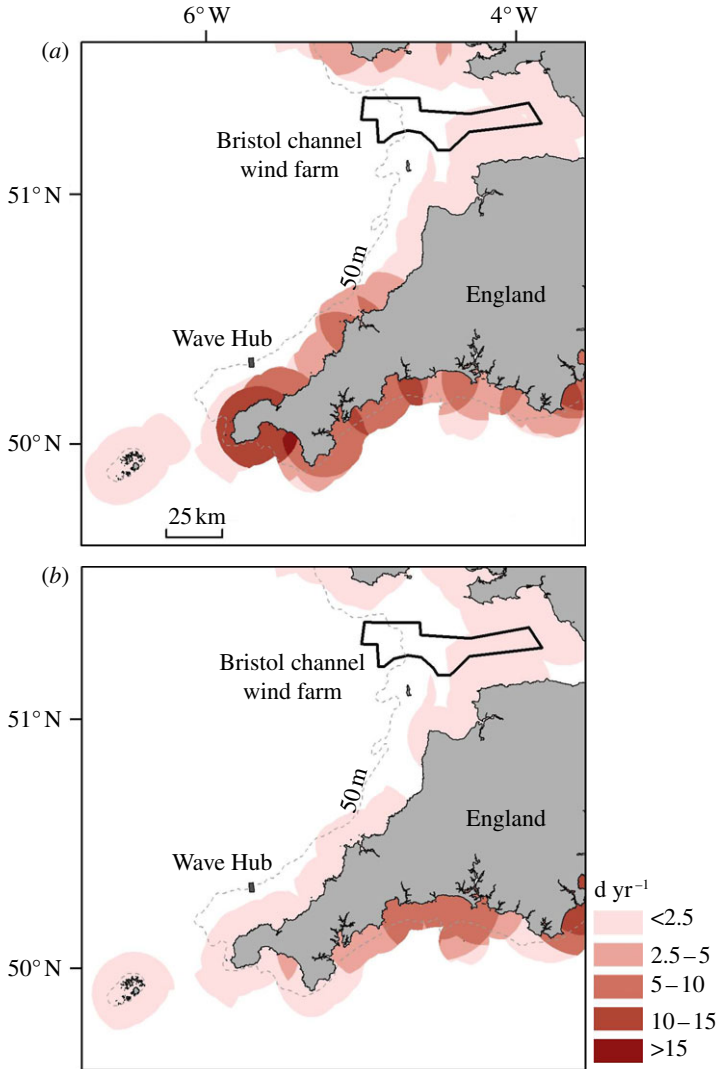


Figure 6. Modelled distribution of coastal fisheries. Estimated maximum number of fishing days km⁻² yr⁻¹ for fishing vessels using (a) static and (b) mobile fishing gear types, derived from UK Government statistics on fishing vessel activity for 2007.

the surface accompanied by CTD upcasts undertaken at the Wave Hub and at control regions).

The earlier-mentioned methods involve direct measurements of species abundance or biodiversity of a small area. It is also possible to estimate pelagic biodiversity, through the use of Earth observation (EO) satellite remote sensing, by assuming that the ecosystem has a relatively simple structure, with energy flowing from phytoplankton primary producers, through zooplankton to pelagic schooling fish and finally to a variety of top predators, including fish, marine mammals and seabirds [107]. Estimates at the base of the food chain can then provide surrogate measures of the overall biodiversity of the pelagic ecosystem.

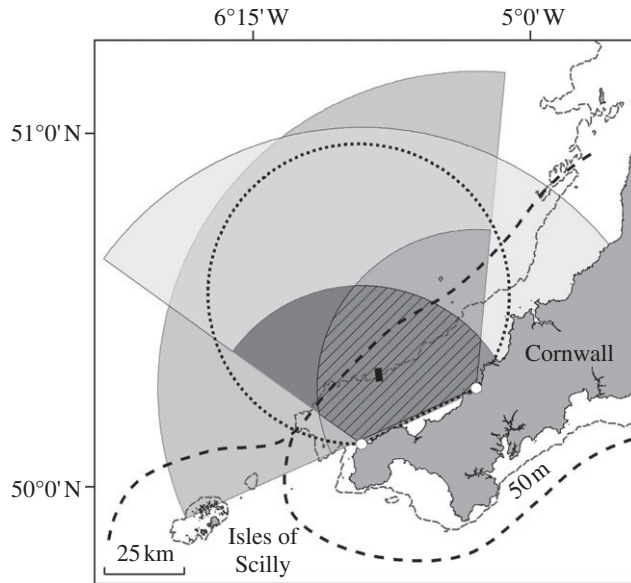


Figure 7. Map of the Wave Hub study region indicating high-frequency radar coverage. Hatched region indicates region where fully directional wave spectra and surface currents will be available, while surface currents and parametric wave information are available throughout the shaded region. Approximate position of coastal front (black broken line), Wave Hub (black filled polygon) and radar stations (white circles).

EO indicators, such as sea surface temperature, the position and density of thermal fronts [108] (figure 8) and ocean colour, may also contribute to an understanding of potential effects of wave energy, by estimating the likely abundance and distribution of key species known to inhabit the area. This process would require detailed studies of the relationship between tagged or surveyed animals and these EO environmental parameters. Similarly, studies of fishing effort or catches and EO data may help us to minimize the economic impacts of the MREI. During the construction of an MREI, it may be possible to exploit the near-real-time capability of EO data to minimize acoustic impacts of construction (for example) on marine mammals. For instance, the recent strength and movement of thermal fronts could advise a strategy for selecting the optimal times of operations. EO indicators may also be studied as part of a post-deployment impact assessment. While it is not yet known whether such techniques have sufficient sensitivity or resolution to detect changes in the shelf-sea physics, biology or optics caused by a disturbance in turbulence or sediment concentration, against a background of high natural variability, ocean colour can be used to detect regime shifts in plankton from diatoms to dinoflagellates, or increased occurrence of algal blooms.

4. Conclusion

Large-scale wave energy developments have yet to commence and the potential effects on biodiversity are likely to be complex and multifaceted. As such, wave

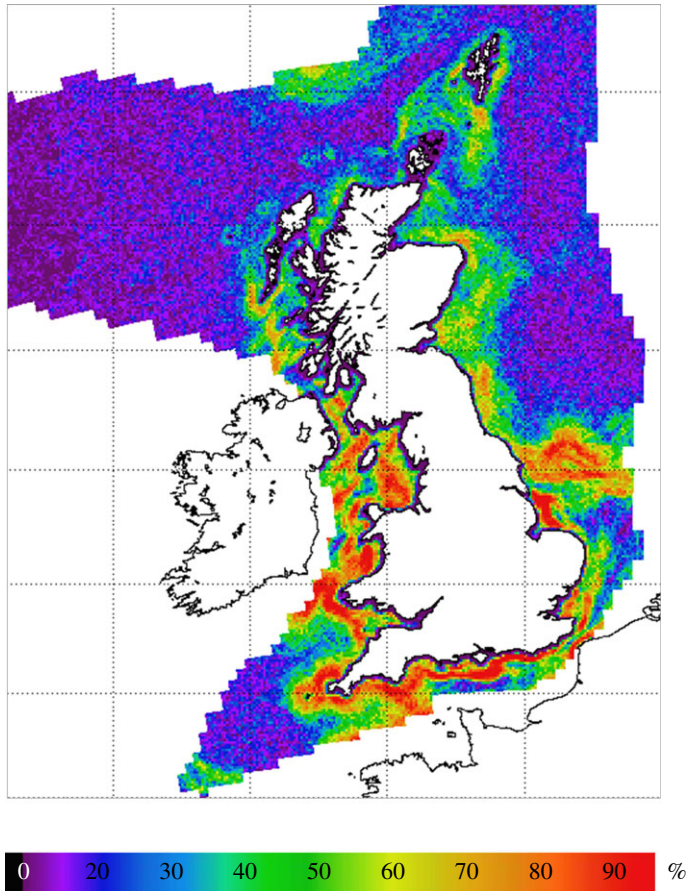


Figure 8. Satellite oceanic front maps as a proxy for pelagic diversity. Seasonal (summer) frequent front map for UK continental shelf, indicating the percentage of time that a strong front was observed at each location [109].

energy demonstrator sites require long-term, detailed, interdisciplinary work using methodological approaches that can be interfaced across multiple locations (countries and ecosystems), over multiple spatial scales and potentially across differing marine energy sectors (wave, wind and tidal) for issues with similar uncertainty. Knowledge from these efforts will ensure that, as commercial-scale wave farms are developed, work is performed within a framework of understanding regarding associated effects on biodiversity at local and regional levels.

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Appendix A. Habitat generation: MREIs as artificial reefs and aquaculture installations

Any hard structure immersed in the sea will become colonized by sessile marine life and may also attract mobile organisms such as fish and crustaceans. Hence, an area of particular interest is the potential for MREIs to increase the abundance of mobile species such as fish and crustaceans and provide habitat for sessile epibiota in a similar way to artificial reefs or to be used for aquaculture.

Artificial reefs have been created for various purposes including recreational activities and as a means of aggregating and or enhancing fish stocks [110], and to mitigate for lost habitat [111], biodiversity and productivity [112,113]. Recruitment and survival are strongly linked to the amount and quality of refuge present, and there is good evidence that artificial reefs can increase the diversity and abundance of species compared with surrounding areas [52,113,114]. In addition to their primary role in the generation of power, MREI pylons, anchors, cables and associated scour defence effectively form artificial reefs, and increased densities of bottom-dwelling fish have been reported around wind farms [56].

A central issue for all artificial reefs is establishing whether the reefs have increased production or have merely resulted in the aggregation of previously dispersed individuals without creating stock enhancement *per se* [115]. Experiments in the intertidal zone have shown that small-scale modifications to the surface of marine engineering used in coastal defences, that is analogous to scour defence, can be used to increase local species diversity and to provide refuges for juvenile commercially exploited molluscs [53] (figure 9). Hence, there may be benefits from modifying the type/size and or configuration of scour defence used around MREIs in order to increase structural complexity and habitat/refuge availability [116,117]. It may also be possible to tailor the type of habitat provided in order to provide opportunities for particular species. The outcomes of such habitat generation will be most effective in locations where the amount of similar natural habitat is an important factor that is otherwise limiting population growth. Further potential for stock enhancement will occur if arrays of structures exclude fishing activities, such as trawling [118], and so, in effect, create marine protected areas, which have been shown to increase stocks of commercially exploited species with potential spillover effects to the surrounding area/fishery [119,120]. The placement and configuration of arrays could also be considered in order to maximize the extent of biological connectivity between structures [20].

Some promising directions are in generating suitable habitat for crabs (*Cancer pagurus*), lobsters (*Homarus gammarus*) and demersal fish [52,117,118]. In addition to direct provision of habitat, colonization of structures by invertebrates may also provide potential food resources for fish and crustaceans. In addition to generation of artificial reefs to promote wild stocks, mariculture of molluscs, including mussels, oysters and algae are feasible around and between MREI structures [22]. It may also be possible for caged culture of finfish, but this will be restricted by depth in shallow-water deployments such as wind farms [52]. More work is needed to establish the efficacy of MREIs as artificial reefs and for aquaculture. This will be best achieved through experiments to compare specific types of habitat generation and aquaculture, long-term monitoring of existing

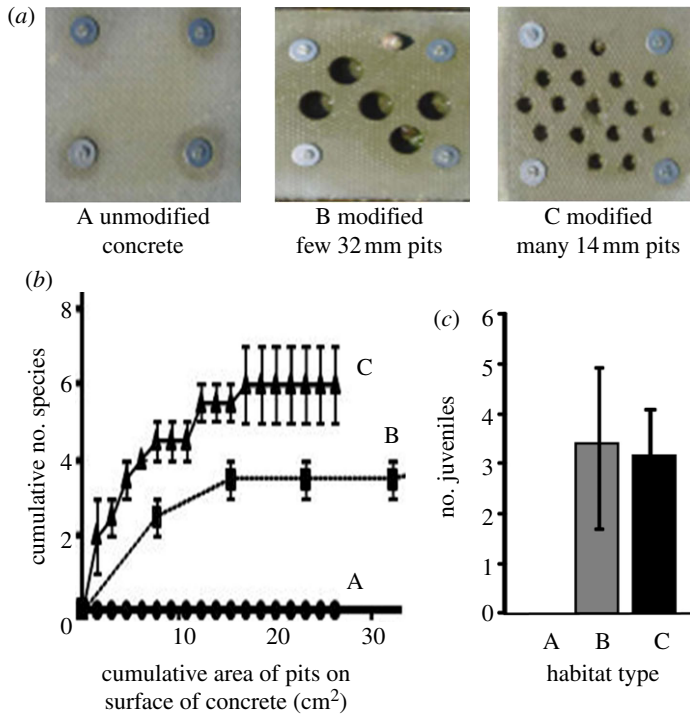


Figure 9. Experimental modification of materials used in coastal defence construction: (a) addition of habitat complexity to concrete surfaces resulted in (b) significantly increased diversity of intertidal organisms within five months at sites in SW England (mean \pm 1 s.e.; Thompson *et al.* 2011, unpublished data); and (c) similar modification of a sea wall, in the Azores, Portugal, increased the abundance of juvenile commercially important molluscs (mean \pm 1 s.e., number of individuals per 25 cm²; here A unmodified surface = 0 individuals; B was 24 mm and C was 12 mm pits; adapted from Martins *et al.* [53]).

installations and predictive modelling approaches to scale outcomes up to that of an array or group of arrays within a region.

While MREIs will undoubtedly generate some new habitat, they will also remove the habitats that were present originally. In many cases, soft sedimentary habitat and associated infaunal assemblages will be replaced by epibiota on hard surfaces. The presence of epibiota and the aggregation of fish and crustaceans are also likely to influence the neighbouring soft bottom assemblage that remains, for example, as a consequence of increased organic inputs from filter feeders or predation by fish [21,117].

It does, however, remain unclear whether the colonization of MREIs represents a positive or negative effect. Addition of novel structure to habitats may also provide substrate for invasive species and, as such, more detailed research is required at MREIs to elucidate the species and magnitude of colonization so that ecological effects and impacts may be considered. There will be both winners and losers in terms of habitats and species, and it will be important to consider the net effect of MREIs on a site-by-site basis in order to make an appropriate assessment of the ecological consequences of such developments.

References

- 1 Fabry, V. J., Seibel, B. A., Feely, R. A. & Orr, J. C. 2008 Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.* **65**, 414–432. (doi:10.1093/icesjms/fsn048)
- 2 Royal Society 2005 *Ocean acidification due to increasing atmospheric carbon dioxide*. London, UK: Royal Society. See <http://royalsociety.org/policy/publications/2005/ocean-acidification/>.
- 3 Richardson, A. J. 2008 In hot water: zooplankton and climate change. *ICES J. Mar. Sci.* **65**, 279–295. (doi:10.1093/icesjms/fsn028)
- 4 Lehodey, P. *et al.* 2006 Climate variability, fish, and fisheries. *J. Climate* **19**, 5009–5030. (doi:10.1175/JCLI3898.1)
- 5 Frederiksen, M., Harris, M. P., Daunt, F., Rothery, P. & Wanless, S. 2004 Scale-dependent climate signals drive breeding phenology of three seabird species. *Glob. Change Biol.* **10**, 1214–1221. (doi:10.1111/j.1529-8817.2003.00794.x)
- 6 Newson, S. E. *et al.* 2009 Indicators of the impact of climate change on migratory species. *Endangered Species Res.* **7**, 101–113. (doi:10.3354/esr00162)
- 7 Robinson, R. A. *et al.* 2009 Travelling through a warming world: climate change and migratory species. *Endangered Species Res.* **7**, 87–99. (doi:10.3354/esr00095)
- 8 Herbert, G. M. J., Iniyani, S., Sreevalsan, E. & Rajapandian, S. 2007 A review of wind energy technologies. *Renew. Sustain. Energy Rev.* **11**, 1117–1145. (doi:10.1016/j.rser.2005.08.004)
- 9 Taylor, D. 2004 Wind energy. In *Renewable energy: power for a sustainable future* (ed. G. Boyle), pp. 244–293. Oxford, UK: Oxford University Press.
- 10 Michel, J., Dunagan, H., Boring, C., Healy, E., Evans, W., Dean, J. M., McGillis, A. & Hain, J. 2007 *Worldwide synthesis and analysis of existing information regarding environmental effects of alternative energy uses on the outer continental shelf*. Minerals Management Service, OCS Report MMS 2007-038. Herndon, VA: US Department of the Interior, Minerals Management Service. See <http://www.boemre.gov/itd/pubs/2007/2007-038.pdf>.
- 11 Ferro, B. D. 2006 Wave and tidal energy: its emergence and the challenges it faces. *Refocus* **7**, 46–48. (doi:10.1016/S1471-0846(06)70574-1)
- 12 Cada, G., Ahlgrimm, J., Bahleda, M., Bigford, T., Stavrakas, S. D., Hall, D., Moursund, R. & Sale, M. 2007 Potential impacts of hydrokinetic and wave energy conversion technologies on aquatic environments. *Fisheries* **32**, 174–181. (doi:10.1577/1548-8446(2007)32[174:PIOHAW]2.0.CO;2)
- 13 Boehlert, G. W., McMurray, G. R. & Tortorici, C. E. (eds) 2008 *Ecological effects of wave energy development in the Pacific northwest*. US Department of Commerce, National Oceanic and Atmospheric Administration & National Marine Fisheries Service, NOAA Technical Memorandum NMFS-F/SPO-92. Washington, DC: US Department of Commerce. See <http://spo.nwr.noaa.gov/tm/Wave%20Energy%20NOAATM92%20for%20web.pdf>.
- 14 Nelson, P. A. *et al.* 2008 *Developing wave energy in coastal California: potential socio-economic and environmental effects*. California Energy Commission, PIER Energy-Related Environmental Research Program & California Ocean Protection Council, PIER Final Project Report CEC-500-2008-083. Sacramento, CA: California Energy Commission. See <http://www.energy.ca.gov/2008publications/CEC-500-2008-083/>.
- 15 Carbon Trust 2006 *Future marine energy. Results of the marine energy challenge: cost competitiveness and growth of wave and tidal stream energy*. Report CTC601. London, UK: Carbon Trust. See <http://www.carbontrust.co.uk/publications/pages/publicationdetail.aspx?id=CTC601>.
- 16 Kerr, D. 2007 Marine energy. *Phil. Trans. R. Soc. A* **365**, 971–992. (doi:10.1098/rsta.2006.1959)
- 17 Pelc, R. & Fujita, R. M. 2002 Renewable energy from the ocean. *Mar. Policy* **26**, 471–479. (doi:10.1016/S0308-597X(02)00045-3)
- 18 Gill, A. B. 2005 Offshore renewable energy: ecological implications of generating electricity in the coastal zone. *J. Appl. Ecol.* **42**, 605–615. (doi:10.1111/j.1365-2664.2005.01060.x)
- 19 Sutherland, W. J. *et al.* 2008 Future novel threats and opportunities facing UK biodiversity identified by horizon scanning. *J. Appl. Ecol.* **45**, 821–833. (doi:10.1111/j.1365-2664.2008.01474.x)

- 20 Inger, R. *et al.* 2009 Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *J. Appl. Ecol.* **46**, 1145–1153. (doi:10.1111/j.1365-2664.2009.01697.x)
- 21 Boehlert, G. W. & Gill, A. B. 2010 Environmental and ecological effects of ocean renewable energy development: a current synthesis. *Oceanography* **23**, 68–81. (doi:10.5670/oceanog.2010.46)
- 22 Wilhelmsson, D. *et al.* 2010 *Greening blue energy: identifying and managing the biodiversity risks and opportunities of off shore renewable energy*. Gland, Switzerland: International Union for Conservation of Nature. See http://www.iucn.org/about/work/programmes/marine/marine_resources/?5713/.
- 23 Shields, M. A. *et al.* 2011 Marine renewable energy: the ecological implications of altering the hydrodynamics of the marine environment. *Ocean Coastal Manag.* **54**, 2–9. (doi:10.1016/j.ocecoaman.2010.10.036)
- 24 Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C. V., Somerfield, P. J. & Karakassis, I. 2006 Global analysis of response and recovery of benthic biota to fishing. *Mar. Ecol. Prog. Ser.* **311**, 1–14. (doi:10.3354/meps311001)
- 25 Desholm, M. & Kahlert, J. 2005 Avian collision risk at an offshore wind farm. *Biol. Lett.* **1**, 296–298. (doi:10.1098/rsbl.2005.0336)
- 26 Desholm, M., Fox, A. D., Beasley, P. D. L. & Kahlert, J. 2006 Remote techniques for counting and estimating the number of bird–wind turbine collisions at sea: a review. *Ibis* **148**, 76–89. (doi:10.1111/j.1474-919X.2006.00509.x)
- 27 Perrow, M. R., Skeate, E. R., Lines, P., Brown, D. & Tomlinson, M. L. 2006 Radio telemetry as a tool for impact assessment of wind farms: the case of little terns *Sterna albifrons* at Scroby Sands, Norfolk, UK. *Ibis* **148**, 57–75. (doi:10.1111/j.1474-919X.2006.00508.x)
- 28 Brown, M. J., Linton, E. & Rees, E. C. 1992 Causes of mortality among wild swans in Britain. *Wildfowl* **43**, 70–79.
- 29 Garthe, S. & Hüppop, O. 2004 Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *J. Appl. Ecol.* **41**, 724–734. (doi:10.1111/j.0021-8901.2004.00918.x)
- 30 De Lucas, M., Janss, G. F. E., Whitfield, D. P. & Ferrer, M. 2008 Collision fatality of raptors in wind farms does not depend on raptor abundance. *J. Appl. Ecol.* **45**, 1695–1703. (doi:10.1111/j.1365-2664.2008.01549.x)
- 31 Larsen, J. K. & Guillemette, M. 2007 Effects of wind turbines on flight behaviour of wintering common eiders: implications for habitat use and collision risk. *J. Appl. Ecol.* **44**, 516–522. (doi:10.1111/j.1365-2664.2007.01303.x)
- 32 Arnett, E. B. *et al.* 2008 Patterns of bat fatalities at wind energy facilities in North America. *J. Wildl. Manag.* **72**, 61–78. (doi:10.2193/2007-221)
- 33 Henderson, I. G., Langston, R. H. W. & Clark, N. A. 1996 The response of common terns *Sterna hirundo* to power lines: an assessment of risk in relation to breeding commitment, age and wind speed. *Biol. Conserv.* **77**, 185–192. (doi:10.1016/0006-3207(95)00144-1)
- 34 Grecian, W. J., Inger, R., Attrill, M. J., Bearhop, S., Godley, B. J., Witt, M. J. & Votier, S. C. 2010 Potential impacts of wave-powered marine renewable energy installations on marine birds. *Ibis* **152**, 683–697. (doi:10.1111/j.1474-919X.2010.01048.x)
- 35 Wilson, B., Batty, R., Daunt, F. & Carter, C. 2007 *Collision risks between marine renewable energy devices and mammals, fish and diving birds, Report to the Scottish Executive*. Strategic Environmental Assessment of Marine Renewable Energy Development in Scotland. Oban, UK: Scottish Association for Marine Science. See http://www.seaenergyscotland.net/public_docs/Appendix%20C7.B%20Collisions_report_final_12_03_07.pdf.
- 36 Langton, R., Davies, I. M. & Scott, B. E. 2011 Seabird conservation and tidal stream and wave power generation: information needs for predicting and managing potential impacts. *Mar. Policy* **35**, 623–630. (doi:10.1016/j.marpol.2011.02.002)
- 37 Horowitz, C. & Jasny, M. 2007 Precautionary management of noise: lessons from the US. Marine Mammal Protection Act. *J. Int. Wildl. Law Policy* **10**, 225–232. (doi:10.1080/13880290701769288)
- 38 Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C. & Popper, A. N. 2010 A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends Ecol. Evol.* **25**, 419–427. (doi:10.1016/j.tree.2010.04.005)

- 39 André, M. *et al.* 2011 Low-frequency sounds induce acoustic trauma in cephalopods. *Front. Ecol. Environ.* (doi:10.1890/100124)
- 40 Madsen, P. T., Wahlberg, M., Tougaard, J., Lucke, K. & Tyack, P. 2006 Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. *Mar. Ecol. Prog. Ser.* **309**, 279–295. (doi:10.3354/meps309279)
- 41 Edrén, S. M. C., Teilmann, J., Dietz, R. & Carstensen, J. 2004 *Effects from the construction of Nysted offshore wind farm on seals in Rødsand seal sanctuary based on remote video monitoring*. Technical report to Energi A/S. Roskilde, Denmark: National Environmental Research Institute Roskilde.
- 42 Carstensen, J., Henriksen, O. D. & Teilmann, J. 2006 Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Mar. Ecol. Prog. Ser.* **321**, 295–308. (doi:10.3354/meps321295)
- 43 Andersson, M. H., Dock-Akerman, E., Ubral-Hedenberg, R., Ohman, M. C. & Sigray, P. 2007 Swimming behavior of roach (*Rutilus rutilus*) and three-spined stickleback (*Gasterosteus aculeatus*) in response to wind power noise and single-tone frequencies. *AMBIO J. Hum. Environ.* **36**, 636–638. (doi:10.1579/0044-7447(2007)36[636:SBORRR]2.0.CO;2)
- 44 Masden, E. A., Fox, A. D., Furness, R. W., Bullman, R. & Haydon, D. T. 2010 Cumulative impact assessments and bird/wind farm interactions: developing a conceptual framework. *Environ. Impact Assess. Rev.* **30**, 1–7. (doi:10.1016/j.eiar.2009.05.002)
- 45 CMACS 2003 *A baseline assessment of electromagnetic fields generated by offshore windfarm cables*. COWRIE Report EMF-01–2002 66. Liverpool, UK: Centre for Marine and Coastal Studies.
- 46 Wiltschko, W. & Wiltschko, R. 2005 Magnetic orientation and magnetoreception in birds and other animals. *J. Compar. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **191**, 675–693. (doi:10.1007/s00359-005-0627-7)
- 47 Luschi, P., Benhamou, S., Girard, C., Ciccione, S., Roos, D., Sudre, J. & Benvenuti, S. 2007 Marine turtles use geomagnetic cues during open-sea homing. *Curr. Biol.* **17**, 126–133. (doi:10.1016/j.cub.2006.11.062)
- 48 Gould, J. L. 2008 Animal navigation: the evolution of magnetic orientation. *Curr. Biol.* **18**, R482–R484. (doi:10.1016/j.cub.2008.03.052)
- 49 Westerberg, H. & Lagenfelt, I. 2008 Sub-sea power cables and the migration behaviour of the European eel. *Fish. Manag. Ecol.* **15**, 369–375. (doi:10.1111/j.1365-2400.2008.00630.x)
- 50 Öhman, M. C., Sigray, P. & Westerberg, H. 2007 Offshore windmills and the effects of electromagnetic fields on fish. *AMBIO J. Hum. Environ.* **36**, 630–633. (doi:10.1579/0044-7447(2007)36[630:OWATEO]2.0.CO;2)
- 51 Bickel, S. L., Malloy Hammond, J. D. & Tang, K. W. 2011 Boat-generated turbulence as a potential source of mortality among copepods. *J. Exp. Mar. Biol. Ecol.* **401**, 105–109. (doi:10.1016/j.jembe.2011.02.038)
- 52 Linley, E. A. S., Wilding, T. A., Black, K., Hawkins, A. J. S. & Mangi, S. 2007 *Review of the reef effects of offshore wind farm structures and their potential for enhancement and mitigation*. Report to Department for Business, Enterprise and Regulatory Reform (BERR), No. RFCA/005/0029P Plymouth. London, UK: Department for Business, Enterprise and Regulatory Reform.
- 53 Martins, G., Thompson, R., Neto, A., Hawkins, S. & Jenkins, S. 2010 Enhancing stocks of the exploited limpet *Patella candei* d’Orbigny via modifications in coastal engineering. *Biol. Conserv.* **143**, 203–211. (doi:10.1016/j.biocon.2009.10.004)
- 54 Petersen, J. K. & Malm, T. 2006 Offshore windmill farms: threats to or possibilities for the marine environment. *AMBIO J. Hum. Environ.* **35**, 75–80. (doi:10.1579/0044-7447(2006)35[75:OWFTTO]2.0.CO;2)
- 55 Thurstan, R. H., Brockington, S. & Roberts, C. M. 2009 The effects of 118 years of industrial fishing on UK bottom trawl fisheries. *Nat. Commun.* **1**, 1–6. (doi:10.1038/ncomms1013)
- 56 Wilhelmsson, D., Malm, T. & Ohman, M. C. 2006 The influence of offshore windpower on demersal fish. *ICES J. Mar. Sci.* **63**, 775–784. (doi:10.1016/j.icesjms.2006.02.001)
- 57 Fayram, A. H. & de Risi, A. 2007 The potential compatibility of offshore wind power and fisheries: an example using bluefin tuna in the Adriatic Sea. *Ocean Coast. Manag.* **50**, 597–605. (doi:10.1016/j.ocecoaman.2007.05.004)

- 58 Castro, J. J., Santiago, J. A. & Santana-Ortega, A. T. 2001 A general theory on fish aggregation to floating objects: an alternative to the meeting point hypothesis. *Rev. Fish. Biol. Fish.* **11**, 255–277. (doi:10.1023/A:1020302414472)
- 59 Nelson, P. A. 2003 Marine fish assemblages associated with fish aggregating devices (FADs): effects of fish removal, FAD size, fouling communities, and prior recruits. *Fish. Bull.* **101**, 835–850.
- 60 Osterblom, H., Casini, M., Olsson, O. & Bignert, A. 2006 Fish, seabirds and trophic cascades in the Baltic Sea. *Mar. Ecol. Prog. Ser.* **323**, 233–238. (doi:10.3354/meps323233)
- 61 Friedlander, A. M., Brown, E. & Monaco, M. E. 2007 Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Mar. Ecol. Prog. Ser.* **351**, 221–233. (doi:10.3354/meps07112)
- 62 Stewart, G., Pullin, A. & Coles, C. 2007 Poor evidence-base for assessment of windfarm impacts on birds. *Environ. Conserv.* **34**, 1–11. (doi:10.1017/S0376892907003554)
- 63 Rosenzweig, M. 2003 *Win-win ecology: how the Earth's species can survive in the midst of human enterprise?* Oxford, UK: Oxford University Press.
- 64 BERR 2008 *Atlas of UK marine renewable energy resources*. London, UK: Department for Business, Innovation & Skills.
- 65 Mills, C. M., Townsend, S. E., Jennings, S., Eastwood, P. D. & Houghton, C. A. 2007 Estimating high resolution trawl fishing effort from satellite-derived vessel monitoring system data. *ICES J. Mar. Sci.* **64**, 248–255. (doi:10.1093/icesjms/fsl026)
- 66 Witt, M. J. & Godley, B. J. 2007 A step towards seascape scale conservation: using vessel monitoring systems (VMS) to map fishing activity. *PLoS ONE* **2**, e1111. (doi:10.1371/journal.pone.0001111)
- 67 Foden, J., Rogers, S. & Jones, A. 2010 Recovery of UK seabed habitats from benthic fishing and aggregate extraction: towards a cumulative impact assessment. *Mar. Ecol. Prog. Ser.* **411**, 259–270. (doi:10.3354/meps08662)
- 68 Rees, H. L., Pendle, M. A., Waldock, R., Limpenny, D. S. & Boyd, S. E. 1999 A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. *ICES J. Mar. Sci.* **56**, 228–246. (doi:10.1006/jmsc.1998.0438)
- 69 Stobart, B. et al. 2007 A baited underwater video technique to assess shallow-water Mediterranean fish assemblages: methodological evaluation. *J. Exp. Mar. Biol. Ecol.* **345**, 158–174. (doi:10.1016/j.jembe.2007.02.009)
- 70 Sheehan, E. V., Coleman, R. A., Attrill, M. J. & Thompson, R. C. 2010 A quantitative assessment of the response of mobile estuarine fauna to crab-tiles during tidal immersion using remote underwater video cameras. *J. Exp. Mar. Biol. Ecol.* **387**, 68–74. (doi:10.1016/j.jembe.2010.02.008)
- 71 Holme, N. A. 1985 Use of photographic and television cameras on the continental shelf. In *Underwater photography and television for scientists* (eds J. D. George, G. I. Lythgoe & J. N. Lythgoe), pp. 88–99. Oxford, UK: Clarendon Press.
- 72 Berkelmans, R. 1992 Video photography: a quantitative sampling method. *Reef Res.* **2**, 10–11.
- 73 Parry, D. M., Kendall, M. A., Pilgrim, D. A. & Jones, M. B. 2003 Identification of patch structure within marine benthic landscapes using a remotely operated vehicle. *J. Exp. Mar. Biol. Ecol.* **285**, 497–511. (doi:10.1016/S0022-0981(02)00546-4)
- 74 Sheehan, E. V., Stevens, T. F. & Attrill, M. J. 2010 A quantitative, non-destructive methodology for habitat characterisation and benthic monitoring at offshore renewable energy developments. *PLoS ONE* **5**, e14461. (doi:10.1371/journal.pone.0014461)
- 75 Underwood, A. J. 1992 Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *J. Exp. Mar. Biol. Ecol.* **161**, 145–178. (doi:10.1016/0022-0981(92)90094-Q)
- 76 Leitão, F., Santos, M. N., Erzini, K. & Monteiro, C. C. 2008 Fish assemblages and rapid colonization after enlargement of an artificial reef off the Algarve coast (southern Portugal). *Mar. Ecol. Evol. Perspect.* **29**, 435–448. (doi:10.1111/j.1439-0485.2008.00253.x)
- 77 Bohnsack, J. A. 1989 Are high-densities of fishes at artificial reefs the result of habitat limitation or behavioural preference? *Bull. Mar. Sci.* **44**, 631–645.

- 78 Grossman, G. D., Jones, G. P. & Seaman, W. J. 1997 Do artificial reefs increase regional fish production? A review of existing data. *Fisheries* **22**, 17–23. (doi:10.1577/1548-8446(1997)022<0017:DARIRF>2.0.CO;2)
- 79 Sims, D. W., Nash, J. P. & Morritt, D. 2001 Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Mar. Biol.* **139**, 1165–1175. (doi:10.1007/s002270100666)
- 80 Sims, D. W. *et al.* 2006 Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *J. Anim. Ecol.* **75**, 176–190. (doi:10.1111/j.1365-2656.2005.01033.x)
- 81 Polunin, N., Bloomfield, H., Sweeting, C. & McCandless, D. 2009 Developing indicators of MPA effectiveness: finfish abundance and diversity in a Yorkshire prohibited trawl area. Report to MFA, London.
- 82 Priede, I. G. & Merrett, N. R. 1996 Estimation of abundance of abyssal demersal fishes; a comparison of data from trawls and baited cameras. *J. Fish Biol.* **49**, 207–216. (doi:10.1111/j.1095-8649.1996.tb06077.x)
- 83 Heagney, E., Lynch, T., Babcock, R. & Suthers, I. 2007 Pelagic fish assemblages assessed using mid-water baited video: standardising fish counts using bait plume size. *Mar. Ecol. Prog. Ser.* **350**, 255–266. (doi:10.3354/meps07193)
- 84 Ehrich, S., Stelzenmuller, V. & Adlerstein, S. 2009 Linking spatial pattern of bottom fish assemblages with water masses in the North Sea. *Fish. Oceanogr.* **18**, 36–50. (doi:10.1111/j.1365-2419.2008.00495.x)
- 85 Reiss, H. *et al.* 2010 Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES J. Mar. Sci.* **67**, 278–293. (doi:10.1093/icesjms/fsp253)
- 86 Certain, G. & Bretagnolle, V. 2008 Monitoring seabirds population in marine ecosystem: the use of strip-transect aerial surveys. *Remote Sens. Environ.* **112**, 3314–3322. (doi:10.1016/j.rse.2008.01.019)
- 87 Greenwood, J. J. D. & Robinson, R. A. 2006 General census methods. In *Ecological census techniques: a handbook* (ed. W. J. Sutherland). Cambridge, UK: Cambridge University Press.
- 88 Ropert-Coudert, Y. & Wilson, R. P. 2005 Trends and perspectives in animal-attached remote sensing. *Front. Ecol. Environ.* **3**, 437–444. (doi:10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2)
- 89 Masden, E. A., Haydon, D. T., Fox, A. D., Furness, R. W., Bullman, R. & Desholm, M. 2009 Barriers to movement: impacts of wind farms on migrating birds. *ICES J. Mar. Sci.* **66**, 746–753. (doi:10.1093/icesjms/fsp031)
- 90 Votier, S. C., Grecian, W. J., Patrick, S. & Newton, J. 2011 Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PTT tracking, radio-tracking and stable isotope analysis. *Mar. Biol.* **158**, 355–362. (doi:10.1007/s00227-010-1563-9)
- 91 Votier, S. C., Bearhop, S., Witt, M. J., Inger, R., Thompson, D. & Newton, J. 2010 Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *J. Appl. Ecol.* **47**, 487–497. (doi:10.1111/j.1365-2664.2010.01790.x)
- 92 Macleod, K., Fresne, S. D., Mackey, B., Faustino, C. & Boyd, I. 2010 Approaches to marine mammal monitoring at marine renewable energy developments. Sea Mammal Research Unit St Andrews, St Andrews, UK.
- 93 Hammond, P. *et al.* 2002 Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *J. Appl. Ecol.* **39**, 361–376. (doi:10.1046/j.1365-2664.2002.00713.x)
- 94 Hammond, P. S. 2007 Final report on small cetacean abundance in the European Atlantic and North Sea (SCANS-II). Department for Environment, Food and Rural Affairs, London, UK.
- 95 Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. 2001 *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.
- 96 Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P. & Matsumoto, H. 2007 An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography* **20**, 36–45. (doi:10.5670/oceanog.2007.03)
- 97 Philpott, E., Englund, A., Ingram, S. & Rogan, E. 2007 Using T-PODs to investigate the echolocation of coastal bottlenose dolphins. *J. Mar. Biol. Assoc.* **87**, 11–17. (doi:10.1017/S002531540705494X)

- 98 Verfuß, U. K., Honnef, C. G., Meding, A., Dahne, M., Mundry, R. & Benke, H. 2007 Geographical and seasonal variation of harbour porpoise (*Phocoena phocoena*) presence in the German Baltic Sea revealed by passive acoustic monitoring. *J. Mar. Biol. Assoc.* **87**, 165–176. (doi:10.1017/S0025315407054938)
- 99 Todd, V. L. G., Pearse, W. D., Tregenza, N. C., Lepper, P. A. & Todd, I. B. 2009 Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations. *ICES J. Mar. Sci.* **66**, 734–745. (doi:10.1093/icesjms/fsp035)
- 100 Bailey, H., Clay, G., Coates, E. A., Lusseau, D., Senior, B. & Thompson, P. M. 2010 Using T-PODs to assess variations in the occurrence of coastal bottlenose dolphins and harbour porpoises. *Aquatic Conserv. Mar. Freshwater Ecosyst.* **20**, 150–158. (doi:10.1002/aqc.1060)
- 101 Edrén, S. M. C., Andersen, S. M., Teilmann, J., Carstensen, J., Harders, P. B., Dietz, R. & Miller, L. A. 2010 The effect of a large Danish offshore wind farm on harbor and gray seal haul-out behavior. *Mar. Mamm. Sci.* **26**, 614–634. (doi:10.1111/j.1748-7692.2009.00364.x)
- 102 McConnell, B. J., Chambers, C., Nicholas, K. S. & Fedak, M. A. 1992 Satellite tracking of grey seals (*Halichoerus grypus*). *J. Zool.* **226**, 271–282. (doi:10.1111/j.1469-7998.1992.tb03839.x)
- 103 Leeney, R. H., Broderick, A. C., Mills, C., Sayer, S., Witt, M. J. & Godley, B. J. 2010 Abundance, distribution and haul-out behaviour of grey seals (*Halichoerus grypus*) in Cornwall and the Isles of Scilly, UK. *J. Mar. Biol. Assoc.* **90**, 1033–1040. (doi:10.1017/S0025315409991512)
- 104 Eastwood, P. D., Mills, C. M., Aldridge, J. N., Houghton, C. A. & Rogers, S. I. 2007 Human activities in UK offshore waters: an assessment of direct, physical pressure on the seabed. *ICES J. Mar. Sci.* **64**, 453–463. (doi:10.1093/icesjms/fsm001)
- 105 Lee, J., South, A. B. & Jennings, S. 2010 Developing reliable, repeatable, and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. *ICES J. Mar. Sci.* **67**, 1260–1271. (doi:10.1093/icesjms/fsq010)
- 106 Vanstaen, K., Clark, R., Ware, S., Eggleton, J., James, J. C. W., Cotteril, C., Rance, J., Manco, F. & Woolmer, A. 2010 Assessment of the distribution and intensity of fishing activities in the vicinity of aggregate extraction sites. MALSF-MEPF Project 08/P73. Cefas, Lowestoft, UK.
- 107 Jennings, S., Dinmore, T. A., Duplisea, D. E., Warr, K. J. & Lancaster, J. E. 2001 Trawling disturbance can modify benthic production processes. *J. Anim. Ecol.* **70**, 459–475. (doi:10.1046/j.1365-2656.2001.00504.x)
- 108 Miller, P. I. 2009 Composite front maps for improved visibility of dynamic sea-surface features on cloudy SeaWiFS and AVHRR data. *J. Mar. Syst.* **78**, 327–336. (doi:10.1016/j.jmarsys.2008.11.019)
- 109 Miller, P. I., Christodoulou, S. & Saux-Picart, S. 2010 Oceanic thermal fronts from Earth observation data: a potential surrogate for pelagic diversity. Report to Department of Environment, Food and Rural Affairs. Defra Contract No. MB102. Plymouth Marine Laboratory.
- 110 Jensen, A. C., Collins, K. J., Lockwood, A. P. M., Mallinson, J. J. & Turnpenny, W. H. 1994 Colonization and fishery potential of a coal-ash artificial reef, Poole Bay, United Kingdom. *Bull. Mar. Sci.* **55**, 1263–1276.
- 111 Hueckel, G. J., Buckley, R. M. & Benson, B. L. 1989 Mitigating rocky habitat loss using artificial reefs. *Bull. Mar. Sci.* **44**, 913–922.
- 112 Pickering, H., Whitmarsh, D. & Jensen, A. 1998 Artificial reefs as a tool to aid rehabilitation of coastal ecosystems: investigating the potential. *Mar. Pollut. Bull.* **37**, 505–514. (doi:10.1016/S0025-326X(98)00121-0)
- 113 Jensen, A. 1999 Artificial reefs of Europe: perspective and future. In *Proc. 7th Int. Conf. on Artificial Reefs and Related Aquatic Habitats, San Remo, Italy*, pp. S3–S13.
- 114 Charbonnel, E., Serre, C., Ruitton, S., Harmelin, J. G. & Jensen, A. 2002 Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). *ICES J. Mar. Sci.* **59**, S208–S213. (doi:10.1006/jmsc.2002.1263)
- 115 Bohnsack, J. A., Ecklund, A. M. & Szmant, A. M. 1997 Artificial reef research: is there more than the attraction–production issue? *Fisheries* **22**, 14–16.
- 116 Andersson, M. H., Berggren, M., Wilhelmsson, D. & Ohman, M. C. 2009 Epibenthic colonization of concrete and steel pilings in a cold-temperate embayment: a field experiment. *Helgoland Mar. Res.* **63**, 249–260. (doi:10.1007/s10152-009-0156-9)

- 117 Langhamer, O. & Wilhelmsson, D. 2009 Colonisation of fish and crabs of wave energy foundations and the effects of manufactured holes: a field experiment. *Mar. Environ. Res.* **68**, 151–157. (doi:10.1016/j.marenvres.2009.06.003)
- 118 Wilson, J. C., Elliott, M., Cutts, N. D., Mander, L., Mendao, V., Perez-Dominguez, R. & Phelps, A. 2010 Coastal and offshore wind energy generation: is it environmentally benign? *Energies* **3**, 1383–1422. (doi:10.3390/en3071383)
- 119 Russ, G. R. & Alcala, A. C. 1996 Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar. Ecol. Prog. Ser.* **132**, 1–9. (doi:10.3354/meps132001)
- 120 Gaylord, B., Gaines, S. D., Siegel, D. A. & Carr, M. H. 2005 Marine reserves exploit population structure and life history in potentially improving fisheries yields. *Ecol. Appl.* **15**, 2180–2191. (doi:10.1890/04-1810)