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CONFUSION REIGNS? A REVIEW OF MARINE MEGAFANNA INTERACTIONS WITH TIDAL-STREAM ENVIRONMENTS

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Abstract Energetic tidal-stream environments are characterised by frequent, variable yet broadly predictable currents containing ephemeral flow structures that change across multiple spatiotemporal scales. Marine mammals and seabirds (marine megafauna) often frequent such sites but increasingly these locations are targeted for renewable energy extraction; little is known however about how marine megafauna use these habitats and any potential impacts. This review aims to summarise existing knowledge concerning usage by marine megafauna and considers their wider ecological significance. The review describes the physical processes occurring within tidal-stream environments that generate the oceanographic structures of potential ecological relevance such as jets, boils, eddies and fronts. Important physical features of these environments include lateral transport, turbulence-driven 3-dimensional flow structure at various spatial scales, and upwelling. Foraging opportunities appear to be the main attractor to marine megafauna, likely driven by enhanced prey abundance, vulnerability and/or diversity. Many megafauna associate with particular tidal phases, current strengths and flow structures, likely in response to tidally-forced prey distribution and behaviours. Occupancy patterns, distributions and foraging behaviours are discussed. Local site fidelity by ‘tidal-stream experts’ suggest non-uniform conservation risks within larger metapopulations. The review discusses data gathering techniques and associated challenges, the significance of scaling and information gaps.

Introduction

Understanding the various factors (both intrinsic and external) that drive the distribution and abundance of species is a fundamental element in the science of ecology (Begon et al. 1996). Accordingly, there is a significant literature on how individuals and species distribute themselves in response to these factors (Gaston 2003). These processes can be self-selecting, such as the differential growth success of widely broadcast seeds (e.g. Putz 1983), or weakly targeted, as in the settlement of planktonic larvae (e.g. Hawkins & Hartnoll 1982). For many animal
species, however, distribution patterns can be both spatially and temporally dynamic within the lifetime of individuals (e.g. Cowley et al. 2001). These more dynamic distributions emerge from the interplay of individual mobility, and that of conspecifics and other species (including prey, competitors and parasites) superimposed on (typically more stable) abiotic factors (Gaston 2003). There are, however, situations where additional complexity is created due to the inherent dynamic nature of abiotic factors. For example, as the Earth moves along its orbit around the Sun, seasonal changes in the extent of exposure to solar radiation produce predictable changes in temperature, day length, ice coverage and so on. Other abiotic factors vary on much shorter timescales and at smaller spatial scales. From a research perspective, the responses of organisms to such dynamic environments may expose pertinent insights into the precise nature and extent of the habitat drivers at work (Fraenkel & Gunn 1940). Furthermore, mismatches resulting from organisms finding themselves out of step with their environment can provide opportunities to predators, competitors and others, which take advantage of organisms’ confusion based on incomplete perception of their environment. The visual acuity of tropical reef fishes is an elegant example, where piscivorous predators appear to exploit the visual vulnerability of both diurnal and nocturnal specialist species by hunting in the half-light of dusk (Munz & McFarland, 1973). In this review, current knowledge of the consequences of a predictable but complex class of dynamic abiotic factors in the marine environment – turbulent tidal streams – are explored for two groups of air-breathing vertebrate predators: marine mammals and seabirds, hereafter referred to as marine megafauna.

The primary drivers for tidal movements of water are global variations in the gravitational forces exerted by the Moon and the Sun coupled with the rotation of the Earth. The influences of tidal changes in sea surface height on littoral communities are well studied and have revealed much about the complex interplay among species and fine-scale environmental features (Connell 1961; Helmuth et al. 2006). Far less is known about the consequences of the associated tidal currents. These currents are known as tidal streams and typically oscillate on cycles of just over 12 hours, split between flood and ebb flows with periods of lower flow (slack) in between. While tidal currents are universal, their amplitude, extent and patterns of motion are modified by features of the basins which contain them. Tidal currents in coastal waters, for example, are often accentuated around headlands, through narrow straits or over shallow features such as reefs or banks. Many sites of rapid tidal currents have been known for centuries as navigational hazards, while some subsequently have assumed wider cultural significance (e.g. the Moskstraumen or Maelström off Lofoten, northern Norway; Poe 1841; Melville 1851; Verne 1870). Despite the difficulties of working in and around the highly dynamic water associated with tidal streams, these sites offer significant opportunities to investigate the ecology of the marine megafauna that target them. Tidal-stream environments, by their very nature, offer highly predictable and repeated opportunities for studying animal behaviour relative to variation at half-daily (ebb-flood) and fortnightly (spring-neap) scales.

Interactions between marine megafauna distributions and tides occur in three broad environments:

- Intertidal environments: Many fish and other marine species display marked movement into intertidal habitats during the rising tide to gain access to foraging and spawning opportunities as peripheral areas (intertidal mudflats,
seagrass beds etc.) become briefly accessible (e.g. Morrison et al. 2002; Krumme 2004; Childs et al. 2008). This may attract marine megafauna (e.g. Harzen 1998; Hobbs et al. 2005; Fox & Young 2012). Conversely, many pinniped species haul out on intertidal areas between trips to sea.

- Estuarine environments: Tidal forcing in estuaries generates transient features (fronts, salt wedges and other discontinuities) through the interaction between fresh and saline water (Simpson & Nunes 1981; Huzzey 1982). Such features may be sought out by marine megafauna, presumably because of enhanced foraging opportunities (Mendes et al. 2002).

- Tidal-stream environments: A range of flow features are associated with strong tidal streams which occur where flow is constrained, including through straits, around headlands, and across banks or sills (‘tidal streaming’; Couch & Bryden 2006) or resonant (e.g. in the Bay of Fundy; Garrett 1972). Flow speeds in these sites may exceed 1 ms\(^{-1}\), and contain much structure, such as eddies, boils and fronts. These tidal-stream environments will form the main focus of this review.

Although features generated by tidal forcing in estuarine environments are both complex and ephemeral, the underlying physical processes that generate them are quite different from those found in tidal-stream environments; stratification, in particular, often occurs in estuaries but is not expected to persist in more energetic tidal-stream environments (Simpson et al. 1990).

It has long been known that marine megafauna seek out energetic tidal-stream environments. Zamon (2001, 2003) put forward the “tidal-coupling hypothesis”, echoing concepts previously formulated by other authors (e.g. Uda & Ishino 1958; Wolanski & Hamner 1988), to describe the apparent influence of tidal phase on piscivorous marine megafauna in tidal-stream environments. Under the tidal coupling hypothesis, interactions between currents and coastline lead to distinctive and spatiotemporally predictable flow structures such as jets, eddies and boils. Through various small-scale physical processes these features drive predictable variability in zooplankton distribution, abundance and/or availability, which are thought to attract small fish, which in turn attract piscivorous predators (Zamon 2003). Questions remain, however, about the precise mechanism(s) by which prey species are made available to be preyed upon by marine megafauna, and whether these mechanisms remain applicable in the most rapid flows (2 - 4 ms\(^{-1}\) or even greater) observed at many sites (Shields et al. 2011). Moreover, there may be other reasons why marine megafauna make use of tidal-stream environments.

One reason why these environments remain comparatively poorly known is the range of logistical and technological difficulties in studying them and the ecology contained within them, as strong currents make it difficult to deploy and retrieve scientific moorings or to undertake vessel surveys. In recent years, industrial interest in these environments as a source for renewable energy has increased considerably (Lewis et al. 2011; Ernst & Young 2013). While generating energy using tidal barrages has been undertaken for many decades (Frid et al. 2012), there is an increasing focus on harnessing the kinetic energy associated with tidal streams (Elliott 2013). Present development sites are widespread but focused on coastal areas with strong tidal-stream resources, particularly off Scotland (UK), Northern Ireland (UK), Brittany (France), the Bay of Fundy (USA/Canada), Puget Sound/Strait
Tidal energy generation is a new industry which presents several novel impacts to marine megafauna (e.g. collision, noise) that may differ in scale, location or characteristics to existing interactions with other industries. These potential impacts remain poorly understood (Inger et al. 2009; Shields et al. 2011; Scott et al. 2014), largely due to the complexity of tidal stream sites, the significant technological difficulties of conducting research on mobile species in fast-moving water, and the lack of background information on how these areas are typically used by marine megafauna and their prey. Standard survey practices typically do not offer opportunities for in-depth study of heterogeneity in marine megafauna habitat use at appropriate scales, and may indeed be impractical for fast-flowing turbulent conditions. Analyses of the potential significance of tidal-stream environments to wider marine mammal or seabird populations are often similarly lacking. Given the absence of an extensive knowledge base, regulatory agencies are likely to opt for a risk-averse precautionary approach when making consenting decisions, requiring increasingly detailed information on small-scale distribution and habitat use of marine megafauna within these sites (ICES 2014). While many scientific studies and environmental impact assessments have been conducted to date, many have focused on single sites over short timescales. This has resulted in a scattered literature that has complicated efforts to understand the broader significance of tidal-stream features in marine megafauna ecology. A comprehensive review is therefore timely to improve understanding of potential animal-industry interactions but also to consider the wider ecological significance of these discrete, ephemeral, but highly predictable features to marine mammals and seabirds. Due to the global distribution and accessibility of tidal-stream environments, the development of tidal-stream energy generation has been primarily concentrated in temperate waters of the Northern Hemisphere, including Europe, North America and eastern Asia (Ernst & Young 2013). This development has to some extent mirrored the historic expansion of marine megafauna research activities, e.g. in the North Atlantic and Pacific oceans. As a result, most focused studies of marine megafauna in tidal-stream sites to date describe a particular subset of species which may or may not be representative of marine megafauna globally.

This review will begin with an overview of the various oceanographic features that may be found within tidal-stream environments, the physical processes that underpin them and the potential consequences to animals of these features. This is followed by a review of marine megafauna which make use of such environments. More detailed discussion of the ecological significance of tidal-stream environments for marine megafauna follows, and the review ends with a description of current research approaches and data gaps that would benefit from further study. This review is based on peer-reviewed scientific literature, as well as additional sources of information including doctoral theses and Environmental Impact Assessments, where such sources were accessible. As is perhaps to be expected given the technical difficulties of studying fast-flowing waters, most studies to date refer to sites with maximum flow speeds of ≤1.5 ms⁻¹, although currents in some locations can flow considerably faster than this (Shields et al. 2011). The review considers fast-flowing tidal straits as well as the discrete and ephemeral oceanographic features that these currents generate in their surrounding transitional zones.
Tidally-driven flow structures

Scales of motion: tides, turbulence and energy cascade

Rapid tidal flows are inherently turbulent, meaning that flow occurs across a broad range of scales with an element of unpredictability. There is, however, structure to this turbulence: in the relationship between scales, in the manner in which energy moves (or ‘cascades’) between scales, and in the more organised (‘coherent’) flow structures that provide energy to the turbulent cascade. Animals experience and respond to the differing scales of motion within a turbulent environment according to how these scales compare to their body size and separation from other individuals and prey, so the scale structure of turbulence is of key importance here. The relative predictability of the coherent elements of the flow contrasts with the turbulent component and means that these structures may be more easily exploited by animals.

Tides arise from variations in the strength of gravitational attraction to the moon and the sun. The resulting ‘tide generating force’ varies on a large (global) scale. The creation of smaller scale tidal structure results from the ocean’s oscillating, wave-like response to this forcing, and interactions with its complex coastline and sea floor topography. Over long timescales the energy supplied to tides at the global scale must balance the energy lost frictionally at very small scales. Around 75% of the global tidal energy supply is dissipated in shelf seas (Wunsch & Ferrari 2004), and this occurs disproportionately in the regions of strongest tidal flow, so a substantial proportion of global tidal energy ultimately feeds the turbulent structure of the most energetic tidal flows.

The range of scales that can be present in a turbulent fluid is limited at large scales by the fluid’s extent (the water depth and its horizontal scale) and at small scales by its viscosity, which dissipates small scale current shear to heat. Flow structures significantly larger than the water depth are essentially two-dimensional as they are constrained vertically by the surface and bed but less so laterally. This is important as the behaviour of three-dimensional (unconstrained) turbulence is rather different from two-dimensional turbulence. In three-dimensional turbulence that has established ‘steady’ energetics, there is a predictable distribution of energy across scales. Between the scales of energy supply and dissipation (the ‘inertial range’) energy spectra follow Kolmogorov’s “minus five-thirds” power law (Kolmogorov 1941), and energy flows, or ‘cascades’, from large to small scales. Subject to assumptions, the level of viscous dissipation can be measured using turbulence shear probes, and this provides an estimate of the energy cascading through all scales within the inertial range. Viscous effects become important at the Kolmogorov scale and below, and this scale depends on the level of dissipation; in more energetic and dissipative systems the viscous scales are smaller meaning that current shear persists at smaller scales. A typical Kolmogorov scale is of the order of millimetres. However, rapid tidal flows are among the most dissipative of all oceanic environments so they have a correspondingly smaller Kolmogorov scale and shear penetrates to substantially sub-millimetre scales, with implications for plankton (Peters & Marrasé 2000).
Figure 1  Schematic of tidal flow through a strait and jetting into open water, showing a range of coherent flow structures that arise in such a system through instabilities and coastline interactions.

Idealised two-dimensional turbulence (essentially horizontal eddies with scales larger than the water depth) shows a contrasting 'inverse cascade', in which energy passes from small to large scales (Kraichnan 1967). This also applies close to the surface in deep water where otherwise three-dimensional structures become increasingly two-dimensional (Kumar et al. 1998). In real-world, shallow-water situations a horizontal eddy in contact with the bed will also scatter energy to small scales through its interaction with the seafloor (see below), meaning that the energy flow between scales is rather more complex.

The coherent flow structures that extract energy from large scale tidal flows and feed turbulence are identifiable structures that have some measure of spatiotemporal predictability (i.e. coherence; Venditti 2013). These include persistent or repeatedly-forming eddies or instabilities. Figure 1 provides an overview of some of the flow structures associated with tidal flow through a strait. Here these features will be considered according to whether they arise from interaction with the bed, the coastline, or occur in open water.

Bed-derived flow structures: Kolks, bursts and boils

The principal source of turbulence in a tidal flow is interaction with the seabed. Frictional stress against the bed reduces the near-bed flow speed, leading to a vertically-sheared boundary layer. Kolks, i.e. vortices within the water column, may result from either instability of this shear or from flow separation at seafloor irregularities (Stoesser et al. 2008). In the former case, which may occur over a perfectly flat bed, hairpin vortices develop, consisting of a rotating tube of water with a tightly bent ‘head’ and counter-rotating ‘legs’ aligned with the flow direction (Figure 2). Such vortices form immediately above the bed and rise through the water column.
A ubiquitous feature of shallow regions of strong flow is the surface patchwork of ‘boils’, convergences and vortices (Kumar et al. 1998). Boils (Figure 3; Nimmo Smith et al. 1999) represent the ‘bursting’ of bottom-generated kolks on the surface. These smooth and roughly circular areas of surface water may be associated with a visible upwelling/divergence of water, bordered by convergent regions of downwelling/convergence in which the water surface is distinctly roughened by short, steep surface waves (Longuet-Higgins 1996). The size of surface boils is comparable to the water depth and they are relatively short-lived (minutes); in the example shown in Figure 3, the mean boil diameter was 42 m in 45 m water depth, and each persisted for at least seven minutes.

Kolks rising through the water column transport the fluid that they contain, so a boil bursting at the surface represents a surface release of near-bed water and any material or entrained organisms that may be transported with it. This leads to a net overturning of the water column as near-bed water is continually lifted to the surface. Buoyant surface material concentrates in the surface convergences, although this material is continually reworked as flow structures decay and are replaced by newly forming structures. It is important to note, however, that passively transported material or organisms cannot be concentrated by such mechanisms, as this would imply compression of the fluid containing them. Changes in concentration can only occur when the material does not perfectly track surrounding fluid, for instance due to differing buoyancy or behaviour (e.g. swimming).

Coastline-derived eddies and wakes

The frictional effect of a coastline on an alongshore flow leads to a slowing of its shallow, nearshore flank. The resultant shear has vorticity (in this case an effective rotation about a vertical axis). If flow along a curved coastline is sufficiently rapid, it separates from the boundary, transporting its vorticity into open water where it has a tendency to roll up into an eddy (Signell & Geyer 1991). Such coastal eddies typically
Top) Sonar and (bottom) composite video images of surface boils in a tidally-mixed area of the North Sea. Images are from the same location but at different times. The scale bar shows 50 m and the water depth is 45 m. The y-axis is spatial across the flow. While the x-axis is also spatial, in the sonar case it is derived from a time series using a measured velocity. The effective flow is from right to left. Artificially introduced oil shows filamentary structure (A, B). Features C-F are described in the source. (Reprinted by permission from Macmillan Publishers Ltd. Nature. Nimmo Smith, W., Thorpe, S. & Graham, A. Nature 400, 251-254, 1999. Copyright 1999)

form in the lee of a headland (or in a bay) and have scales of 1-10 km. The detailed behaviour of such systems depends on the size of the coastline feature relative to the tidal excursion (the distance covered during a tidal cycle) and frictional scales. Alternating eddies form on either flank according to the flow direction. The evolving nature of a tidal flow is important, with eddies developing in the initial stages of ebb or flood flow and being released when the tidal current reverses. When the tidal excursion is considerably larger than the scale of the headland, the starting eddy is transported downstream and the system approaches the steady flow situation in which the strongest flow separates from the headland as a shear layer which extends downstream and bounds an area of low-flow inshore.

In a shallow tidal system, small-scale tidal eddies are frictionally retarded near the bed. This means that there is an excess inward pressure gradient here which draws water into a near-bed convergence, upwelling through the core of the eddy and diverging at the surface. Dense material and sediment will therefore be concentrated in the core of the eddy (Pingree & Griffiths 1978), while passively transported material will be upwelled towards the surface (White & Deleersnijder 2007). The closed flow paths within an eddy provide a retention mechanism in which water and material is isolated from alongshore tidal flow, then potentially returned to the main flow when the tidal current reverses.
Figure 4  Aerial photograph of a vortex street downstream of a 160 m diameter island in Rupert Bay, Quebec, Canada. (Reproduced with permission from Ingram, R.G. & Chu, V.H. Journal of Geophysical Research: Oceans (1978–2012) 92, 14521–14533, 1987. Aerial photographs [copyright 1976] in the original article were reproduced from the collection of the National Air Photo Library with permission of Energy, Mines and Resources Canada.)

In the case of an island, the two lateral flanks have a tendency to generate eddies with opposing rotation direction, and these eddies may interact. Several flow regimes can be identified according to the value of the island wake parameter (Wolanski et al. 1984) which incorporates the effects of flow speed, island width, water depth and vertical eddy viscosity. As flow speed increases, the sequence is:

1. No wake (flow remains attached to the coastline)
2. Attached wake (a trapped pair of counter-rotating eddies develops)
3. Unsteady wake (alternating eddies are shed as a von Kármán vortex street)

The speeds at which transitions occur depend on the other parameters. Strong tidal flows with small islands/obstructions fall into the third regime, generating unsteady wakes which shed vortices downstream (Figure 4). This is the case for Beamer Rock, a 50 m island in the Firth of Forth, Scotland (Neill & Elliott 2004) which, in a 1.1 m s⁻¹ tidal flow, sheds eddies with a periodicity of 12 minutes, of a size comparable to the island, and with a downstream wavelength of around 5 island diameters. Attached eddies might be expected to have a quite different ecological role driven by their retention of water and material. Rattray Island in the Great Barrier Reef, Australia is an elongated island presenting a maximum extent of 1.5 km to a tidal flow of 0.6 m s⁻¹. In this case an attached wake forms with a trapped eddy pair (Wolanski, et al. 1984) within which a near-bed convergence drives an upwelling flow (White & Deleersnijder 2007). In high-energy tidal environments, eddy retention is only expected behind large islands or in relatively weak flows, either before and after peak ebb/flood, or in peripheral areas of weaker flow.
Open water tidal jets and their stability

Open water tidal jets form when flow is sufficiently rapid to separate from a coastline. The case of a headland has been described above, however a somewhat different case occurs when flow is initially confined between two coastlines but separates from them as they diverge, as at the mouth of a tidal inlet or strait. In this case, coastal friction imparts the two flanks of the flow with opposite vorticity and the separating jet rolls up into two vortices of opposite sign. These vortices are initially attached to their respective coastlines but subsequently travel into open water as an eddy pair (dipole), leading a tidal jet (Fujiwara et al. 1994, Old & Vennell 2001, Figure 1). Typical eddy sizes are on the order of a kilometre. Dipoles are relatively stable structures with a natural tendency to propagate through ambient fluid. The flanks of the trailing jet remain strongly sheared, and these sheared zones are themselves unstable with a tendency to spin up into smaller eddies (Chen and Jirka 1998, Socolofsky and Jirka 2004, Figure 5).
When the tide reverses direction, flow is widely funnelled back into the opening as a ‘sink flow’ (Figure 1). This asymmetry between flood and ebb dynamics, also influenced by local topography, means that water that was not part of the jet is drawn into the opening. For a sufficiently strong tidal flow and/or narrow gap, the water contained in the dipole escapes the returning tidal flow (Wells & van Heijst 2003). There are a number of properties of such systems that are of ecological significance. Firstly, this mechanism acts as a pump which exchanges water between the bodies of water at either end of the channel or strait and extends the tidal mixing influence to a considerably wider region than would be the case if a single body of water moved back and forth repeatedly through the most tidally energetic region (i.e. the strait). Secondly, water that accelerates as it passes through a strait may retain kinetic energy even as the tide reverses direction. A pulse of energy moves out into open water (Old & Vennel 2001) and becomes independent of the tidal forcing (López-Sánchez & Ruiz-Chavarría 2013), creating a more dependably energetic site for animals which exploit such environments.

Stratification and strong tidal flows

A stratified water column has less potential energy than the mixed water column that would be created by homogenising it; therefore, an energy input is required to achieve such mixing. In regions of strong tidal flow, this energy is provided by the flow itself via bed stress and resulting turbulence. Stratification is not expected to persist in such environments, except when spatial scales are small and stratified water is drawn directly into a high-flow environment before it has received enough turbulent energy to mix thoroughly. This occurs over fjordic sills where complex internal lee waves and hydraulically-controlled flows may arise (Farmer & Dungan Smith 1980, Inall et al. 2004, Klymak & Gregg 2004). Lateral convergence of tidal flows of differing density can also produce a density front with rich dynamic structure (Farmer et al. 1995). In high-flow environments where stratification persists, kolks and other turbulent structures are able to punch through density surfaces, overturning the water column leading to the weakening or eradication of stratification.

A large scale tidally-energetic region may be vertically well-mixed while its low-energy surroundings are stratified. The transition between the two occurs at a tidal mixing front where the provision of energy for mixing balances the energy required to overcome stratifying influences. The location of this transition can be predicted, in summer, by the ratio between the bottom depth and the tidal current speed cubed (Pingree & Griffiths 1978, Simpson & Hunter 1974). Associated with such a front is an along-front jet with secondary surface convergence and downwelling (Hill et al. 1993). While the Simpson & Hunter (1974) approach predicts similar fronts bracketing smaller scale tidally-energetic regions (e.g. straits and headlands), the situation is more complex when the tidal excursion scale is comparable to or larger than the scale of environmental changes. A complex interplay is to be expected between mixed and stratified water, tidal advection and open water jets, eddies and convergences.

Summary of energetic tidal flow features from an ecological perspective

1. Rapid tidal flows provide the opportunity for (and threat of) significant lateral transport. Eddies in the lee of bedforms and coastal features offer a refuge from tidal flow and a potential retention mechanism.
2. Turbulence provides three-dimensional flow structure on scales from kilometres to planktonic, with impacts on different species according to body size, swim speed, agility, perception and ability to move vertically in the water column.

3. Material and organisms from the lower water column are upwelled to the surface, both in persistent (hours) and predictable features (eddies, tidal mixing fronts) and in short-lived (minutes) and less predictable features (kolks, turbulent boils).

**Use of tidal-stream environments by marine megafauna**

Usage of tidal-stream environments is not uniform across marine megafauna, and is likely to differ between populations, gender and/or age classes of the same species. Most megafauna are long-lived animals and individual experience may play an important role in exploiting these features. In some cases, for animals that live in social groups, cultural transmission of such expertise through social learning may ensure continued use of sites by successive generations (Whitehead et al. 2004). As with other foraging specialities, the expertise needed to successfully exploit these energetic environments may be limited to particular populations and individuals, rather than available to all members of the species. Caution is therefore required when attempting to extrapolate patterns of use observed at one site to others.

Marine megafauna occupy a wide range of habitats, and not all species are likely to make regular use of tidally energetic sites. For example, species that predominantly reside in offshore oceanic environments are unlikely to be encountered in inshore sites where the confluence of flow, constriction and bathymetry combine to produce tidal-stream features (see above). As indicated previously, the historic concentration of studies of tidal-stream environments in the Northern Hemisphere, and most particularly in northwestern Europe and North America, means that far more is known about the significance of tidal-stream sites to a particular subset of species. This is reflected in the quantity of published material relating to these species.

**Cetaceans**

Whales, dolphins and porpoises (cetaceans) can be broadly divided into Odontocetes (toothed whales), which forage on individual prey and have echolocation capabilities, and Mysticetes (baleen whales) which forage on large concentrations of small prey items (krill [Euphausiacea] or other zooplankton, and fish) using their baleen plates for filtering. Toothed whales, as a group, feed on a wide range of prey items from benthic crustaceans to a variety of pelagic and benthic fish, cephalopods and even other marine mammals. Many species are deep divers while others are specialised in living in coastal waters.

**Toothed whales (Odontocetes)**

Among the toothed whales, several species have been reported to make use of tidal-stream features. Of the six major subdivisions within this group, sperm whales ( Physeteridae, Kogiidae) and beaked whales ( Ziphiidae) occur primarily offshore; these species are therefore considered unlikely to regularly exploit tidal-stream environments.
Beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*), the only members of the Monodontidae, are confined to Arctic/subarctic waters. Beluga are known to associate with dynamic areas including fronts, estuaries and edges of glaciers (Lydersen et al. 2001, Hobbs et al. 2005, Stafford et al. 2013), but little information is available regarding small-scale tidal features. Several beluga populations reside in inshore waters regularly experiencing strong tidal currents (e.g. Disenchantment Bay, Alaska: Castellote et al. 2013, Cook Inlet, Alaska: Lammers et al. 2013, Gulf of St. Lawrence: Simard et al. 2008) which are expected to influence the whales’ small-scale distribution and behaviour. Castellote et al. (2013) suggested that belugas prefer faster-flowing tides in some areas, although no empirical flow speed data were available. Historic records of the now nearly-extinct Ungava Bay beluga stock also indicate a positive association with strong tidally-driven currents in this highly tidal area (Finley et al. 1982). In contrast, there are currently no indications that narwhal make regular use of tidal straits, although locally strong currents may prevent formation of sea ice resulting in permanent areas of open water (polynyas) which are a crucial winter habitat for this and other Arctic species.

River dolphins (Platanistidae, Iniidae, Pontoporiidae) generally occur in fresh waters that fall outside the scope of this review. Franciscana (*Pontoporia blainvillei*) are, however, found in inshore coastal waters of southeastern South America and are associated with strong tidal currents of up to 1.8 ms⁻¹ in particular coastal embayments (Bordino 2002). The wider significance of such features to this species remains unclear.

At least three of the six species of porpoises (Phocoenidae) appear to make use of tidal-stream features, although some species are better studied than others. Harbour porpoises (*Phocoena phocoena*) have been reported in or near tidal-stream features in many locations throughout their range including UK waters (Scotland: Evans 1997, Wilson et al. 2012, 2013, Wales: Pierpoint 2008, Isojunno et al. 2011, Northern Ireland: Savidge et al. 2014; England: Goodwin 2008), the southeastern North Sea (Germany: Skov & Thomsen 2008, the Netherlands: Boonstra et al. 2013), the Gulf of Maine/Bay of Fundy in USA/Canada (Johnston et al. 2005a), British Columbia (Hall 2011), California (Sekiguchi 1995), Washington State, USA (Raum-Suryan & Harvey 1998) and Alaska (Taylor & Dawson 1984). The species’ prevalence in sites of interest for tidal energy development has led to a considerable amount of information being gathered in recent years. Nevertheless, the relationship between porpoise presence and tidal flow speed appears complex and does not appear consistent in all areas, with uncertainty remaining as to whether porpoises target or avoid fast tidal flows. Many studies carried out in the UK (Evans 1997, Calderan 2003, Goodwin 2008, Pierpoint 2008, Marubini et al. 2009) and the Bay of Fundy (Johnston et al. 2005a) indicate that porpoises preferentially target, or are found in elevated densities in, areas of fast tidal flows. In contrast, Embling et al. (2010), analysing results from dedicated cetacean surveys from the southern Inner Hebrides (Scotland), found that porpoise distribution was best explained by tidal currents, with higher densities predicted in areas of low current. A follow-on study encompassing the entire Hebrides (Booth 2010, Booth et al. 2013) found that depth, steep slopes and proximity to land were all significantly more important than current speed in explaining areas of high porpoise density at spatial resolutions of 2 km, and Booth (2010) considered that if current speed was important it would have to be at
finer scales than were captured in his study (i.e. at the scale of eddy fields and tidal jets, below his smallest resolution of 2 km). The importance of scale was similarly highlighted by Hall (2011) who reported strong positive links between porpoises and particular tidal flow sites in British Columbia (Canada), in contrast to earlier studies conducted at larger scales in adjacent areas (Flaherty & Stark 1982, Baird & Guenther 1991). Recent work in individual tidal straits in western Scotland indicates that harbour porpoises here may spend less time in the tidal straits themselves, but concentrate in the turbulent eddies generated in more open waters downstream as tidal flows exit the channels, with significant spatial heterogeneity across scales of less than 1 km (Wilson et al. 2012, 2013). Harbour porpoises, therefore, appear to favour energetic sites in various locations but their distribution and behaviour are structured at comparatively small spatial scales, consistent with the features themselves.

Although finless porpoises (Neophocaena phocaenoides) have been less well studied than harbour porpoises, individual populations have also been observed in tidal environments in several locations (Hong Kong, China: Hung 2014, Kanmon Strait, Japan: Akamatsu et al. 2008, Omura Bay, Japan: Akamatsu et al. 2010). Both the Kanmon Strait and Omura Bay studies involved finless porpoises from small resident populations making extensive use of narrow tidal straits, possibly linked to seasonal presence of prey. Where direction of movement could be established, finless porpoises appeared to mostly travel downstream with the current (Akamatsu et al. 2008, 2010). In-depth observations by Hall (2011) indicated that Dall’s porpoises (Phocoenoides dalli) in southern British Columbia (Canada) also made use of tidal-stream habitats, although they appeared to prefer slower flowing waters (0.5 - 0.8 ms^{-1}) than harbour porpoises (0.5 - 2.0 ms^{-1}) where both species overlapped. This confirms observations by Miller (1989, in Raum-Suryan 1995) who reported that sightings of Dall’s porpoises in Puget Sound (Washington, USA) were often associated with flood tides. Cowan (1944, in Jefferson 1988) reported that the species could be found in deep, open-ended channels “with strong currents”. Although often considered a pelagic species, Dall’s porpoises are regularly observed in inshore waters off western Canada, Alaska, Kamchatka and Japan where such strong currents occur (Jefferson 1988). Other porpoise species are currently not explicitly known to frequent tidal-stream habitats, although this may be partially due to a lack of focused research to date. Burmeister’s porpoise (Phocoena spinipinnis) occurs in coastal waters along southern South America, including southern Chile, Patagonia and Tierra del Fuego where tidal-stream habitats are likely to occur (Molina-Schiller et al. 2005 and references therein). Observations of this species being captured in the Beagle Channel, where tidal flow speeds can reach at least 1.8 ms^{-1}, further suggest that it may also be associated with these habitats (Goodall et al. 1995, Aquatera 2014).

Within the family Delphinidae (dolphins and their allies), several species are known or suspected to make use of tidal features. Many coastal populations of bottlenose dolphin (Tursiops truncatus/T. aduncus) have been studied in detail in recent decades. This species has been observed in tidal straits and tidally-influenced waters in many locations including Scotland (Moray Firth: Wilson et al. 1997, Mendes et al. 2002, Bailey & Thompson 2010; Figure 6), Ireland (Shannon estuary: Berrow et al. 1996, Ingram & Rogan 2002), Portugal (Sado estuary: Harzen 1998), the Bosphorus/Turkish strait system (Altuğ et al. 2011), Florida (Sarasota Bay: Irvine et
Bottlenose dolphins (*Tursiops truncatus*) swimming along a tidal front in the Moray Firth, Scotland. Photo © WDC/Charlie Phillips.

al. 1981, Sanibel Island: Shane 1990), Mexico (La Paz Bay: Acevedo 1991, upper Gulf of California: Silber et al. 1994), Ecuador (Gulf of Guayaquil: Félix 1994), Argentina (Golfo San José: Würsig & Würsig 1979), and Brazil (Patos Lagoon: Mattos et al. 2007). Bottlenose dolphins display a wide range of behavioural patterns in these habitats, a fact commented upon by several authors (e.g. Gruber 1981, Shane 1990). The considerable behavioural plasticity generally exhibited by this species allows it to forage in a wide range of marine habitats, including associating with fast-flowing tidal currents in constricted channels (e.g. Irvine et al. 1981, Acevedo 1991, Bailey & Thompson 2010). Not all populations engage in these behaviours and for those that do, local environmental opportunities appear most important in defining the exact nature of their behaviour.

Humpbacked dolphins (*Sousa* spp.) are highly coastal in their distribution and are often associated with estuaries and embayments (e.g. Karczmarski et al. 2000, Jefferson & Karczmarski 2001, Chen et al. 2010, Bijukumar & Smrithy 2012, Lin et al. 2013). Foraging behaviours appear linked to tidal cycles in some areas (e.g. Mozambique: Peddemors & Thompson 1994), although there are presently no documented instances of these species strongly associating with tidal-stream environments. Risso’s dolphins (*Grampus griseus*) primarily occur offshore across the continental shelf and slope as well as in oceanic waters (Jefferson et al. 2014). Recent observations in Bardsey Sound (Wales: De Boer et al. 2014) suggest that Risso’s dolphins may preferentially associate with tidal fronts and island wakes near some tidal-stream environments, although results from this study suggest that the species may prefer areas with relatively low spatial variation in current speed. Killer whales (*Orcinus orca*) have a worldwide distribution in both inshore and offshore
waters and are subdivided into numerous ecotypes, each apparently specialised in feeding on particular prey types (e.g. Bigg et al. 1987, Pitman & Ensor 2003, Dahlheim et al. 2008). In inshore waters of the northeastern Pacific, where this species has been studied extensively, at least some animals make use of tidal-stream environments: fish-eating Southern Resident killer whales tended to move with flood currents and against ebb currents, appearing to travel between aggregations of migrating salmon forming predictably at slack water (Felleman et al. 1991). Mammal-eating transient killer whales in Alaska appeared to focus on narrow channels among the Aleutian islands to intercept migrating grey whales (*Eschrichtius robustus*, Matkin et al. 2007, Barrett-Lennard et al. 2011). In this case, however, it is unclear whether the strong tidal currents in these channels (e.g. Stabeno et al. 2002) helped or hindered prey capture. Dolphins of the genus *Cephalorhynchus* appear to favour turbulent inshore environments, being frequently observed in inshore waters, estuaries or coastal fjords. Of the four species in this genus, Commerson’s dolphins (*Cephalorhynchus commersonii*) have been reported in association with narrow tidal straits with strong currents in the Strait of Magellan (Argentina: Lescrauwaet et al. 2000) although this may not be a fundamental habitat requirement across this species’ range (Leatherwood et al. 1988, Loizaga de Castro et al. 2013). Similarly, Hector’s/Maui’s dolphins (*C. hectori*/*C. hectori* ssp. *maui*; Reeves et al. 2008) are known to frequent energetic inshore waters including inlets to estuaries and large bays where strong tidal currents regularly occur (e.g. Rayment et al. 2011). No other odontocete species are currently known to make regular use of tidal-stream environments.

**Baleen whales (Mysticetes)**

There is limited information available on the significance of tidal-stream environments for baleen whales (Mysticetes). Grey whales (*Eschrichtius robustus*) use narrow channels between islands during their annual migrations and seek out coastal lagoons for reproduction (Jones et al. 1984, Matkin et al. 2007); strong tidal currents may be expected to occur in these environments but their significance to this species is presently unclear. Gill & Hall (1983) observed grey whales in coastal lagoons apparently foraging in fast-flowing tidal streams, always facing into the prevailing current and typically associated with strongest tidal velocities of up to 1.2 ms\(^{-1}\). Similar observations have been made of bowhead whales (*Balaena mysticetus*) foraging in the high Arctic (Würsig et al. 1985), although it remains unclear how significant these environments are to bowheads. Individual North Atlantic right whales (*Eubalaena glacialis*) have been observed to be predictably displaced by tidal currents on their feeding grounds in the Bay of Fundy (Baumgartner et al. 2003, Pike 2008). This tidally-assisted movement allowed the whales to remain near copepod concentrations which were similarly moved by tidal currents, thereby presumably enhancing foraging success.

Among the rorqual whales, some species such as the humpback (*Megaptera novaeangliae*) and blue whale (*Balaenoptera musculus*) make use of channels between islands for travelling (Viddi et al. 2010) but the influence of currents on such movements remains unknown. There is, however, increasing evidence that baleen whales are attracted to ephemeral fronts that may be tidally generated (e.g. Doniol-Valcroze et al. 2007). Minke whales (*Balaenoptera acutorostrata*) and fin whales (*B. physalus*) have been observed foraging among a predictably occurring island wake feature in the Bay of Fundy (Johnston et al. 2005b, Ingram et al. 2007, Johnston &
Read 2007). During this study, many individuals from both species exhibited a consistent preference for slower current speeds, and were typically observed within eddy fields associated with tidal currents running past an island. Johnston et al. (2005b) suggested that both whale species were exploiting aggregations of prey organisms retained among these eddies, while Ingram et al. (2007) discussed potential habitat partitioning between these two species within the same environment. Minke whales off western Scotland were found to be significantly more likely to forage in areas of stronger current influenced by tides (Anderwald et al. 2012). Humpback whales were found to be associated with similar conditions, particularly wake features forming around headlands in Glacier Bay, Alaska (Chenoweth et al. 2011). It appears possible that many baleen whales exploit tidal-stream environments at least occasionally.

**Pinnipeds**

Pinnipeds mostly forage by pursuing benthic and pelagic fish and other prey, although some (e.g. walrus [Odobenus rosmarus], crabeater [Lobodon carcinophagus], and leopard seal [Hydrurga leptonyx]) have more specialised diets (shellfish, krill, and large fish and other marine vertebrates, respectively). Some species (e.g. elephant seals, Mirounga spp.) dive to great depths but most remain within comparatively shallow waters (uppermost several hundred metres). They spend most of their lives foraging at sea, but routinely return to land to haul out on shore. Given their intrinsic link with the land, it is not surprising that these species are regularly sighted in coastal waters.

**Fur seals, sea lions (Otariidae) and walrus (Odobenidae)**

Fur seals are widely distributed throughout the Southern Hemisphere (nine species, Riedman 1990) with one species, the northern fur seal (Callorhinus ursinus), occurring in the Bering Sea and North Pacific Ocean (Gentry 1998). The majority of species can be described as generalist predators often favouring small pelagic prey species (Harcourt et al. 2002). The Australian fur seal (Arctocephalus pusillus doriferus) is an exception, and is primarily a benthic forager (Arnould & Kirkwood 2007). While lactating and migratory fur seals are now known to utilise both mesoscale frontal features (de Bruyn et al. 2009, Georges et al. 2000, Lea et al. 2006) and submesoscale surface fronts such as eddies and filaments (Ream et al. 2005, Nordstrom et al. 2013, Sterling et al. 2014) in pelagic habitats, few studies have described the fine-scale, coastal behaviour of fur seals in relation to short temporal scale variability in oceanographic features. Northern fur seals of various age classes migrate through regions of fast tidal flow (up to 0.5 ms⁻¹, Stabeno et al. 2005) in the Aleutian Passes, Alaska (Ragen et al. 1995, Ream et al. 2005, Lea et al. 2009). However, to date these movements have not been documented at sufficient temporal and spatial resolution to assess the diurnal relationships between tidal currents and foraging. Most recently Pelland et al. (2014) have combined *in situ* oceanographic data collected by seagliders in waters fortuitously used by instrumented northern fur seal females to illustrate the fine-scale relationships between fur seal diving and shoaled mixed layer depths within the Columbia River Plume. The diving behaviour of female fur seals within the plume is likely related to the incidence of vertically migrating prey species.
Of all the pinnipeds, sea lions are most likely to interact with tidal stream features (Figure 7). Far less migratory than many other pinnipeds, the six species of sea lions display strong site fidelity to natal and foraging regions (Thompson et al. 1998, Trites et al. 2006). One such species and also the largest sea lion, the Steller sea lion (*Eumetopias jubatus*), is distributed around the North Pacific rim and along the Aleutian islands (Loughlin et al. 1992), noted above as a region of high tidal stream flow. Preying on a diverse array of species (Sinclair et al. 2005) Steller sea lions forage near the seabed and also target seasonally abundant, energy-rich pelagic prey species such as Pacific Herring (*Clupea pallasii*), Pacific eulachon (*Thaleichthys pacificus*) and capelin (*Mallotus villosus*; Womble & Sigler 2006), which often aggregate in high flow conditions (Sigler et al. 2004).

Fine-scale, active real-time tracking of juvenile animals in southeastern Alaska (Lea & Wilson 2006) has shown that juvenile sea lions are primarily distributed within tens of metres of the coastline and regularly aggregate at points and island tips (Wilson et al. unpublished data; Figure 8). While this behaviour may be anti-predatory it is also likely that interactions between strong tidal flow and such habitat features enhance foraging opportunities (cf. Johnston et al. 2005a, b).

Commonly associated with sea ice, walrus (*Odobenus rosmarus*) are widely distributed throughout northern polar latitudes in the Pacific and Atlantic Oceans (*O. r. rosmarus* and *O. r. divergens* respectively). Walrus are generally benthic foragers, using their tusks to create furrows along sandy ocean floors (Bornhold et al. 2005) while searching for benthic invertebrates (Jay et al. 2012). As sea ice diminishes within the Arctic region (Kwok & Rothrock 2009), the loss of this valuable offshore habitat is leading to a greater reliance by walrus on more coastal areas (Jay et al. 2012). While walrus pose distinct challenges for the study of habitat use at fine temporal and spatial scales, there currently is little evidence for the use of tidal-stream environments by this species.

Clearly, more targeted fine-scale studies of the interrelationships between the Otariidae and Odobenidae and their foraging environments are needed to better establish the daily and seasonal importance of such features to these pinniped families.
Figure 8  Steller sea lions in a high-energy tidally enhanced environment in Sitka Sound, Alaska. Photo © Jamie Womble.

Seals (Phocidae)

Phocid seals are geographically widespread in diverse range of marine habitats with most species occupying colder waters of the Northern and Southern Hemispheres. Some species, notably harbour/common seal (Phoca vitulina) and grey seal (Halichoerus grypus), have been regularly reported in coastal areas of high tidal flow. For example, Suryan & Harvey (1998) followed individual harbour seals using radio telemetry, and noted foraging seals aggregated in coastal waters near areas with topographic relief and strong currents. Similarly, observations of harbour seals in the Moray Firth (Scotland) showed that a deep, narrow channel subject to strong tidal flows was routinely used as a feeding area by up to 44 individuals (Thompson et al. 1991). Furthermore, tracking of individual seals using VHF telemetry showed that at least one female seal was regularly located in the vicinity of this tidal strait. Prey sampling in this area revealed that herring (Clupea harengus), sprat (Sprattus sprattus) and whiting (Merlangius merlangus) were particularly abundant in the deepest parts (20-40 m) of the channel suggesting that the intensive use of this area by seals was related to prey availability. Brown & Mate (1983) also reported harbour seals waiting for salmon runs during the incoming tide at a constriction in Netarts Bay (Oregon, USA). In high-latitude areas during periods of sea ice cover, harbour seals have been reported to use restricted localities with tidal jets and swift currents. While this is also assumed to be related to foraging, the underlying mechanism appears to be that swift currents provide small areas that remain ice-free throughout the winter (Mansfield 1967). Similarly, other species of ice-breeding seals have been reported to routinely use small-scale polynyas, created in part by tidal currents, during the winter; these include ringed (Pusa hispida) and bearded seals (Erignathus barbatus; Stirling 1980).
Despite many reports, there are few quantitative studies on the patterns of use of tidal areas by seals or of the underlying significance of these areas. In a tidal strait in San Juan Islands, Washington State, Zamon (2001) studied the temporal and spatial patterns of harbour seals (Phoca vitulina richardsi) in relation to tidal phase. Counts of seals at the water surface were made from shore and were compared between different states of the tide. Results showed a clear tidal pattern in seal presence in the channel with greatest median counts during flood tides. More recently, a small number of dedicated individual-based studies using animal-borne GPS tags have focused specifically on the use of tidal areas by seals. For example, in 2012, nine adult harbour seals were tagged in a narrow coastal channel on the west coast of Scotland (Kyle Rhea) during the summer period when significant numbers of seals are present in the channel (Cunningham et al. 2010). The majority of tagged seals stayed within 20 km of their capture site and all of them made repeated transits through the narrow channel. It was concluded that the arrival of large numbers of seals and their intense diving activity within the channel is indicative of a concentrated and valuable seasonal food resource during the summer (Thompson 2013). Similarly, between 2006 and 2010 harbour seal movements were studied within a narrow channel connecting a large inland sea loch with the Irish Sea (Royal Haskoning 2011). Thirty-six seals were fitted with GPS tags. Results indicated that seals routinely used the narrow channel, transiting between haul-out sites in the loch and offshore foraging areas. Transits through the channel were made at a relatively higher rate during periods of slack tide. To support this, land-based observations of seals at the surface recorded substantially higher sighting rates at high and low water. There were also marked differences in sightings between tidal states, with approximately 2.5 times the number of seals seen during flood tides compared to ebb tides (Royal Haskoning 2011).

A study of the movements and diving behaviour of juvenile grey seals (Halichoerus grypus) in tidally energetic areas was carried out around Wales in 2009 and 2010; GPS tags were attached to 20 recently weaned grey seal pups at breeding beaches close to high tidal current areas (Thompson 2012). Results showed that a proportion of these seals made extensive (in some cases almost exclusive) use of tidally energetic areas, appearing to move forwards and backwards with the tide and repeatedly diving to the seabed. The authors noted that in some cases, after seals left the tidally energetic area next to their natal beaches, they subsequently seemed to prefer other high tidal current areas (Thompson 2012). This raises the intriguing possibility that individual seals may specialise in using tidally energetic habitats. It is clear that some species of phocid seals, like other marine megafauna, routinely use areas of high tidal flow. Although the underlying significance of these features remains poorly understood, it is generally assumed that spatial and temporal patterns are related to prey availability or foraging efficiency. However, for some species these areas also appear to be important for a range of other functions including transit to offshore foraging areas or as bottlenecks for interception of conspecifics in the breeding season (Van Parijs et al. 1999, Hayes et al. 2004).

Seabirds

Seabirds, as a group, display a wide range of prey preferences. Some (e.g. gulls, phalaropes, storm petrels, albatrosses) forage at or near the surface, feeding on plankton or carrion, but many other species dive in pursuit of their prey. Of these, some (e.g. gannets, terns) hover in mid-air and then plunge-dive onto prey,
sometimes to considerable depths below the surface (e.g. gannets, using their wings for additional propulsion; Langton et al. 2011). Other species dive down to depths of tens of metres, using either webbed feet (cormorants, seaducks, divers) or wings (auks, penguins) for propulsion. Prey items include plankton (e.g. auks, kittiwakes), krill (e.g. shearwaters, auks), fish and squid (e.g. cormorants, divers, auks). Many seabird species forage primarily at the ocean surface although some (e.g. some auks and seaducks) forage near the seabed for fish, shellfish and other epifauna. However, there are also distinct dietary variations at species-level, even within geographically similar areas, both between individuals (Elliott et al. 2008) and for the same individuals over time (Grémillet et al. 1998). It is crucial to consider these distinct foraging and feeding specialisations in order to determine the significance of tidal-stream environments to seabirds.

**Penguins (Spheniscidae)**

Penguins (Spheniscidae) have not been intensively studied in relation to tidal-stream environments to date, but Rey et al. (2010) reported breeding Magellanic penguins (*Spheniscus magellanicus*) in Tierra del Fuego (Argentina) reducing their commuting costs to and from foraging areas by taking advantage of directional tidal currents. In extreme cases of high tidal flow penguins travelling upstream walked rather than swam (Wilson et al. 2001).

**Albatrosses, shearwaters and petrels (Procellariiformes)**

Albatrosses, shearwaters, petrels and their allies (Order Procellariiformes) are primarily surface foragers and require prey items to be brought near the sea surface. However, while species could benefit from hydrodynamic features (such as boils) within tidal-stream habitats, they are generally associated with oceanic fronts (Bost et al. 2009, Dean et al. 2012, Edwards et al. 2013), and there is little evidence of them associating with tidal-stream environments. Northern fulmar (*Fulmarus glacialis*) have been observed to feed among slicks associated with tidally-driven eddies (Ladd et al. 2005).

**Gulls and terns (Laridae/Sternidae)**

Gulls (Laridae) and terns (Sternidae) are exclusively surface foragers and require prey items to be brought near the sea surface. These species could also benefit greatly from the hydrodynamic features within tidal-energy environments, such as boils, and they are often found associated with these habitats. Assemblages of gulls and terns, including Arctic terns (*Sterna paradisaea*), common terns (*S. hirundo*), Bonaparte’s gulls (*Chroicocephalus philadelphia*) and common gulls (*Larus canus*) have been observed foraging within tidal-stream environments near Deer Island (Bay of Fundy, Canada, Braune & Gaskin 1982) and Active Pass (British Columbia, Canada, Vermeer et al. 1987). In the nearby San Juan Islands (Washington State, USA), several species including glaucous-winged gull (*L. glaucescens*) and Heermann’s gull (*L. heermanni*) similarly exploited herring (*Clupea harengus*) and sand lance (*Ammodytes hexapterus*) in a turbulent island wake (Zamon 2003). Black-legged kittiwakes (*Rissa tridactyla*) have also been observed congregating, and apparently foraging, among tidal-stream features in Scotland (Elliott 2004, Langston 2010, RSPB 2011a).
Auks (Alcidae)

Auks (Alcidae) are pursuit divers, foraging for prey ranging from zooplankton to small fish. While pelagic-foraging auks do not require prey items to be brought towards the sea surface, they could benefit from shorter dive times and disorientated prey items and schools found in tidal-stream environments. Several species of planktivorous auklets (Aethia sp.) exploited strong currents between Unalga and Kavalla Islands (Aleutians, Alaska, Hunt et al. 1998). Similarly, planktivorous ancient murrelets (Synthliboramphus antiquus) were strongly associated with high currents and turbulence near Vancouver Island (Holm & Burger 2002). Piscivorous rhinoceros auks (Cerorhinca monocerata) were reported to feed on herring and sand lance in a turbulent island wake in the San Juan Islands (Washington State, USA, Zamon 2003), and Atlantic puffins (Fratercula arctica), razorbills (Alca torda) and common guillemots (Uria aalge) were observed foraging in fast currents containing upwellings and turbulence in Orkney (Scotland, Slater 1976, J. Waggitt & B. Scott, unpublished data) and the Great Race (Scotland, Elliott 2004; RSPB 2011b, c). Tufted puffins (F. cristata) were recorded foraging within tidal streams between the Aleutian Islands (Ladd et al. 2005). Some benthic-foraging alcids appear particularly closely associated with tidal-stream habitats, at least in some locations (Bradstreet & Brown 1985). Pigeon guillemots (Cepphus columba) and closely related black guillemots (C. grylle) have been reported foraging in strong currents (~2 ms⁻¹) in tidal streams including near Vancouver Island (Canada, Holm & Burger 2002), Bluemull Sound (Shetland, UK, Robbins et al. 2014), and Fall of Warness (Orkney, UK, J. Waggitt & B. Scott, unpublished data).

Cormorants (Phalacrocoracidae)

Cormorants (Phalacrocoracidae) are pursuit divers that feed on benthic and pelagic fish (Watanuki et al. 2008). There are many observations of various species, including great cormorant (Phalacrocorax carbo), European shag (P. aristotelis), Brandt's cormorant (P. penicillatus) and pelagic cormorant (P. pelagicus), foraging at the edges of fast-flowing waters in tidal-stream environments (Holm & Burger 2002, Elliott 2004, Ladd et al. 2005, Wade et al. 2013, J. Waggitt & B. Scott, unpublished data). Pelagic cormorants were noted for their propensity to forage within boils (Holm & Burger 2002).

Gannets & boobies (Sulidae)

Deep plunge-diving northern gannets could also benefit from prey items being brought towards the water surface in tidal-stream environments. Elliott (2004) reported northern gannets (Morus bassanus) plunge-diving and feeding in the tidal stream of the Gulf of Corryvreckan (Scotland). Shallow upwellings near skerries attracted large aggregations of northern gannets in the Fall of Warness (Orkney, Scotland; J. Waggitt & B. Scott, unpublished data).

Divers (Gaviidae)

Most divers (Gaviidae) appear to avoid energetic sites (Furness et al. 2012), although great northern divers (Gavia immer) were often observed in fast currents in the Fall of Warness (Orkney, Scotland, J. Waggitt & B. Scott, unpublished data).

Seaducks (Anatidae)

Similarly, most seaducks (Anatidae) appear to avoid energetic sites (Furness et al. 2012), although eiders (Somateria sp.) have been observed overwintering in sea ice-
bound polynya environments which are kept open by strong currents (>1 ms\(^{-1}\), Heath et al. 2006) as well as in shallow waters alongside strong currents within the Fall of Warness (Orkney, Scotland, J. Waggitt & B. Scott, unpublished data). Long-tailed duck (\textit{Clangula hyemalis}) were also observed in strong, although not turbulent, currents by Holm & Burger (2002).

\textit{Phalaropes (Scolopacidae: genus Phalaropus)}

Phalaropes (Scolopacidae) are among the most pelagic of waders, feeding on zooplankton and other floating prey items in the uppermost layer of the water column. They appear strongly associated with small-scale tidally-driven features that aggregate zooplankton, at least during migration (Thorne & Read 2013).

Summary

In summary, a wide range of marine megafauna have been observed within tidal-stream environments, although most remain comparatively poorly-studied within these environments, particularly those species occurring in tropical waters, the Arctic, Antarctic and temperate waters in the Southern Hemisphere. Further baseline studies of such species are therefore required to generate a clearer picture of the significance of tidal-stream sites to marine megafauna at a global scale.

\textbf{Why do marine megafauna seek out these environments?}

Tidal streams are, by their very nature, likely to be challenging environments for marine megafauna to exploit due to periodically fast flow and three-dimensional turbulence. However, there are many reports of these species using such features (see preceding section) and there are several possible reasons why animals might seek them out. There has been a general assumption that tidally-driven features offer enhanced foraging opportunities. Tidal flows may, however, provide other opportunities such as facilitating movement or interacting with conspecifics travelling through a confined area.

\textbf{Movement}

For species whose primary mode of transport is swimming, channels between islands, headlands etc. form natural routes for travel, whether on short foraging excursions or on annual migrations. Because they are spatially constricted, many of these channels are subject to strong tides which may significantly influence animals’ ability to travel through them. Many benthic fish and invertebrates make use of Selective Tidal Stream Transport (STST), which involves entering the water column and being passively transported with the current during one phase of the tide, and returning to the seabed during the opposing phase of the tide, resulting in net directional lateral movement (Metcalfe et al. 1990, Forward & Tankersley 2001, Gibson 2003). Pelagic fish species (e.g. Atlantic mackerel \textit{Scomber scombrus}; Atlantic herring \textit{Clupea harengus}) have also been reported to use directional tidal currents to assist spawning migrations (Castonguay & Gilbert 1995, Lacoste et al. 2001). Although marine megafauna tend to be stronger swimmers than fish, they may use currents in a similar way to aid directional movement. Small-scale tidally-driven movement towards foraging areas has been demonstrated for various megafauna including harbour porpoise (De Boer et al. 2014), North Atlantic right whale (Pike 2008) and Magellanic penguin (Rey et al. 2010). To date it is unknown whether large whales, which are known to use channels between islands on annual
migration routes, synchronise their passage with the tidal cycle. Potential advantages of such behaviour could include energy savings, particularly for females accompanied by calves, as well as minimising exposure to predators within narrow channels (Matkin et al. 2007). Alternatively, marine megafauna may time their use of these channels to coincide with slack water, possibly to minimise exposure to fast currents while travelling.

While some seabirds, such as gulls and terns, will readily fly over land, many others, such as most cormorants, auks and gannets, appear reluctant to do so (Ashmole 1971). Channels could therefore be significant corridors for travelling between breeding and foraging areas, particularly for colonial breeders. Channels, headlands and islands associated with high-current habitats could also represent important visual cues during foraging or migratory movements. Landscape features represent important visual cues during terrestrial birds' fine-scale movements between foraging and breeding/roosting sites (e.g. Braithwaite & Guilford 1991, Gagliardo et al. 2001, Holland 2003). Although direct evidence is absent to date, recognisable landmarks such as channels, headlands and islands could guide seabirds' fine-scale movements during foraging or migration, although other mechanisms are likely to contribute to their general orientation (e.g. Nevitt & Bonadonna 2005, Guildford et al. 2011).

**Interactions with conspecifics**

In the case of phocid seals which often seek out sheltered haul-out sites, tidal straits may be located between haul-out sites and offshore foraging locations. Increased sighting rates of seals (or indeed any species) in such areas may therefore merely reflect increases in the relative density of animals as they move through geographic constrictions to offshore foraging areas (the 'bottleneck effect') as haul-out sites are inundated by the rising tide. However, this does not necessarily diminish the biological significance of these increases in the relative density of seals. In fact, it may underpin distinctive spatial and temporal patterns in the use of such geographic constrictions by seals attempting to maximise encounters with conspecifics. Specifically, during the breeding season, male harbour seals have been shown to use narrow channels to maximise encounters with females moving between haul-out locations and offshore foraging areas. In the Moray Firth and Orkney (Scotland) the highest densities of male seals producing breeding vocalisations were found along narrow constrictions in the transit routes between haul-out sites and foraging areas (Van Parijs et al. 1999). Furthermore, the number of males calling varied significantly with the tide, with the peak at high tide clearly coinciding with the period when most females were in the water (Van Parijs et al. 1999). Similar observations of male-display territories along female-traffic corridors have been made in other locations (Hayes et al. 2004), suggesting that narrow channels may be significant local features in the context of seal reproduction.

**Foraging**

There is considerable observational evidence to indicate that marine megafauna may be attracted to tidal-stream sites due to enhanced foraging opportunities (e.g. Zamon 2001, 2003, Johnston et al. 2005a, b, Pierpoint 2008, Bailey & Thompson 2010, Robbins et al. 2014; Figure 9). Foraging theory predicts that predators should concentrate their efforts in areas of abundant and/or accessible prey in order to maximise their energy intake (MacArthur & Pianka 1966, Stephens & Krebs 1986).
Various mechanisms to explain this attraction in the context of tidal-stream environments have been proposed to date, and are discussed in some detail below. It is, however, important to consider that multiple mechanisms may be operating concurrently in these environments, and may have different effects on different predators.

The features of tidal-stream environments have the potential to make prey more abundant, in absolute terms. In more stable marine environments, such elevated levels of abundance may have come about due to prey (e.g. zooplankton) being concentrated in predictable zones of convergence (Alldredge & Hamner 1980, Wolanski & Hamner 1988), with prey species (e.g. small fish) targeted by marine megafauna being attracted to such zooplankton concentrations. These processes are well understood in more stable hydrodynamic conditions (Wolanski & Hamner 1988) where fronts and eddies can persist for hours or days and stimulate elevated primary and secondary production. It remains unclear, however, whether these mechanisms are equally important in energetic tidal-stream environments where such features form and disappear much more rapidly, albeit in predictable patterns.

It is unlikely that concentrations of zooplankton can form within fast-flowing turbulent environments in a central tidal strait, although they may be forcibly advected from adjacent productive areas (Zamon 2002). Depending on local water speeds, fish and other pelagic species in tidal streams can use the currents to assist migration (see above) or find themselves similarly advected when caught in tidal streams faster than their maximum swimming speed (Lavoie et al. 2000, Simard et al. 2008). Exploring this mechanism by studying small-scale movement patterns of
fish under the energetic conditions found in these sites remains a considerable technological challenge (Johnston et al. 2005a).

Marine megafauna can also be attracted to tidal-stream environments, not because prey are abundant, but rather because of the enhanced vulnerability of prey to capture in such environments. There is a considerable body of evidence suggesting that prey vulnerability, rather than prey abundance, drives seabirds’ foraging distributions at fine spatiotemporal scales (e.g. Fauchald et al. 2000, Fauchald 2009, Embling et al. 2012, Cox et al. 2013, Scott et al. 2013), and similar processes are thought to operate in marine mammal foraging (Ferguson et al. 2012). Concentrating foraging efforts at times and locations of increased prey vulnerability has been shown to significantly enhance predator foraging success (Quinn & Creswell 2004, Hopcraft et al. 2005, Crook & Davoren 2014). Strong turbulence provides a mechanism to confuse or disorient prey and imposes a metabolic cost as prey try to maintain orientation (Zamon 2002, Enders et al. 2003, Liao 2007). Strong currents can also impact cohesion among schooling species (e.g. Gomez-Guitierrez & Robinson 2006, Robinson et al. 2007), potentially leading to the breakup of schools which facilitates predation of individuals (Enstipp et al. 2007, Vabø & Nøttestad 1997). Prey may be unwilling to cross boundaries between fast-moving water masses to avoid being subjected to shear stresses (Čada et al. 2006, Tarrade et al. 2008) and predators could ‘trap’ prey against such mobile boundaries (Johnston et al. 2005b, Simard et al. 2008). Such behaviours have not yet been recorded, but marine megafauna have been observed making use of similar real or perceived boundaries, such as the sea surface, mud plumes or ‘bubble curtains’, to enhance foraging success (Similä & Ugarte 1993, Lewis & Schroeder 2003, Wiley et al. 2011). Steep velocity gradients associated with tidal streams allow predators to briefly enter fast-flowing currents to pursue prey before returning into calmer (or counterflowing) adjacent waters or eddies (Johnston et al. 2005b). Vertical water movements associated with kolks, boils and eddy fields can transport prey to the surface. In this case, predators’ energetic costs associated with foraging dives are likely to be reduced, even taking into account strong currents prevalent within boils. Finally, tidal straits between islands are often relatively narrow as well as shallow and will, by their very nature, restrict prey movements within a confined space, thereby eliciting more predictable prey behaviour and providing improved foraging opportunities for top predators (Matkin et al. 2007).

Tidal-stream environments may also be attractive foraging areas for marine megafauna because of the increased variety of available prey. Pelagic prey species may be advected laterally with the current, while both pelagic and benthic prey species may be transported to the surface by upwelling (boils etc.). Tidal mixing fronts have been shown to broaden the range of prey sizes available for predators by concentrating small prey to sufficiently high densities to make foraging on them worthwhile (Vlietstra et al. 2005), and similar mechanisms may operate in tidal-stream environments.

Irrespective of which of the above processes enhance foraging success in tidal-stream environments, the regularity inherent in daily and monthly tidal cycles results in favourable foraging conditions occurring predictably in approximately the same locations over short timescales (days to weeks). This predictability is likely to be attractive to marine megafauna that otherwise range widely in search of food, even if
more abundant, yet less predictable, prey are available elsewhere (Irons 1998, Weimerskirch 2007). This particularly applies to central place foraging species (pinnipeds and seabirds) with constrained time budgets during breeding seasons (Orians & Pearson 1979).

**Risks**

Although tidal-stream environments offer important foraging opportunities to marine megafauna, there are risks associated with foraging in these energetic conditions, particularly for marine mammals. If currents are sufficiently strong they may drown young animals, separate them from their mothers or otherwise impact social cohesion of groups. The highly localised, predictable concentrations of megafauna may similarly attract their predators such as killer whales (Matkin et al. 2007), which may be increasingly difficult to detect acoustically as ambient noise levels rise during peak flow (Carter 2013). Animals’ foraging behaviours are modified by risk of predator exposure (Wirsing et al. 2008), and this is also likely to influence the extent to which animals make use of tidal-stream sites. Other individuals will seek to avoid these sites altogether because they are too young, weak or otherwise unable to forage efficiently in fast-flowing waters, and/or due to the possible risks outlined above. Some animals will therefore choose to actively avoid tidal-stream environments despite potentially enhanced foraging opportunities.

**Behaviour in tidal-stream environments**

**General considerations**

The highly variable tidal-stream environments are likely to be exploited by marine megafauna in a variety of ways. Animals attempting to forage in tidal-stream conditions may adapt foraging strategies used in calmer waters, or display novel strategies rarely seen outside these energetic environments. The distribution of marine megafauna in tidal streams will be influenced by many factors, including prior experience, current speeds, local bathymetry, particular oceanographic conditions, and the density, distribution, energy content and behaviour of different prey species. These factors may interact in particular ways which will result in a range of behavioural patterns, across tidal cycles at the same site, between sites, and within the same species. A high degree of behavioural flexibility in the face of rapidly changing conditions is a likely feature of animals foraging in these demanding environments.

**Current speeds and orientation**

Tidal-stream environments display a wide range of current speeds over the course of daily and monthly tidal cycles (Shields et al. 2014). Accurately determining the effect of current speeds throughout the water column on marine megafauna behaviour may be difficult, and many studies describe current speeds in broad qualitative terms (Holm & Burger 2002). Nonetheless, some animals are able to reside in faster currents than others, although there is large intra- and interspecific variability. For example, in some locations (e.g. the Shannon estuary, Ireland: Berrow et al. 1996, Ensenada de la Paz, Mexico: Acevedo 1991), bottlenose dolphins appear to forage preferentially at peak tidal flow when currents are strongest, but this is not the case at other sites (Bailey et al. 2013).
Although many megafauna display a strong association with tidally-driven environments, several authors have commented on the variability observed among animals’ orientation towards the direction of current. This has been most commonly observed in cetaceans, although some observations exist for seabirds as well (e.g. Heath et al. 2006). In some cases, animals will travel with the prevailing current (e.g. Würsig & Würsig 1979, Irvine et al. 1981), while in other sites animals of the same species are typically seen swimming against the current (e.g. Acevedo 1991, Pierpoint 2008, Hall 2011). In yet other studies (Félix 1994) no significant relationship between animal orientation and flow direction was apparent. Given that most tidal-stream environments experience strong currents flowing first in one direction, then in another during the course of the tidal cycle, any relationship between flow and animal orientation is likely to be influenced by local environmental features, prey and foraging tactics that may defy easy generalisation.

Moreover, there is the need for caution when interpreting observed animal movements in tidal currents. Specifically, observers are at risk of devising a circular argument when reporting that more or fewer animals move against tidal currents, as animals that have to move against currents will inherently be available for sighting by observers at a particular geographical location for longer than those moving with currents. Where data are available, sighting rates should therefore ideally be related to flow speeds and directions prevalent at appropriate tidal phases.

Seabirds which dive from sitting on the surface do not respond consistently to directionality of flow, with some species always diving against the flow, while others appear to dive with the current flow significantly more often than against it. Most diving seabirds, however, appear to surface at or upstream from the point where they began individual dives (Heath & Gilchrist 2010, Wade et al. 2013). This indicates that diving seabirds are not merely passively drifting downstream as they dive, but are actively moving against the current for short periods. Some species such as benthic-foraging black and pigeon guillemots (Cepphus spp.) repeatedly drift downstream while diving in tidal-stream environments, only to fly back upstream and repeat the process (Holm & Burger 2002, Robbins et al. 2014). This behaviour may allow these alcids to rapidly increase foraging intensity over suitable substrata at reduced energetic cost. While this species is often reported from fast-flowing tidal stream environments (Holm & Burger 2002, Robbins et al. 2014, J. Waggitt & B. Scott, unpublished data), Nol & Gaskin (1987) and Elliott (2004) reported that black guillemots avoided stronger currents, potentially suggesting heterogeneity in habitat use. Marine mammals may use eddies adjacent to the main current in a similar way to return to upstream areas with comparatively little effort (Hastie, Benjamins, Wilson; unpublished observations), but further work is required to evaluate the frequency of such behaviours.

At slightly larger spatial scales, animals may consistently move against currents to retain access to prey. Movements of Southern Resident killer whales (British Columbia, Canada) were strongly associated with tidal currents, with whales tending to move with flood currents and against ebb currents (Felleman et al. 1991). This movement pattern mirrored that of migrating adult salmon (Oncorhynchus sp.), the killer whales’ principal prey, which travelled towards their spawning rivers on the flood tide and held position during the ebb tide (Stasko et al. 1976). Such
observations indicate the crucial role of prey movements in determining appropriate foraging tactics in relation to tidal currents.

**Tidal occupancy patterns**

The relationship between occupancy and tidal phase is complex for many marine megafauna, in that populations of the same species may associate with opposite tidal phases in different sites. Tidal-stream environments typically exhibit tidal asymmetries (variations between ebb and flood phases of the tidal cycle; e.g. Neill et al. 2014), resulting in recurring variability in current strength, extent and/or intensity of hydrodynamic features such as boils and kolks. Such tidal asymmetry could lead to changes in prey availability, resulting in preferences among marine megafauna for entering tidal streams at particular tidal phases. For example, sighting rates of harbour porpoises within Ramsey Sound (Wales) were significantly higher during ebb tides, whereas porpoises were observed to largely leave the area during flood tides. During this time, porpoises were observed in adjacent tidal areas several kilometres away, suggesting that these animals may successively exploit several similar sites in the general area (Pierpoint 2008). Conversely, observations in the tidal strait of Kyle Rhea (Scotland) suggest that porpoises exploit eddy fields developing downstream of the channel whichever direction the tide is running (Wilson et al. 2013). However, observations of porpoises within the actual channel were comparatively rare. The eddy fields on either end of the channel may have been exploited by different porpoise groups present in both adjacent basins rather than a single group travelling between both basins (Wilson et al. 2013). Bottlenose dolphins foraging in the outer Shannon Estuary (Ireland) were strongly associated with ebb tides (Berrow et al. 1996) but this relationship was inconsistent from year to year among dolphins in the inner Moray Firth (Scotland, Bailey et al. 2013). Pelagic-foraging auks, gulls and terns, which may rely upon fast currents and hydrodynamic features to promote prey availability, also usually favour particular tidal states.

Temporal trends have been shown to differ between sites depending upon tidal asymmetry direction and topography/bathymetry. At the Fall of Warness (Scotland), faster ebb currents in conjunction with steep slopes facing towards the direction of ebb currents means that hydrodynamic features are intensified during ebb tides, and higher abundances of Atlantic puffins and common guillemots often occurred during ebb tides (J. Waggitt & B. Scott, unpublished data). Complex bathymetry facing towards the direction of currents between Unalga and Kavalla Islands (Aleutians) maintained intense hydrodynamic features through maximum tides, and abundances of least (*Aethia pusilla*), crested (*A. cristatella*) and parakeet auklets (*A. psittacula*) increased during both maximum flood and ebb tides (Hunt et al 1998). Similar increases in abundance of gull species during maximum flood tides in the San Juan Islands (Washington State, USA, Zamon 2003) and Active Pass (British Columbia, Canada, Vermeer et al. 1987) also reflected tidal periods when hydrodynamic features intensified.

When studying how pinnipeds use tidal-stream environments, several important caveats need to be considered. Given that the availability of haul-out sites is usually restricted to particular tidal states (generally during low tide, Pauli & Terhune 1987), it is important to avoid the conflation of tidal patterns that are driven by currents with those that are driven by haul-out site availability. For example, the availability of haul-out sites in Zamon’s (2001) study showed that harbour seals exhibited a diurnal haul-
out pattern; the greatest number hauled-out during the middle of the day and during low tide, and seals left the beach in the evening regardless of tidal phase. It would therefore appear that the distinctive tidal pattern observed in the use of the channel was not primarily driven by haul-out site availability (Zamon 2001). Similarly, seals observed hauling-out within a narrow tidal strait off the west coast of Scotland exhibited a pattern that did not appear to be directly related to the availability of haul-out sites; seal numbers increased during the ebbing tide, with highest numbers observed from about 3.5 hours before low tide until half an hour after (Cunningham et al. 2010).

Despite many reports of seals in tidal-stream environments, few studies have quantified patterns of use by seals or of the underlying significance of these areas. However, Zamon (2001) studied the temporal and spatial patterns of harbour seals (Phoca vitulina richardsi) in relation to tidal phase in a tidal strait in the San Juan Islands (Washington State, USA). Counts of seals at the surface were made from shore and were compared between different states of the tide. Results showed a clear tidal pattern in seals’ presence in the channel with median counts being greatest during flood tides. Moreover, observations of seals catching prey (primarily salmon, Oncorhynchus sp.) indicated that more large-fish captures occurred on the flooding tides and in areas near the channel constriction. The episodic nature and tidal patterns in capture events implied that seals took advantage of salmon migration runs. Zamon (2001) suggested that spatial constrictions in tidal flow might benefit seals because interactions between currents and prey movement were potentially predictable in time and, rather than searching for dispersed prey in large, open volumes of water, the seals may choose to focus effort in a smaller volume where topography causes either encounter rates, densities of prey, or vulnerability of prey to be greater than in surrounding habitat (Zamon 2001). Results of a study of harbour seal movements within a narrow channel connecting a large inland sea loch with the Irish Sea suggested that transits by individual seals through the channel were made at a relatively higher rate during periods of slack tide (Royal Haskoning 2011). The close links between tidal cycles and habitat use among different marine megafauna have implications for undertaking appropriate surveying of such environments.

**Foraging strategies**

Foraging behaviours can be considered across a spectrum between active pursuit and passive ambush strategies (Pianka 1966, Perry 1999). Most marine megafauna are active predators pursuing individual prey or prey aggregations (the latter particularly in the case of baleen whales), although there are some exceptions (Yates et al. 2007). Observations of marine megafauna holding station in tidal-stream environments, in contrast, suggest a temporary switch towards an ambush strategy where predators ‘lie in wait’ for prey being swept towards them by the current (e.g. Gill & Hall 1983, Akamatsu et al. 2010, Hall 2011, Wade et al. 2013). Such a strategy is common amongst predatory fish living in fast-flowing freshwater environments (Grant & Noakes 1988, Metcalfe et al. 1997).

Shane (1990) suggested that observations of dolphins holding station or swimming against the current might indicate foraging behaviour. Similarly, Hall (2011) proposed the “Conveyor Belt Hypothesis” on the basis of observations of harbour porpoises in British Columbia (Canada) to describe apparent feeding
behaviour where porpoises positioned themselves in the path of the oncoming current to intercept prey being carried downstream. Specifically, groups of porpoises were seen “facing into the current, then synchronously allowing the current to carry them subsurface to their initial starting positions. Each group surfaced in unison, and the pattern repeated itself over and over” (Hall 2011, p.72). Similar behaviours were described for harbour porpoises in Ramsey Sound (Wales) by Pierpoint (2008) who frequently observed animals maintaining their approximate position against the prevailing current, suggesting some form of ambush strategy.

Which strategy is adopted likely depends on complex interactions between current strength and the ability of both prey and predator to effectively manoeuvre in such environments. Theoretical modelling studies suggest that ambush foraging strategies are most effective in cases where prey move at least as fast as predators and/or where movement is directional (Scharf et al. 2006, Avgar et al. 2008). In tidal-stream sites, it may therefore be more energetically efficient for a predator to remain approximately stationary in the central part of a current (where prey movements are likely to be highly directional) rather than attempt pursuit, as long as the predator can maintain its position. This suggests that predators may be periodically forced to abandon this strategy in particular areas in very fast currents and relocate downstream or outside the main flow where currents are weaker. As a result, animals may use tidal-stream features differently during the course of a single tidal cycle. For example, although Pierpoint (2008) was unable to record current speeds while studying harbour porpoises in southern Ramsey Sound (Wales), subsequent studies have recorded current speeds of up to ~1.9 ms$^{-1}$ during ebb tides, and up to ~3.5 ms$^{-1}$ during flood tides, in the adjacent northern part of this tidal strait (Evans et al. 2013). Assuming these flow speeds are comparable to those in the site studied by Pierpoint (2008), who reported far fewer harbour porpoises during flood tides, this suggests that speeds ≥ 3 ms$^{-1}$ may exceed porpoises’ ability to maintain their positions against the current and make this behaviour less attractive during this tidal phase. A similar suggestion was made by Akamatsu et al. (2010) for finless porpoise in Omura Bay (Japan) where tidal flow rates ranged up to 4.4 ms$^{-1}$, well above swimming speeds normally attained by this species. Tidal currents may therefore only be occupied by particular animals for comparatively short periods of time.

Marine megafauna may use the main flow of a tidal current to forage on prey that is either actively migrating with the current, being passively carried along with the current, or attempting to hold position near a particular location (Lavoie et al. 2000, Lacoste et al. 2001, Simard et al. 2002). If prey are actively swimming with the current, as in the case of migrating fish, marine megafauna may choose to pursue them downstream (if flow speeds are sufficiently slow for them to retain manoeuvrability) or seek out a suitable position to intercept them. This latter tactic may also be best for foraging on passively advected prey, given its unpredictable pattern of arrival and distribution. For prey that are actively trying to hold station (i.e. migratory fish working against the current), predators face a choice between swimming with the current or swimming/holding station against the current near the prey. The former strategy allows predators to approach prey at greater speeds assisted by the water flow, but this may result in predators being observed by the prey resulting in avoidance behaviour, as well as potentially being carried past the prey with the current, reducing time available for predation. The latter strategy would be more energetically costly but would minimise these drawbacks by allowing
predators to slowly approach prey from behind, potentially retaining an element of surprise (Felleman et al. 1991). Prey in slightly calmer waters further downstream are likely to be actively pursued by predators much as they would be outside a tidal-stream environment (e.g. Johnston et al. 2005a, b).

There is limited information available about how individual marine megafauna capture prey within tidal-stream environments (but see Watanuki et al. 2008, Crook & Davoren 2014). It is generally assumed that prey are located and captured in a broadly similar manner to outside the tidal stream. Vision is likely to remain the principal sense for seabirds (e.g. Regular et al. 2011), although cormorants have relatively poor vision and could also use tactile cues while foraging upon the seabed (Martin et al. 2008). Marine mammals will employ a number of different sensory modalities. Odontocetes are likely to use active acoustics (echolocation) and vision to locate prey, but passively listening for prey may be less practical than elsewhere due to high levels of ambient noise (Wilson et al. 2012). It is unclear whether echolocation signals would be affected by turbulence in tidal-stream environments, which could potentially allow odontocetes to remain outside the main tidal flow until they detect prey within it. Analogous behaviours using different sensory modalities have been reported in fish (Helfman 1981). Baleen whales are thought to mainly forage using vision (Goldbogen et al. 2013, but note Stimpert et al. 2007 for a potential acoustic pathway). Pinnipeds rely on a combination of vision and mechanosensation through their vibrissae (Dehnhardt et al. 2001), but it is currently unknown how rapid flow rates and turbulence in tidal streams influence the efficiency of the latter sensory system.

**Prey behaviour**

Peak flow speeds in many tidal-stream environments are likely to present challenging conditions for most species of fish and other prey. When cruising speed data for a range of fish species (commonly expressed in body lengths s⁻¹; Videler & Ward 1991) were converted to absolute speeds (ms⁻¹), most values did not exceed 2 ms⁻¹ (Videler & Hess 1984; Videler & Ward 1991). Even fast-swimming species like Atlantic mackerel (S. scombrus) were found to reach estimated maximum cruising speeds of 3.8 ms⁻¹, below net flow speeds detected in various tidal stream sites, let alone small-scale discontinuities. The discrepancy between maximum fish cruising speeds reported in the literature and current speeds observed in tidal streams suggests that assumptions that prey fish actively pursue concentrations of zooplankton into and out of these features may not be realistic unless they make heavy use of sheltered regions and eddies to remain within the tidal strait (e.g. Zamon 2003, Johnston & Read 2007). This element of the tidal-coupling hypothesis, as originally advanced by Zamon (2003), requires further consideration, as it may only apply to flows below a particular threshold.

Fish in strong tidal streams are therefore likely to be travelling with the current, although migratory species may hold position during the opposing tidal phase. Some fish may be tidal-stream residents, seeking out shelter near the seabed and only entering the water column around slack water. Although fish commonly display positive rheotaxis (facing upstream; Arnold 1974), there is little knowledge about how fish in tidal-stream environments orient themselves with respect to the direction of main and local current. In particular it is unclear whether fish that are entrained within a large body of laterally-moving water (rather than actively swimming with the
current) perceive the surrounding water to be mobile or approximately stationary. In
the latter case, fish may not orient themselves in relation to the current while being
moved by tidal streams. Lateral displacement in fast tidally-driven currents may also
result in reduced ability of fish to maintain cohesive schools. When current speeds
exceed fishes’ ability to orient properly, the efficiency of schooling breaks down, and
as fish are forced to act more as individuals they appear far more likely to be
successfully captured by predators (e.g. Enstipp et al. 2007, Crook & Davoren 2014).
Observations by Viehman & Zydlewksi (2014) using active acoustic detectors in a
tidal stream of up to 2 ms\(^{-1}\) indicated that a range of pelagic fish species moved
through the study site as coherent schools, suggesting that school breakup might
only occur at greater velocities.

Avoiding vertical displacement may be important for fish in tidal streams, and
particularly for physoclistous species possessing an un-vented swim bladder, as
sudden changes in pressure may result in injury and potentially mortality through
barotrauma (defined as “physical damage caused by the decrease in ambient
pressure as the fish is brought to the surface from deeper depths”; Brown et al. 2009,
Schreer et al. 2009, Stephenson et al. 2010). Barotrauma-related injuries among fish
include a bloated or ruptured swim bladder, stomach and anal eversions, bulging of
the eyes, gas bubbles in eyes and fins, inability to maintain equilibrium,
haemorrhaging, organ torsion, and formation of gas bubbles in the circulatory
system, gills, heart, and brain (Feathers & Knable 1983, Morrissey et al. 2005,
Hannah & Matteson 2007, Gravel & Cooke 2008). Although often associated with
fish living at greater depth (Hannah & Matteson 2007), recent studies suggest
barotrauma can also occur within comparatively shallow waters (from ~10 m deep;
waters via kolks and boils can result in sudden vertical displacement of fish towards
the surface, including both pelagic species entrained within the moving water and
benthic species dislodged from the seabed. This vertical movement may be
sufficiently abrupt to induce barotrauma-related injuries that can significantly impair
fishes’ swimming capabilities through the loss of their ability to remain neutrally
buoyant, thereby making them more vulnerable to predation (Brown et al. 2009).
Other fish species, particularly those that lack a swim bladder (such as gobies
[Gobiidae] but also some pelagic species such as mackerel) and physostomous
species (such as herring) which are able to rapidly release expanding gas from the
swim bladder through the anal duct (Wilson et al. 2004), may be less vulnerable to
such displacement. It is unclear to what extent marine megafaunal foraging within
tidal-stream environments is facilitated by barotrauma-related injuries among fish or
other prey species, but it may be important when foraging on physoclistous fish (e.g.
Orders Gadiformes, Perciformes) that lack the capacity to rapidly adjust internal gas
pressure in their swim bladders.

**Seasonal occupancy patterns**

Many seabirds and marine mammals display seasonally variable residency
patterns (e.g. related to reproductive activity), and their different behaviours within
these seasons may drive differences in their use of tidal-stream environments. For
example, many seabirds in the North Atlantic, including Atlantic puffins (*Fratercula
arctica*; Guilford et al 2011), common guillemots (*Uria aalge*; Lorentsen & May 2012,
Linnebjerg et al. 2013), razorbills (*Alca torda*; Linnebjerg et al. 2013), black-legged
citiwakes (*Rissa tridactyla*; Frederiksen et al. 2011) and northern gannets (*Morus
bassanus*; Fort et al. 2012) migrate further offshore during non-breeding seasons.

While benthic-foraging species such as shags (*Phalacrocorax* spp.) and auks (*Cepphus* spp.) might undertake partial migrations during non-breeding seasons (Grist et al. 2014), they remain within coastal habitats throughout the year. The use of tidal-stream environments by such species would thus be expected to continue throughout the year (Robbins et al. 2012, J. Waggitt & B. Scott, unpublished data). Marine megafauna diets often differ across life stages, reflecting different nutritional needs or seasonal prey availability (e.g. Ewins 1990, Tollitt & Thompson 1996) and this could drive concurrent variation in foraging behaviours. It should also be noted that migratory patterns may differ between regions in response to local environmental parameters, even among closely related species. For example, many pelagic-foraging alcids in the North Pacific regularly exploit tidal-stream environments throughout the year, in contrast to the observed behaviours of North Atlantic alcids described above, (Hunt et al. 1998, Holm & Burger 2002, Zamon 2003). Other sites may be exploited by different populations in summer and winter as animals migrate according to seasonal changes (Holm & Burger 2002).

*Intra- and interspecific interactions*

The enhanced foraging opportunities in tidal-stream environments often result in the attraction of multiple marine megafauna, often including both seabirds and marine mammals (e.g. Zamon 2001, 2003, Pierpoint 2008). Many species have been observed to rely heavily upon local enhancement and/or social foraging (Camphuysen 2011, Tremblay et al. 2014) when locating fish schools, and any costs due to increased competition are probably outweighed by increased prey detection rates. Foraging seabirds often benefit from cetaceans driving fish schools towards the sea surface and therefore could enjoy increased foraging efficiency when cetaceans are present (Camphuysen & Webb 1999, Weimerskirch et al. 2010, Benoit-Bird et al. 2011), although interspecific aggression and competition underwater between diving seabirds has been observed (Duffy et al. 1987).

Current strength is likely to be a significant factor in how marine megafauna distribute themselves across tidal-stream environments (Holm & Burger 2002). Marine megafauna that obtain their prey through pursuit diving (marine mammals, diving seabirds) are particularly likely to seek out current speeds in which they can move in a controlled manner, even if travelling downstream with the current. This will automatically restrict the fastest and most turbulent tidal flows to the strongest and/or most manoeuvrable individuals or species, reducing competition (Wanless & Harris 1991, Philpott et al. 2013). Moreover, spatial and temporal habitat heterogeneity are expected to result in niche partitioning of food resources among potential competitors (Amarasekare & Nisbet 2001).
Figure 10  Sightings of foraging black guillemots (*Cepphus grylle*, BG) and European shags (*Phalacrocorax aristotelis*, SH) in breeding (Br) and non-breeding (Nb) seasons in the Fall of Warness, Orkney, UK (based on J. Waggitt & B. Scott unpublished data). Circle sizes indicate numbers of foraging individuals observed, and solid lines delineate an area of consistently fast horizontal currents (mean speeds >2 m s\(^{-1}\)) encountered in the central channel. In the breeding season, both species preferred areas around the edges of the fast-current zone. In non-breeding seasons, many black guillemots also foraged within the central channel. European shags were still seen most often around the edges of the fast-current zone but seemed to exploit a wider area in non-breeding seasons.

Niche partitioning could arise through foraging strategies or prey distributions. For example, cormorant species are foot-propelled foragers and capture benthic prey items following careful searches and ambushes (Martin et al. 2008). Such foraging strategies appear best suited to slower waters, and most observations of cormorants in tidal-stream environments are at the edges of main currents (Holm & Burger 2002, Elliott 2004, Ladd et al. 2005, Wade et al. 2013, J. Waggitt & B. Scott, unpublished data; Figure 10). However, these areas are also characterised by distinctive hydrodynamic features; pelagic cormorants were noted for their propensity to forage within boils (Holm & Burger 2002). Similarly, while both Atlantic puffins (*Fratercula arctica*) and common guillemots (*Uria aalge*) associated with fast currents containing
Figure 11  Sightings of foraging common guillemots (Uria aalge, GM) and Atlantic puffins (Fratercula arctica, PF) in the breeding season in the Fall of Warness, Orkney, UK (based on J. Waggitt & B. Scott unpublished data). Circle sizes indicate numbers of foraging individuals observed. Solid lines in the upper two figures (Spd) indicate an area of consistently fast horizontal currents (mean speeds >2 m s\(^{-1}\)) encountered in the central channel. Solid lines in the lower two figures (Tur) indicate areas of high turbulence around headlands and islands. Whilst many individuals of both species were seen foraging in the zone of fast horizontal currents, large numbers of Atlantic puffins also exploited the high-turbulence areas.

upwellings and turbulence in the Fall of Warness (Scotland), high numbers of Atlantic puffins were observed in turbulent conditions (J. Waggitt & B. Scott, unpublished data; Figure 11). This may be due to these species’ different foraging strategies: puffins typically collect multiple small prey items near the surface and could therefore benefit from high turbulence forcing such items towards the sea surface, whereas guillemots take individual, typically larger, prey items that may not be forced to the same extent, resulting in fewer foraging opportunities for guillemots under these conditions (Wanless et al. 1988).

Differences in prey distribution and prey selection could also promote niche partitioning. In tidal-stream environments, the distribution of different prey species is
likely to be non-uniform, depending at least partially on current speeds and bathymetry. In this manner, small-scale physical processes may drive spatial segregation of marine megafauna across a tidal-stream feature through resource partitioning. For example, three closely related species of auklets (Aethia spp.) foraging in the same Aleutian channel were found to segregate themselves according to availability of preferred prey, which was directly driven by small-scale currents and local turbulence (Hunt et al. 1998). Moreover, the location and extent of these prey concentrations will change over the course of the tidal cycle, potentially resulting in frequent yet predictable redistribution of animals over time.

Finally, resource competition could also drive niche partitioning. In the Fall of Warness (Scotland), black guillemots and European shags occupied similar areas at the edge of tidal streams during breeding seasons. However, during non-breeding seasons black guillemots generally exploited fast-water habitats whereas European shags remained within areas at the edge of the main tidal stream. These seasonal changes in niche partitioning could possibly reflect prey characteristics, with decreased abundances of preferred benthic prey items such as butterfish (Pholis gunnellus) and sandeels (Ammodytidae) in shallower waters driving niche segregation between these species or niche expansion among black guillemots (J. Waggitt & B. Scott, unpublished data).

In Ramsey Sound (Wales), harbour porpoise mothers and calves were most often observed in peripheral areas outside the main tidal strait (where flow rates of ~1 ms\(^{-1}\) or less were expected; Pierpoint 2008, Evans et al. 2013). Assuming mother-calf pair sighting probabilities were not significantly different from those of other porpoises, this suggests that female porpoises with young calves may avoid flow speeds >1 ms\(^{-1}\), presumably because calves lack the skills and strength to successfully accompany females into tidal currents. Similar spatial variability in distribution among age-classes may occur among other megafauna, although this variability is likely to be most pronounced for diving species such as porpoises, seals or auks, rather than surface-foraging species such as gulls.

Although there are many observations of groups of marine megafauna of multiple species feeding in close proximity within tidal-stream sites (e.g. Zamon 2001, 2003, Pierpoint 2008), there is little information to confirm or refute whether cooperative foraging between conspecifics occurs. Conversely, it is not known whether individual animals could actively exclude conspecifics from particularly productive feeding sites within tidal streams to monopolise resources ("resource defence", Grant 1993). Whether resource defence occurs depends on several factors, including population density, resource density, the degree to which the resource is localised in space and time, and the extent to which the availability of the resource can be predicted. In the case of marine megafauna foraging in tidal-stream environments, the comparatively low predictability of resource availability (in terms of the arrival rates of individual prey) may well preclude resource defence in most situations, but this type of small-scale interaction deserves further study. Evidence from stream-feeding salmonid fish, which forage on invertebrates carried downstream by the current, suggests that as flow speed increased from zero, fish initially became more aggressive in defending the area around them from conspecifics. As flow speeds (and thereby prey arrival rate) increased still further, levels of aggression declined, presumably because of increased costs of defence and reduced foraging efficiency at greater speeds (Grant
Similar processes may operate among marine megafauna in tidal-stream environments. Prey distribution in a tidal site may depend on various stochastic processes (e.g. school breakup due to turbulence), making prey delivery rates highly variable. This suggests that resource defence is not an appropriate tactic at higher flow speeds. Male harbour seals do, however, appear to actively try and defend territories in tidal straits to gain increased access to females, which could be considered a different type of resource defence strategy (Van Parijs et al. 1999, Hayes et al. 2004).

Predators will tailor their foraging techniques to suit local prey diversity (Garthe et al. 2007, Elliott et al. 2008, Watanuki et al. 2008). As described above, different marine megafauna target a wide range of prey (from plankton to fish and invertebrates, up to marine mammals in the case of killer whales) at a range of depths using specific foraging techniques (e.g. surface foraging versus pursuit diving). Given these differing foraging requirements, each species will likely seek out preferred microhabitats within tidal-stream environments where their preferred prey are most abundant and/or available. Some marine megafauna appear to prefer particular oceanographic features such as turbulent waters (Holm & Burger 2002). While baleen whales might prefer to forage among eddies and outside the fastest currents to take advantage of larger, more predictable food patches aggregated within these features (Johnston et al. 2005b), pinnipeds, porpoises and auks might prefer targeting individual prey in the main current (Thompson 2012, J. Waggitt & B. Scott, unpublished data). Regions of strong upwelling present a special case: on theoretical grounds, air-breathing species such as marine mammals or seabirds might be expected to forage preferentially within boils and other areas of upwelling as prey is carried towards the surface, allowing predators to forage at shallower depths and be carried back to the surface themselves. Some observations support this hypothesis (Holm & Burger 2002, Elliott 2004) but more work is needed to accurately link marine megafauna to particular tidal-stream features.

**Location of tidally-driven flow structures**

Marine megafauna likely locate tidal streams across scales of kilometres on the basis of visual and/or acoustic cues, which are detectable over considerable distances. Chemical cues (e.g. scent), which are used by marine megafauna to locate plankton concentrations associated with more stable oceanographic fronts (Kowalewsky et al. 2006, Nevitt 2008, Thewissen et al. 2011), are unlikely to be effective in tidal-stream sites due to the rapidly changing configurations of water types. Potential tidally-driven visual cues might include whitecaps, fronts, tidal slicks and other oceanographic features associated with strong currents (Davoren et al. 2003, Tremblay et al. 2014). For seabirds, visual observations of distant conspecifics, other birds or other predators are likely to act as important cues indicating foraging opportunities at scales of up to 10-20 km away (e.g. Wittenberger & Hunt 1985, Irons 1998, Thiebot & Weimerskirch 2013, Tremblay et al. 2014). Marine mammals are likely to make use of subsurface acoustic cues, particularly at night. Tidal streams can generate considerable amounts of ambient noise, likely driven by a combination of turbulence, bathymetry and sediment movement, although precise noise characteristics are likely to vary between sites (Wilson et al. 2013). As ambient noise characteristics generated by tidal streams also vary across the tidal cycle in response to changing current speeds (Carter 2013), animals listening for such sounds may potentially obtain information about foraging conditions.
likely to be encountered from some distance. There is limited information available about long-range transmission loss of sound in inshore waters (summarised in Carter 2013), which is likely to vary significantly between sites due to local environmental characteristics. Further research is necessary to investigate the potential acoustic signatures and long-range acoustic detectability of tidal currents by marine megafauna, and the role this may play in locating foraging opportunities.

**Ecological consequences of use of tidal-stream environments**

While individual animals may derive benefits from foraging within tidal-stream features, the broader consequences of animals’ foraging success in these areas to the long-term viability of their local or global populations are often difficult to ascertain, particularly for long-lived species such as marine mammals and seabirds. Many marine megafauna display considerable fidelity towards foraging sites, including those associated with tidal-stream environments (e.g. Dorsey et al. 1990, Irons 1998, Cheney et al. 2012). Foraging success among long-lived species, such as marine mammals and seabirds, is strongly influenced by individual experience and knowledge derived from conspecifics. It may take several years for juvenile animals to successfully acquire appropriate foraging skills (Burger 1980, Greig et al. 1983, Guinet & Bouvier 1995, Daunt et al. 2007, Votier et al. 2011), and animals may benefit by concentrating their foraging activity in areas where resources are predictably abundant or accessible, such as tidal streams. Moreover, animals can build on previous experience of foraging success in such sites, resulting in individual foraging strategies that are particularly suited to these environments (Ollason et al. 1997, Irons 1998, Woo et al. 2008, Kotzerka et al. 2011). This expertise can subsequently be passed on to conspecifics through direct observation (lateral transfer, e.g. seabirds observing distant flocks of other birds; Grünbaum & Veit 2003), information transfer at colonies (Grémillet et al. 2004, Wakefield et al. 2013, Bogdanova et al. 2014) and/or through teaching specific foraging techniques to offspring (vertical transfer or cultural transmission; Whitehead et al. 2004). As tidal-stream environments are geographically restricted and temporally intermittent, animals with this experience may choose to remain near particular sites for extended periods of time, or travel between similar sites to time their arrival with anticipated prey availability at the appropriate tidal phase (‘foraging by expectation’); both approaches are expected to reduce time invested in searching for foraging opportunities (Braune & Gaskin 1982, Vermeer et al. 1987, Hunt et al. 1999). Given the likely spatiotemporal predictability of suitable foraging opportunities among tidal-stream features such as jets and eddy fields, some animals may journey further to obtain reliable access to such predictable food resources (Chaurand & Weimerskirch 1994, Lescroël & Bost 2005). Further studies are, however, needed to better understand how individuals balance and benefit from these predictable but intermittent opportunities.

As nutritional demands of marine mammals and seabirds are particularly high during the reproductive season, animals may seek to breed near tidal streams to reduce travelling times and thus maximise the benefits afforded by enhanced foraging opportunities in these sites. Some tidal straits in the Northern Hemisphere are known to be seasonally frequented by considerable numbers of harbour seals during the breeding season (Cunningham et al. 2010, Thompson 2012), with seal diving behaviour in the tidal strait indicating significant foraging activity. A study of
movements and diving behaviour of juvenile grey seals in tidally energetic areas showed that a proportion of these seals made extensive (in some cases almost exclusive) use of tidal-stream environments, appearing to move forwards and backwards with the tide and repeatedly diving to the seabed. The authors noted that in some cases, after seals left the tidally energetic area next to their natal beaches, they subsequently appeared to preferentially use other high tidal current areas (Thompson 2012).

Animals such as these, which regularly forage in tidal-stream environments, may to a greater or lesser extent be considered tidal-stream specialists, i.e. individuals that use their experience to forage more successfully in these environments than generalist conspecifics lacking such expertise. Tidal-stream specialists may form a comparatively small proportion of larger regional (meta-)populations of marine mammals or seabirds, and may be largely restricted to areas near tidal-stream sites (particularly in the case of colonial breeders such as many seabirds). Conversely, wide-ranging migratory species may travel considerable distances between foraging hotspots which may include tidal-stream sites, and possibly move from one such site to another (Read & Westgate 1997, Johnston et al. 2005a, Sveegaard et al. 2011, Thompson 2012). Particular sites may thus be occupied by animals from different populations from one season to the next. Establishing the extent of this connectivity between tidal-stream sites and potentially distant breeding populations is important in order to accurately assess their ecological value and potential risks of their alteration. Any impacts resulting from marine renewable energy generation may be more significant for such groups of specialised animals than might be expected if tidal-stream environments were being used equally frequently by all individuals of the wider population. There is no evidence to suggest that such putative tidal-stream specialists are at a competitive disadvantage when foraging outside tidal-stream environments. However, in the event of significant mortality of such tidal-stream specialists at particular sites, recolonisation by these species may take time as the required foraging skills may need to be reacquired by initially-naive individuals (Berger et al. 2001, Stamps et al. 2007).

Current research techniques: considerations and recommendations
Scale of analysis

Determining the relationship between the physical parameters of tidal streams and the distribution or behaviour of marine megafauna within them requires an assessment of appropriate spatial and temporal scales at which to undertake such analyses. Tidal streams present a highly complex and variable array of habitats at scales of metres (individual kolks and boils) to kilometres (tidal jets, large downstream eddy fields), which develop and change over temporal scales of seconds to hours. This fine-scale habitat heterogeneity in both space and time complicates attempts to pinpoint the components of tidal-stream environments that are most heavily used by marine megafauna across the tidal cycle.

Determining which temporal and spatial scales are ecologically relevant for different marine megafauna is crucial to assessing their habitat use within these sites. High-resolution data are evidently desirable but many standard survey methodologies may not be able to resolve habitat heterogeneity to appropriate scales.
(Wiens 1989). Similarly, data on potentially significant environmental parameters (flow speed, bathymetry etc.) may not be available at appropriate resolutions. Allen et al. (2001) reported variability in foraging-related habitat selection by bottlenose dolphins within scales of hundreds of metres, emphasizing the importance of using appropriate spatial scales for analysing habitat preferences for this species. Similar concerns were raised by Booth et al. (2013) concerning association of harbour porpoises with energetic tidal habitats, which were not identified in models with 1-2 km grid resolution. Fauchald et al. (2000) emphasized the hierarchical nature of spatial distributions of seabirds at different scales, based on underlying distributions of prey patches.

As a result, understanding of detailed behavioural patterns within these environments remains limited for many species, and results obtained at coarse scales may not reliably identify small-scale habitat use. For example, de Boer et al. (2014) suggested that the association of Risso’s dolphins with low spatial variation in current speed, in areas known to contain tidally-driven eddy fields and upwelling, could be an artifact of the comparatively coarse (300 x 300 m) ADCP data resolution available for their study. Without undertaking pilot studies it is difficult to predict the appropriate spatiotemporal scales at which to study marine megafauna within particular tidal-stream environments, but some general observations can be made. At a basic level, given the small scales of most tidal-stream sites, high-resolution data (hundreds of metres) are more useful than low-resolution data (>10 km). Observations should take place with regard to both daily and tidal cycles, and preferably also take account of spring-neap cycles, particularly when considering appropriate sample sizes for statistical analysis. It is crucial that observations are gathered throughout the range of current speeds although this may cause logistical problems at greater flows. Similarly, surveys should consider seasonal and interannual variability.

It should also be kept in mind that these environments typically form a limited portion of individual animals’ ranges, but are quite different from surrounding areas, meaning that extrapolating from larger-scale surveys may not be appropriate (ICES 2014). Most marine megafauna are highly mobile and regularly migrate across distances far greater than individual tidal-stream sites. There is therefore a need to consider both large-scale synoptic survey efforts across large areas to provide context and small-scale focused efforts in particular tidal-stream sites (as undertaken through, for example, the U.S. Bureau of Offshore Energy Management’s AMAPPS program; Reeb 2013).

**Industry needs and data gathering techniques**

Although there are a number of scientific questions that arise from the use of tidal areas by marine megafauna, much of the recent interest in tidal-stream environments has been driven by renewable energy development schemes at particular sites. There is typically a requirement on the part of the regulator to put potential impacts on individual animals into a population context (reviewed in ICES 2014). Such considerations are usually based on some form of density estimate with associated confidence intervals (distance sampling: Buckland et al. 2001, Thomas et al. 2010). ICES (2014) summarised the information needs that regulators would likely require during and after the consenting process:
- Species presence
- Regularly updated abundance estimates for all management units (populations) for all species of interest
- Trend analysis of abundance estimates over time and information on demographic parameters (e.g. reproductive rates, survival, etc.)
- Assessments of temporal variability (e.g. seasonal cycles)
- Detailed information on habitat use, including reproductive activity, foraging, migratory pathways, local residency, etc.
- Connectivity between development sites and protected areas
- Local environmental data to aid in habitat modelling
- High-resolution marine mammal survey data collection across tidal cycles, across seasons, using a range of methodologies as needed
- Three-dimensional distribution of animals in the water column

Various methods exist to obtain this information, although most were originally developed for use in less-energetic waters and may therefore require modification to better suit these conditions. Boat-based visual surveys are commonly used to survey seabirds and marine mammals, but turbulence, standing waves etc. may make it difficult to observe animals during peak flow times. Moreover, basic assumptions of the underlying distance sampling methodology may be violated, particularly in narrow tidal straits between islands where currents may preclude an unbiased distribution of survey effort, edge effects may be significant, and water movement may cause animals to be non-randomly distributed relative to survey transects (Buckland et al. 2001, 2004, Wilson et al. 2013). The question of whether animal movement is measured relative to the sea floor versus relative to the moving flow is a potentially important, but often disregarded aspect of studying animals within these environments, particularly when surveys are undertaken from vessels within the same fast-flowing body of water. Aerial surveys have to contend with the small sizes and spatial heterogeneity of tidal sites, potentially leading to depressed sighting rates. Shore-based visual observations are useful (e.g. Pierpoint 2008) but may not be feasible at larger or offshore sites.

Passive acoustic data (mainly relevant for odontocete cetaceans) can be gathered using hydrophone arrays towed behind a survey vessel (offering good spatial coverage) or using moored autonomous acoustic recorders (offering good temporal coverage). Similar considerations apply to towed array surveys as to visual surveys in tidal streams, with additional complications caused by towing a long array behind a vessel in fast currents. Moored detectors typically require robust moorings to remain in place despite currents, adding to mooring weight, complexity and cost, and potentially requiring larger vessels to safely deploy and retrieve them (Dudzinski et al. 2011). Strong currents may deflect recorders towards the bed, increasing the risk of damage or loss, and/or interfere with their recording sensitivity. Tidal streams also produce elevated ambient sound levels which can mask cetacean sounds, particularly during peak tidal flow; finally, the rapid flow of water past the hydrophones in the detectors adds self-noise to the data (Au & Hastings 2008, Bassett et al. 2010). Attaching detectors to passively drifting platforms has recently been found to negate some of these problems, while allowing more precise data on small-scale habitat use to be collected (Wilson et al. 2013, 2014, Gordon et al. 2014).
High-resolution telemetry data, such as those obtained from tagged animals, can provide detailed information on habitat use by individual animals and are therefore extremely valuable (Thompson, 2012, Lea & Wilson 2006, Hastie et al. 2014). Unfortunately the number of animals that can be tagged is typically restricted by financial, logistic and ethical considerations (tag costs, challenges of capturing animals and affixing tags), tag deployment durations may be limited, and there may be severe imbalances in terms of which age classes or genders can be successfully tagged (Evans et al. 2013). Even if animals are tagged, there is typically no guarantee that they will use the particular habitat of interest, negatively affecting the power of the study. This is particularly true for tidal-stream environments because of their discrete locations and often small size. For species that only return to land to breed (i.e. many seabirds), little information is available about nonbreeding adults or juveniles, particularly once animals disperse from breeding sites (Wilson et al. 2002).

**Data gaps**

Although the recent acceleration in tidal renewable energy development has spurred numerous environmental studies, considerable uncertainty remains about small-scale distribution and habitat use of marine megafauna in tidal-stream environments locally and across the world. Most studies to date have taken place in the temperate waters of the Northern Hemisphere, and even here many tidal-stream environments remain poorly studied. Likewise, many sites studied may not have been observed at an appropriate scale to clarify high-resolution habitat use. Conversely, for many species the significance of these small, distinctive sites in the context of the surrounding wider marine environment remains unclear. Further baseline studies of species occurring in tidal-stream environments in tropical waters, high-latitude areas, and temperate waters in the Southern Hemisphere are therefore required to generate a clearer picture of the significance of tidal-stream sites to marine megafauna at a global scale.

Despite advances made in recent years, understanding of the relevance of flow structures in aggregating prey or facilitating prey capture by marine megafauna remains far from complete. Current data gaps include:

- Whether marine megafauna are preferentially associated with particular tidal-stream features (e.g. boils, tidal jets, eddies, fronts)
- How these tidal-stream features might contribute to foraging success
- The ability of animals to detect and capture prey within and across tidal-stream features
- Swim speeds and direction of travel relative to both the current and the sea floor
- The three-dimensional distribution of animals in the water column relative to surface, sea floor and any tidal-stream features of significance
- Resource partitioning between species, age-classes, genders or other categories
- Rates of change of the above parameters across the tidal cycle

The above factors will all likely influence whether marine megafauna are able to successfully forage within a tidal-stream site and where the best foraging opportunities might occur.
There are significant data gaps in terms of understanding how fish and other prey species behave in tidal-stream environments. Addressing these gaps has to date been hampered by logistical difficulties, including how to sample fish using standard equipment under energetic conditions. Current data gaps include:

- Which species, size- and age classes are typically found in tidal-stream environments
- Swimming speeds and direction of travel relative to both the current and the sea floor
- School size and schooling behaviour, as appropriate for different species
- Three-dimensional distribution in the water column
- Rates of change of the above parameters across the tidal cycle

There is only limited information on the extent to which marine megafauna may be nutritionally dependent upon foraging opportunities generated by tidal-stream environments. This is likely to be of particular significance for local populations that breed near these sites. The link between individual animals’ foraging success within tidal-stream environments and long-term population persistence remains poorly understood, complicating efforts to understand impacts of tidal energy developments at the population level. Recent advances in modelling population consequences of non-lethal impacts such as disturbance (the PCAD/PCOD models; NRC 2005, Lusseau et al. 2012, Harwood et al. 2014) may provide potential avenues for investigating these issues further.

**Summary and conclusions**

1. Tidal streams are complex, energetic and highly variable environments; nevertheless this variability is repetitive and broadly predictable. The complex interactions between current strength, direction, and bathymetry, and the impact of all of these factors on prey density and distribution, can result in periodically favourable foraging opportunities for marine megafauna. The ‘tidal-coupling’ hypothesis proposed by Zamon (2003) suggests that predictable aggregations of prey are generated through interactions between tidally-driven currents and bathymetry, although what physical processes are driving these aggregation processes often remains unclear, as does the applicability of such mechanisms to the most energetic, turbulent tidal-stream sites.

2. Different marine megafauna may be attracted to tidal-stream environments for different reasons, including using them as a corridor for travelling, migrating, or for social interactions between conspecífics. The majority of reported interactions are, however, associated with foraging. Marine megafauna may choose to forage in tidal-stream environments because prey are more abundant, more vulnerable (available) to predation and/or more diverse in these locations at particular phases of the tide. The predictability inherent in tidal streams may also constitute an attractive feature of these environments.

3. The wide diversity of foraging preferences between different marine megafauna (planktivores versus piscivores, pelagic versus benthic foragers),
coupled with the varying impacts of currents on different prey species, means that different marine megafauna will distribute themselves across different parts of tidal-stream environments. These distributions are likely to change over short spatiotemporal scales in response to tidally-driven changes in current speeds and flow structures. As such, marine megafauna distribution patterns are likely to vary considerably within and between sites.

4. It is crucial to study tidal-stream environments at ecologically relevant scales to accurately determine their significance to marine megafauna. There is therefore a need to consider both large-scale synoptic surveys to provide context, and small-scale focused efforts in particular tidal-stream sites and temporal states.

5. There is evidence for site fidelity towards tidal-stream environments among some populations of marine megafauna, based on the limited number of studies undertaken to date, suggesting specialisation by small groups that are particularly experienced at foraging in energetic tidal-stream environments. Consequently, any anthropogenic impact on these sites may disproportionately affect local subpopulations, rather than be distributed across larger-scale metapopulations. If these animals are lost, it may take time for naive conspecifics to recolonize these sites.

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References


southern part of the Sea of Marmara, Turkey. *Marine Biodiversity Records* **4**, e65; doi:10.1017/S1755267211000662


Calanus finmarchicus, over diel and tidal time scales. Marine Ecology Progress Series 264, 155-166.


Marubini, F., Gimona, A., Evans, P.G.H., Wright, P. J., and Pierce, G. J. 2009. Habitat preferences and interannual variability in occurrence of the harbour


Pike, E. 2008. Tidal influence on diel movement of North Atlantic right whales (Eubalaena glacialis) in the Bay of Fundy. MSc dissertation, Duke University, Beaufort, N.C., USA.


Vögler et al. (eds.). Stornoway, Scotland: University of the Highlands & Islands, p.57 only.


Stirling, I. 1980. The biological importance of polynyas in the Canadian Arctic. Arctic 33(2), 303-315.


Womble, J.N., & Sigler, M. F. 2006. Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. *Marine Ecology Progress Series*, 325, 281-293.


