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REVIEW

Using the VEMCO Positioning System (VPS) to explore fine-scale movements of aquatic species: applications, analytical approaches and future directions

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ABSTRACT: Recent advancements in telemetry have redefined our ability to quantify the fine-scale movements of aquatic animals and derive a mechanistic understanding of movement behaviours. The VEMCO Positioning System (VPS) is a fine-scale commercial positioning system used to generate highly accurate semi-continuous animal tracks. To date, VPS has been used to study 86 species, spanning 25 taxonomic orders. It has provided fine-scale movement data for critical life stages, from tracking day-old turtle hatchlings on their first foray into the sea to adult fish returning to natal rivers to spawn. These high-resolution tracking data have improved our understanding of the movements of species across environmental gradients within rivers, estuaries and oceans, including species of conservation concern and commercial value. Existing VPS applications range from quantifying spatio-temporal aspects of animal space use and key aspects of ecology, such as rate of movement and resource use, to higher-order processes such as interactions among individuals and species. Analytical approaches have seen a move towards techniques that incorporate error frameworks such as autocorrelated kernel density estimators for home range calculations. VPS technology has the potential to bridge gaps in our fundamental understanding of fine-scale ecological and physiological processes for single and multi-species studies under natural conditions. Through a systematic review of the VPS literature, we focus on 4 principle topics: the diversity of species studied, current ecological and ecophysiological applications and data analysis techniques, and we highlight future frontiers of exploration.

KEY WORDS: VEMCO Positioning System · Telemetry · Movement ecology · Animal tracking · Spatial ecology

1. INTRODUCTION

Movement is pivotal to animal survival and the structuring of ecosystems by facilitating access to essential resources, including food, reproductive mates and refugia, which are regulated by external drivers active over a range of spatial and temporal scales (Nathan et al. 2008). The development of animal tracking technology (acoustic, radio and satellite telemetry and archival biologgers) has enabled the quasi-continuous positioning of diverse species, from those inhabiting the deep sea (Priede et al. 1994) to birds soaring thousands of metres above the earth's surface (Poessel et al. 2018).

The first fine-scale aquatic telemetry positioning system study was published in 1974. This system used time of difference of arrival (TDOA) of transmitted acoustic pulses within a grid array of omnidirectional hydrophones to position tagged cod *Gadus morhua*, with information relayed using a cabled sys-

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tem to an on-shore laboratory (Hawkins et al. 1974). Unlike pre-existing passive acoustic systems, which could only identify animal presence with several hundred metres of accuracy, the hyperbolic TDOA algorithm provided sub-metre positioning accuracy (Hawkins et al. 1974). This innovation significantly improved the resolution and accuracy of underwater movement tracking.

In 1989, the first commercially available positioning system called VRAP ('VEMCO Radio Acoustic Positioning system') (VEMCO) was released (O'Dor et al. 2001). The VRAP system consisted of a computer base station, 3 or 4 surface buoys that contained a receiver and hydrophone and a radio VHF modem (Klimley et al. 2001, Downey et al. 2011). The VEMCO Positioning System (VPS) (Innovasea, formerly VEMCO) was released as a lower-cost alternative that had no upper limit on the number of incorporated receivers (Andrews et al. 2011). The VPS requires fixed deployed receivers to have an overlapping detection ('listening') range in order to record simultaneous detections of a tag on 3 or more receivers for trilateration. Using the TDOA algorithm, the difference in tag detection time between pairs of receivers is converted to a range difference using the speed of sound in water (based on benchmark values for different water types, e.g. freshwater and saltwater) (Smith 2013). In simplest terms (2 dimensions), a range difference and the known locations of 2 receivers define 1 branch of a hyperbola (also referred to as a hyperbolic line of position) (Smith 2013). A third receiver provides an additional hyperbolic line of position, with the intersection of these providing the location of the transmitter (assuming no measurement error). In reality, TDOA is 3-dimensional and uses receiver depth and tag depth (assumed if no depth sensor is present).

Unlike the original positioning systems, the VPS comprises a network of time-synchronised acoustic receivers that are autonomous and do not require a computer base station or buoyed antennas (Smith 2013). For VPS, time synchronisation is achieved using integrated synchronisation ('sync') tags (present in VEMCO VR2Tx, VR2AR or High Residency receivers) or tags paired alongside older technologies (for example, VEMCO VR2W receivers). Sync tags are used to identify and account for clock drift between receivers that would otherwise impact calculated positions (Smith 2013). Reference tags are typically deployed within an array of listening receivers to evaluate spatiotemporal differences in system performance. Following data download on study completion, VEMCO provides a processed dataset of positions (and their associated accuracy). More recently, VEMCO has released licenced software and offers training to enable researchers to conduct autonomous TDOA positioning 'in house'. The VPS system can be used to estimate the positions of multiple tagged animals within freshwater, brackish and saltwater environments (Guzzo et al. 2016, Logan & Lowe 2019). VPS has been used to study the fine-scale movements of diverse species across both natural and altered environmental settings (Wolfe & Lowe 2015, Veilleux et al. 2018).

Given the potential of VPS to advance our fundamental understanding of aquatic animal ecology, the objective of the current study was to undertake a systematic literature review focussed on 4 key topics relevant to fine-scale acoustic telemetry positioning systems: (1) the diversity of species studied, (2) experimental questions that can be addressed including conservation and management foci, (3) common and emerging statistical techniques for handling VPS data, and (4) contemporary areas of ecology which have yet to be explored, but where fine-scale acoustic telemetry approaches present novel opportunities.

2. METHODS

To synthesise existing peer-reviewed VPS literature, a global search was conducted in ISI Web of Science using the keywords 'VPS' OR 'VEMCO Positioning System' OR ('acoustic telemetry' AND 'fine-scale'). Due to the number of extraneous results published in other fields, the resultant search output was filtered to categories including; 'Environmental Sciences', 'Environmental Studies'. 'Zoology', 'Evolutionary Biology', 'Marine Freshwater Biology', 'Fisheries', 'Ecology', 'Biology', and 'Oceanography'. Searches were then repeated using SCOPUS and Google Scholar to ensure all relevant studies were identified. Abstracts were screened for relevance, with duplicate articles removed and only studies that tagged animals included. In addition, relevant literature cited within these studies, not identified directly by the search, was also extracted. All studies identified before 3 November 2021 were included.

Data on the year, species studied, environment (habitat type, water body type, depth), geographic location of the study and key study objectives were extracted for each publication. Study objectives were then categorised under 7 broad topics following an evaluation of all extracted manuscripts: behavioural ecology, conservation measures and assessments,

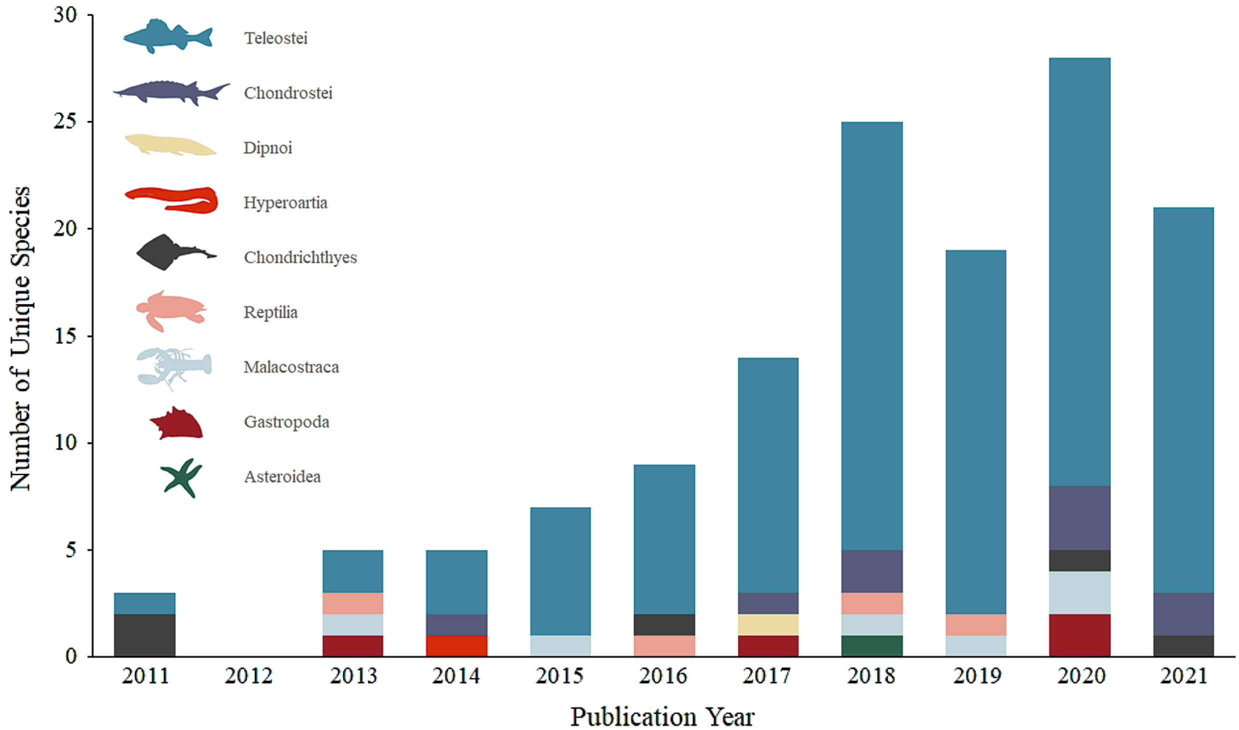

Fig. 1. Diversity of taxa studied using the VEMCO positioning system (VPS) in literature published between 2011 and 2021. Taxa include fishes such as Teleostei (bony fishes), Chondrostei (sturgeons and paddlefishes), Dipnoi (lungfish), Hyperoartia (lampreys), Chondrichthyes (cartilaginous fishes such as sharks, skates and rays), as well as reptiles (Reptilia), shellfish (Malacostraca and Mollusca) and echinoderms (Asteroidea)

fisheries management, land use management, methodological testing, reproductive ecology and the study of other drivers of movement (e.g. oceanographic conditions, temporal and seasonal drivers and extreme weather events). The order of information in the abstract and final objective statement of the introduction was used to categorise each study within these defined topics. The majority of studies addressed several core objectives; therefore, their order of importance was defined according to the abstract.

3. RESULTS

Using Web of Science, 188 articles were identified, of which 26 were deemed relevant. A duplicate search using SCOPUS identified 167 articles; following abstract screening, 26 unique articles remained. A replicated search in Google Scholar yielded 2270 articles, of which 60 unique articles were directly relevant. An additional 4 articles were identified from in-text citations. In total, combined searches yielded 116 peer-reviewed articles, which analysed data from 140 unique species datasets (a full list of articles is available in Section S1 of the Supplement at www.int-res.com/articles/suppl/m687p195_suppl.pdf).

3.1. The diversity of life: species studied over time

Since 2011, VPS has been used to track the movements of 86 species, spanning 25 taxonomic orders. This diversification over time (Fig. 1) has been facilitated by tag miniaturisation, enabling the tracking of smaller species and earlier life stages. Key groups studied include morphologically diverse species ranging from bony and cartilaginous fishes to echinoderms and reptiles. The type of tag chosen by a study remains a trade-off between tag size and battery life. The smallest animal tagged to date is a juvenile European eel *Anguilla anguilla* (Bašić et al. 2019) measuring 37 mm in total length internally implanted with a VEMCO V5 tag (0.65 g in air, 5 mm diameter, 12 mm length). Smaller tags are limited in life span due to the power and capacity required to transmit acoustic signals; therefore, studies tracking juvenile fishes (n unique datasets = 27; 19%) have typically spanned up to 6 mo (n unique datasets = 19; 70%). Adult life stages remain the most commonly tagged (n = 61; 44%), with few studies tracking multiple life stages (adult and juvenile) (n = 16; 11%). Over a quarter of all tracking studies (n = 36; 26%) did not describe the life stage or provide identifiable biometrics of the studied species. The increased battery life of large acoustic tags (up to 10 yr) has generated multi-year VPS data, with the longest VPS study to date spanning over 4 yr (lake trout *Salvelinus namaycush* tracked for 1569 d; Binder et al. 2018).

3.1.1. Fishes

Teleosts are the most widely studied taxonomic group of fishes using VPS, with 85 articles published since 2011, representing 11 taxonomic orders and 66 species. Species include a diverse morphological spectrum, from eel-like body morphs (Anguilliformes, n species = 5) to depressiform benthic flatfish (Pleuronectiformes, n species = 5). Also included are species that occupy a range of functional roles and trophic levels, from key mesopredators in coastal ecosystems such as the great barracuda *Sphyraena barracuda* (Becker et al. 2020) and carnivorous fishes in freshwater systems (northern pike *Esox lucius*, Roy et al. 2021), to abundant mid-level consumers which link lower and upper trophic levels, such as shorthorn sculpin *Myoxocephalus scorpius* in marine systems (Ivanova et al. 2018) and white sucker *Catostomus commersonii* in freshwater reservoirs (Veilleux et al. 2018). Perciformes, the largest order of fish containing ~41% of all teleosts (Pandey & Marthur 2018), are the most studied group (n fish tagged = 1702; 40% of all tagged teleosts).

Prehistoric lineages of fishes, including chondrosteans (subclass Chondrostei), lungfish (subclass Dipnoi) and Hyperoartia (lamprey) have received some attention. Three species of primitive ray-finned bony fishes, namely Atlantic sturgeon *Acipenser oxyrinchus*, lake sturgeon *A. fulvescens* and green sturgeon *A. medirostris*, have been studied with regard to their reproductive ecology, space use and the influence of anthropogenic stressors (n articles = 5). These studies include one of the largest fish tagged in a VPS study, a 96 kg Atlantic sturgeon measuring 216 cm in fork length (Balazik et al. 2020). Lungfish (subclass Dipnoi), the closest living relatives to tetrapods (Irisarri & Meyer 2016), are uniquely adapted to hypoxic conditions through the presence of 1 or 2 primitive lungs derived from the swim bladder. Through contextualising 3D-space movements of freshwater Australian lungfish *Neoceratodus forsteri* derived from VPS with environmental data, it was possible to identify how this ancient lineage may have adapted to survive in an altered riverine system (Roberts et al. 2017).

The class Chondrichthyes contains cartilaginous fishes, including sharks, batoids (rays, skates, guitarfishes and sawfishes) and chimaeras, and comprises over 1100 living species (Weigmann 2016). Despite this, only 4 species of elasmobranch have been studied using VPS: the grey smooth-hound *Mustelus californicus* (Espinoza et al. 2011), the shovelnose guitarfish *Rhinobatos productus* (Espinoza et al. 2011. Farrugia et al. 2011), the spotted wobbegong *Orectolobus maculatus* (Armansin et al. 2016) and the reef manta ray *Mobula alfredi* (Armstrong 2021). These studies include the first published study using the VPS system (Espinoza et al. 2011), which tagged grey smooth-hound (n = 1) and shovelnose guitarfish (n = 2) and tested the feasibility of this technology as well as associated positional accuracy and precision.

3.1.2. Reptiles

Two reptile species have been studied using VPS: hatchling flatback turtles *Natator depressus* at 2 nesting sites in Western Australia (Eco Beach, Thums et al. 2013; Thevenard Island, Wilson et al. 2018) and juvenile green turtles *Chelonia mydas* in Culebra, Puerto Rico (Griffin et al. 2019). Both *N. depressus* studies aimed to identify tagged hatchling direction and swim speed on their first foray from their natal beaches. These data are important given that the mortality rate of sea turtle hatchlings is ~25% in the first 24 h (Gyuris 1994), and the IUCN Red List classifies all 7 species of sea turtle as Threatened (Critically Endangered, n species = 2; Endangered, n = 1; Vulnerable, n = 3) or Data Deficient (n = 1). VPS has provided an approach to elucidate data on a poorly understood developmental stage with a crucial mortality bottleneck.

3.1.3. Shellfish and echinoderms

VPS studies have focussed on lobsters (Malacostraca, n articles = 6, n tagged individuals = 543), molluscs (Gastropoda, n articles = 4, n tagged individuals = 109) and echinoderms (Asteroidea, n articles = 1, n tagged individuals = 18). Malacostraca research has included 3 important commercial species: the European lobster *Homarus gammarus* (Skerritt et al. 2015, Lees et al. 2018) off the northeast coast of England, and the American lobster *H. americanus* (McMahan et al. 2013) and snow crab *Chionoecetes opilio* (Cote et al. 2019, 2020) in North America. Studies of Gastropoda have investigated movement related to population recovery following intensive fishing activity (pink abalone *Haliotis corrugata*; Coates et al. 2013), habitat use under suboptimal conditions (Caribbean queen conch *Aliger gigas*; Stieglitz & Dujon 2017) and the movements of mariculture pests, the Northern Pacific seastar *Asterias amurensis* (Miyoshi et al. 2018) and pest removers (giant triton *Charonia tritonis*; Schlaff et al. 2020).

3.1.4. Conservation status of species studied using VPS

The majority of species studied to date using VPS are considered low conservation risk by the IUCN Red List (i.e. Least Concern or Near Threatened), with far fewer Threatened (Vulnerable, Endangered and Critically Endangered), Data Deficient or Not Evaluated species tracked (Fig. 2). The trend of studying species of low conservation risk is likely a result of reduced administrative barriers (i.e. ease of securing a scientific permit), availability of funding for commercially or recreationally fished species (e.g. industry and governmental partnerships) and practicality (species with known distribution and ease of capture). Despite these factors, improving our understanding of Threatened, Data Deficient and Not Evaluated species remains critical to conservation management.

3.2. Global distribution, habitats and functional roles of species studied

VPS studies have spanned 120 degrees of latitude, ranging from tracking Endangered silver eels *Anguilla dieffenbachii* occupying a freshwater reservoir in New Zealand (Jellyman & Unwin 2019) to studying movement trajectories of the abundant shorthorn sculpin in the Canadian High Arctic (Ivanova et al. 2018, Landry et al. 2019). Tagging effort has been focussed in North America (n unique articles = 49; 49% articles), followed by Europe (n = 21; 21%) and Oceania (n = 16; 16%), with less research undertaken in the Caribbean (n = 5; 5%), East Asia (n = 5; 5%), West and Central Asia (n = 3; 3%) and Mesoamerica (n = 1; 1%) (Fig. 3). No published VPS studies have been conducted in South America, Northern Asia, Antarctica or Africa.

The evident geographic gap in applying this technology could be due to several reasons; the search criteria used in this review, the acquisition and distribution of equipment, mechanisms of knowledge transfer, available funding and geopolitical factors. Firstly, this review only incorporated literature published in journals that accept the English language, which is not the official language of many countries in the regions mentioned above. A duplicate search was run using eLIBRARY.RU, a popular Russian literature search engine that contains over 29 million Russian scientific articles and publications, to assess the impact of this factor on the review output. Using the search term 'VEMCO Positioning System' yielded 3 results that had been identified using our selected search engines. While this search engine did not provide any unique articles relevant to this review, the use of more inclusive search engines should not be overlooked. It should be noted that technical reports were not included in this review, which may be a more popular form of science communication in some regions.

The global distribution of VPS studies mirrors that of acoustic and satellite telemetry studies (see Hussey et al. 2015) (Fig. 3). This pattern may in part be due to regional telemetry networks. Well-established networks and centralised databases are present across North America, Europe, Australia and southern Africa that facilitate equipment sharing and knowledge transfer within these regions. Furthermore, Innovasea (the manufacturer of the VPS, formerly manufactured by VEMCO) is based in Canada. The cost of procuring equipment outside of North America increases further from the source, which may deter researchers from using this technology. This disparity is likely further amplified by the limited funding and capacity in developing countries (Hussey et al. 2015, Barkley et al. 2019). Geopolitical boundaries may also present a challenge. Of all studies conducted to date, only 1 compared the fine-scale movement metrics of an invasive species across 2 distinct geographic locations (Pickholtz et al. 2018). This apparent shortfall in VPS applications across certain regions does not reflect the distribution of unique habitats or species present, which do not conform to sociopolitical boundaries.

Fine-scale tracking studies have predominantly focussed on the marine biome (n unique datasets = 73; 52% of all unique datasets) within coastal (n coastal marine datasets = 42; 67% of unique marine datasets) habitats. VPS technology has been used to track aquatic species across a range of unique coastal habitats, including, but not limited to, restored wetlands (Farrugia et al. 2011), giant kelp forests (Coates et al. 2013), artificial reef systems (Logan & Lowe

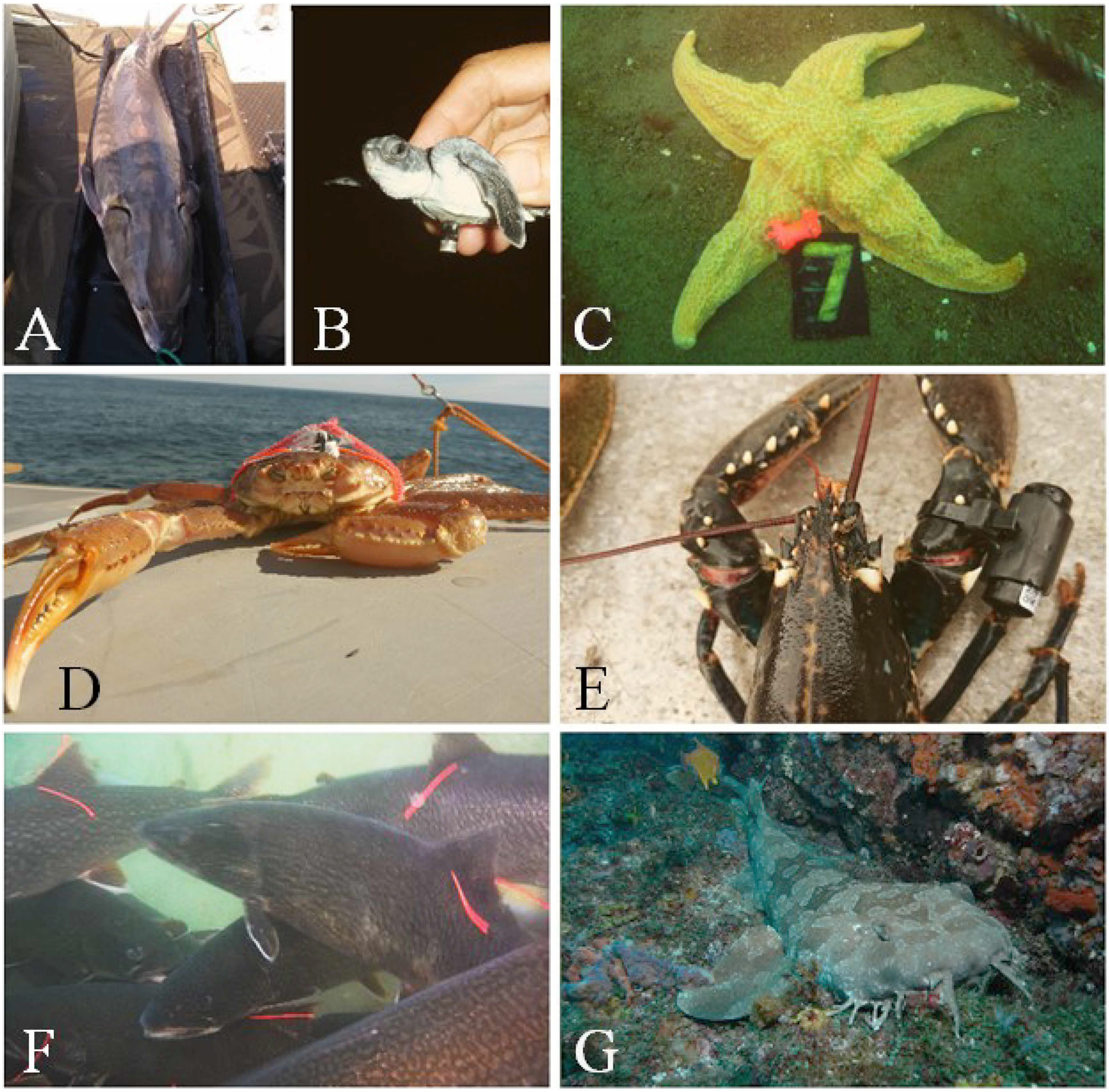

Fig. 2. Diversity of species studied using the VEMCO Positioning System (VPS). (A) The largest fish tagged for a VPS study to date, a 96 kg Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* tracked by Balazik et al. (2020) (photo credit: Matthew Balazik). (B) The smallest animal externally tagged for a VPS study to date, a 31.1 g hatchling flatback turtle *Natator depressus* tracked by Thums et al. (2013) (photo credit: Michelle Thums). (C) A tagged Northern Pacific sea star *Asterias amurensis* tracked in northern Japan to identify its seasonal movements within maricultural fields (Miyoshi et al. 2018) (photo credit: Koji Miyoshi). (D) A snow crab *Chionoecetes opilio* tagged to study fundamental deep-water movement characteristics of this commercial fishery resource (Cote et al. 2019) (photo credit: David Cote). (E) A European lobster *Homarus gammarus* tagged to investigate free-ranging animal behaviour and movements in relation to baited commercial traps (Lees et al. 2018) (photo credit: Kirsty Lees). (F) The largest tagged cohort to date, with 390 lake trout *Salvelinus namaycush* tracked in Lake Huron, Canada, to investigate habitat use during spawning (Riley et al. 2014, Binder et al. 2018) (photo credit: Thomas Binder). (G) An internally tagged potted wobbegong shark *Orectolobus maculatus* tracked to study inter-sociality (Armansin et al. 2016) (photo credit: Robert Harcourt)

2019) and mangroves (Rooker et al. 2018). Offshore marine habitats (>2 km from land) have received some attention (n unique offshore marine datasets = 21; 29%) and have investigated species movements around unique features, including offshore wind farms (van der Knaap et al. 2021), subsea cables

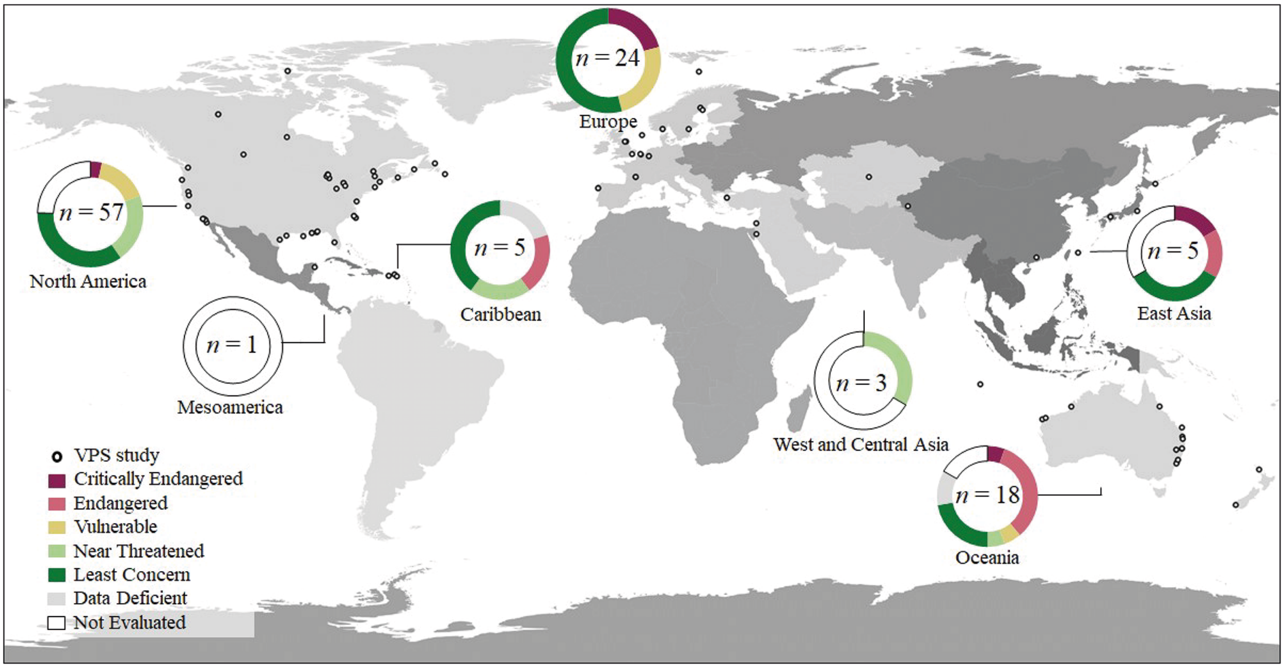

Fig. 3. Global distribution of VEMCO Positioning System (VPS) tagging studies (points). Colour wheels reflect the IUCN Red List Categories and Criteria of study species relative to the total number of unique species tracked (n) within each region (monochromatic shade)

(Cote et al. 2019), marine canyons (Cote et al. 2020) and around wastewater outflow sites (Burns et al. 2019). Studies within freshwater environments (n unique datasets = 52; 37%) and brackish environments (n = 17; 12%) have focussed on lakes (Buchinger et al. 2017, Guzzo et al. 2018), natural flowing rivers (Espinoza et al. 2020), impounded waterways (Whitmore & Litvak 2018, Baker et al. 2020, Fahlman et al. 2021), shipping canals (Vergeynst et al. 2019) and harbours (Teesdale et al. 2015).

Of the species targeted in VPS studies, the majority typically occupy the lower water column (n unique demersal species = 54, 63%; n unique reef-associated species = 16; 19%), followed by those found in the benthopelagic zone (n = 16; 25%). Animals inhabiting the pelagic zone are the least studied (n = 1; 1%) (n = 3; 3% not described). This application gap results from the relative ease of studying species that occupy the lower water column relative to pelagic, highly mobile (horizontally and vertically) species. VPS studies provide detection coverage over relatively small areas (<5 km^2) compared to coarse-scale linear strings of acoustic receivers with non-overlapping detection ranges. Therefore, adequately capturing the range of movement that a pelagic species covers is a challenge.

3.3. Using VPS to address ecological questions

Primary ecological themes addressed using VPS can be categorised under 7 overarching topics: behavioural ecology (n articles = 40; 34% of articles), conservation measures (n = 25; 22%), land use management (n = 14; 12%), fisheries management (n = 12; 10%), methodological testing (n = 11; 9%), reproductive ecology (8; 7%) and the influence of other movement drivers (n = 7; 6%). In addition, 70 fine-scale categories were identified within these core topics, ranging from assessing the impact of boat noise to applying mortality reduction techniques to assist fisheries management (Fig. 4). Over time, these central themes and subsidiary aims have diversified, facilitated in part by technological progress. Technological advances include the enhanced resolution offered by VEMCO High Residency (HR) equipment. In conjunction, statistical progress has been driven by the ease of conducting different analyses via the availability of open-access computational packages (Joo et al. 2020) and 'big' data via data sharing (Thums et al. 2018).

As new statistical approaches emerge in ecology, existing data can be used to drive a new wave of understanding of animal ecology and behaviour. VPS data have been analysed and published using different timeframes, subsets of animals and types of

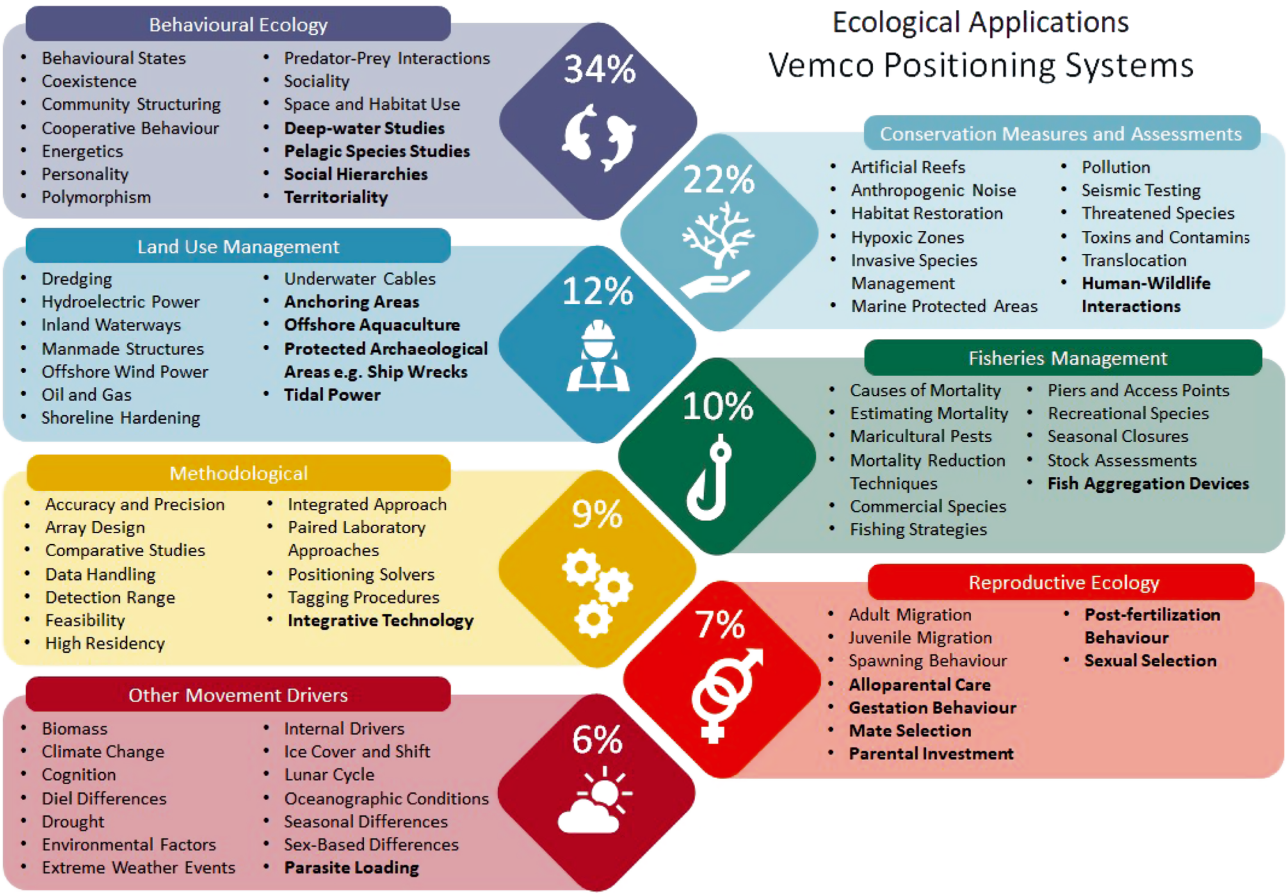

Fig. 4. Key ecological themes addressed using fine-scale VEMCO Positioning Systems (VPS) to date, with future directions highlighted in **bold**

analysis to answer diverse ecological questions. For example, of the 5 articles studying red snapper *Lutjanus campechanus*, 4 articles used different combinations of data generated from a single VPS array (differing time frames and data generated by different tagged individuals) to identify 2D (Piraino & Szedlmayer 2014, Williams-Grove & Szedlmayer 2016a) and 3D (Williams-Grove & Szedlmayer 2017) movements of this species, and the leading causes of mortality (Williams-Grove & Szedlmayer 2016b).

While technological advancement and statistical approaches have the potential to improve our understanding of mechanistic animal behaviour, disseminating these results effectively to non-specialised users is critical. At present, VPS data visualisations are similar to those selected for coarse-scale animal tracking data. From the use of abacus plots to identify animal fate and highlight presence/absence from the study area (Williams-Grove & Szedlmayer 2016b, Carpenter-Bundhoo et al. 2020), to visualisation of 2D home range (Schlaff et al. 2020) along *x*, *y* coordinates. High-resolution data have been paired with environmental data to generate detailed visualisations of space use, for example, by matching water temperature recordings and high-resolution animal depth data (from pressure tags) through time series plots (Freitas et al. 2021) and 3D visualisations of space use during stratification (Roberts et al. 2017). Visualising VPS results is critical to disseminating data to non-technical stakeholders, including natural resource managers, policymakers and the public.

We highlight the need for validation techniques throughout this section and offer common techniques and technologies that can be used. For example, a key validation and cross-comparison technique that VPS studies have not fully taken advantage of are controlled experiments in laboratory settings. Laboratory experiments can be highly effective at testing study design features, including tag retention and responses to novel olfactory stimuli; only 4 VPS studies reported running additional or parallel laboratory studies. These parallel applications have investigated barrier avoidance (Leander et al. 2020), spawning behaviour (Buchinger et al. 2017), personality (Villegas-Ríos et al. 2018) and common behavioural traits (Fahlman et al. 2020). While most VPS studies use field study components alone, there is also the potential to validate and support field observations using controlled environments such as isolated lakes or controlled flumes (Lennox et al. 2021).

3.3.1. Behavioural ecology

Most behaviour-focussed studies have used VPS data to investigate space use metrics, including residency, activity space, and core and extended home range. Other applications include studies using VPS data to investigate coexistence (Guzzo et al. 2016, Becker et al. 2020, Freitas et al. 2021), sociality (measured as the persistence of social networks over time) (Armansin et al. 2016) and physiological drivers (Brownscombe et al. 2017; Fig. 4). Secondary to understanding these characteristics is identifying the drivers of animal movement, for example, abiotic factors such as salinity, temperature, ice cover, seasonal productivity and weather extremes. The majority of studies have used data collected over longitudinal time scales to identify periodicities of movement characteristics, e.g. across diel periods, within and between seasons and over annual timescales (the secondary focus of 50% of articles with a primary focus on behavioural ecology). For example, Moulton et al. (2017) examined the periodicity of movements of 2 sympatric gamefishes, the red drum *Sciaenops ocellatus* and the spotted seatrout *Cynoscion nebulosus*, on both a localised and bay-wide scale. Over 2 yr, animals were tracked using a smaller VPS grid array to identify fine-scale movements and across discontinuous strings of receivers that captured movements within the broader bay. Habitat use by sea trout shifted from seagrass during the day to bare substrate at night, indicative of nocturnal foraging and potential predator avoidance, given that seagrass can attenuate high-frequency vocalisations which dolphins use to echolocate prey (Wilson et al. 2013). Nocturnal foraging was also indicated by the higher calculated rate of movement (ROM) at night (3.4 m min^{-1}) versus day (0.95 m min^{-1}).

VPS studies have used additional data streams from a variety of sources to advance understanding of behaviour, including animal-borne accelerometers to measure activity, environmental sensors to measure abiotic parameters (dissolved oxygen, salinity, temperature, light, current speed and direction, wind speed) and anthropogenic effects such as noise and artificial light. For example, Brownscombe et al. (2017) were able to study the spatiotemporal energy expenditure of bonefish *Albula vulpes* in the wild by pairing swim tunnel respirometers with accelerometers to estimate metabolic rate across several habitat types and behavioural states. Using these techniques, Brownscombe et al. (2017) estimated energy expenditure across a heterogeneous reef flat and identified environmental drivers of movement. One such driver included the avoidance of nearshore areas during temperature extremes.

The ability to track multiple species simultaneously has facilitated an understanding of species interactions and the testing of traditional ecological theory or concepts, including coexistence, niche and resource partitioning (Guzzo et al. 2016). With the acquisition of depth data, there is potential to estimate the degree of spatial overlap in 3D space among individuals and species to reveal a deeper understanding of their co-occurrence and mechanisms driving species interactions. There is also the possibility to incorporate 3D models of space use with autonomous cameras and deep learning models to capture the diversity of non-tagged life and conspecifics on reefs (Villon et al. 2018).

Future applications of VPS could include the study of predator–prey interactions that shape ecosystems over varying scales, from individual decision making and predator avoidance to trophic cascades and food web restructuring (Smith et al. 2020). While joint space use has been studied under the lens of resource partitioning, coexistence and sociality, it also has relevance for epidemiology via disease transmission (Schauber et al. 2007, Gilbertson et al. 2021) as well as population genetics and gene flow (Roffler et al. 2012, Hahn et al. 2019).

3.3.2. Conservation measures

Conservation-driven VPS studies have primarily focussed on the behavioural responses of animals to ameliorative measures (n articles = 13; Fig. 4), as well as noise pollution and contaminants (n = 3), seismic testing (n = 1), hypoxia (n = 1) and the movements of threatened (n = 2) and invasive species (n = 2).

Artificial reefs are the most commonly studied ameliorative conservation measures, with studies on their influence on species' site fidelity, residency and home range (n = 7) and community structuring (n = 1). The geographic scale of artificial reef studies has ranged from deploying VPS arrays around discrete reef units and clusters in coastal marine environments (n receivers = 15; Piraino & Szedlmayer 2014) to a grid of receiver grids across a freshwater bay (n receivers = 27; Marsden et al. 2016). For example, Marsden et al. (2016) studied the relative attraction of tagged spawning lake trout to natural and artificial reefs using an integrated VPS approach in Lake Huron, Canada. Surface- and diver-deployed egg and fry traps were used to validate spawning behaviours identified by a lake-deployed VPS. Using these integrative techniques revealed that the proximity of a new artificial reef to an existing natural reef increased spawning activity. Moreover, by conducting a longitudinal study across 3 spawning seasons, the use of new reefs was shown to be initially low but increased over the assessment period.

The benefits of conservation strategies, including habitat restoration (n articles = 1), marine protected areas (n = 2) and translocation (n = 3), have also been studieFor example, Farrugia et al. (2011) investigated the use of a restored habitat by the shovelnose guitarfish to mitigate habitat loss from the expansion of the Port of Los Angeles, California, USA. In terms of understanding the benefits of marine protected areas (n = 2), Stieglitz & Dujon (2017) paired data from environmental loggers (measuring salinity, temperature, dissolved oxygen and ambient light levels) with telemetered Caribbean queen conch, which spanned a range of developmental stages (n tagged = 38). The study aimed to assess the use of marginal atypical estuarine environment by this species and found that space use was comparable to marine habitats, highlighting the conservation need for this potential nursery habitat.

3.3.3. Land use management

Land use management-focussed VPS studies have primarily investigated the behavioural response of teleosts (n species = 16, n articles = 12) and chondrosteans (n species = 2, n articles = 2) within modified systems including reservoirs, harbours and those influenced by sewage outflows and dredging. These studies typically incorporate multiple data sources such as habitat type from bathymetric surveys (multibeam sonar), vegetation surveys, fish community surveys and categorisation of substrate type. For example, Veilleux et al. (2018) assessed the use of harbour slips in the Inner Harbour of Toronto, 2 of which were ‘enriched’ to increase habitat complexity (i.e. increased overhead cover and presence of in-water structures) and 2 deeper slips with no enrichment.

VPS is often paired with discontinuous strings or gates of receivers. While this trait is not unique to land use management studies, creating ‘checkpoints’ to identify animals that emigrate or exit a fine-scale study area is vital to identifying the relative impact of habitat modification and anthropogenic structures. For example, Vergeynst et al. (2019) deployed a VPS within the Albert Canal in Belgium to investigate the impact of intermediate-head navigation locks on downstream migration success of European eel and Atlantic salmon *Salmo salar*. While this VPS array was positioned at the entrance to a single navigation lock, it formed part of a more extensive acoustic network that validated the tagged fish exiting the study system.

Mortality within aquatic systems is currently identified from patterns observed within telemetric data. Common techniques include identifying rapid changes in vertical profile across a range of depths atypical of the behaviour of a species, a continuous depth profile or detection at a single receiver station (cessation of movement) or abnormal swim speeds outside the range of expected values (Everett et al. 2020, Bacheler et al. 2021). A unifying aspect of these techniques is that species ecology is well known and the study system is well understood. The recent advent of the ‘predation tag’ presents a new frontier to integrate within VPS applications in land use management studies, for example, in impounded systems that experience population bottlenecks, e.g. high-risk areas for juvenile fish migrating out to sea (Boulêtreau et al. 2020). These predation tags are coated in a biologically inert polymer; when a predator consumes a tagged animal, this polymer breaks down, triggering a change in the tag’s emitted identification code (Halfyard et al. 2017). While no published VPS studies to date have used this technology, this will likely become a vital tool in fisheries and land management research. These predation tags also present opportunities to estimate biomass structuring in ecosystems through determining natural predation rates across functional groups.

While VPS has shed light on the influence of riverine and coastal structures on fish movement, future research could explore the association of aquatic animals with structures, including tidal power and protected archaeological areas such as shipwrecks. For example, one avenue of inquiry could include research into the link between tidal power, altered bottom substrates in locations downstream of tidal energy installations and subsequent changes in plant and animal community composition and abundance (DOE 2009, Frid et al. 2012).

3.3.4. Fisheries management

Fisheries management VPS studies have investigated a range of topics from testing techniques to reduce discard mortality (Bohaboy et al. 2020), to bait attraction and catchability (Bacheler et al. 2018, Lees et al. 2018), causes of mortality (Williams-Grove & Szedlmayer 2016b), general movements of species of commercial value within offshore areas (defined here as >2 km from shore, Skerritt et al. 2015) and aquaculture pests within culture areas (Miyoshi et al. 2018).

VPS data have direct applications for improving existing fisheries management tools, for example, by collecting data to inform catch per unit effort (CPUE) estimates. CPUE is a metric used to understand species distribution and abundance (Hinton & Maunder 2004). Lees et al. (2018) used VPS to identify localised behaviours of an important recreationally and commercially fished species, the European lobster, in response to baited traps. This study aimed to understand the probability of attraction to a bait source and quantify the proportion of the population targeted. Understanding the fine-scale behavioural response of animals to different fishing practices has vast potential to aid our understanding of fishing-induced evolution (Uusi-Heikkilä et al. 2008), as well as the design of effective protected areas (Lennox et al. 2017) and improving current estimates of population dynamics (i.e. survivorship/mortality) (Langrock et al. 2012, Lees et al. 2021).

Techniques to validate fisheries management VPS studies have included the use of underwater cameras. When investigating post-release survivorship, Bohaboy et al. (2020) affixed an underwater camera above descender devices to record fish descent and release to evaluate the performance of descender devices to capture possible predator interactions and behaviour of released fish. While no fish were predated during descent, 3 predation events were captured on video post-release, including consumption by a shark (n predated = 2) and a dolphin (n predated = 1), validating the removal of these fish from subsequent analysis. By incorporating complementary technology such as remote underwater video, there is potential to confirm mortality estimates and behavioural modes speculated from positional data (as seen using other biologging techniques; see Nakamura et al. 2015).

3.3.5. Methodological testing

Methodological VPS articles (n = 11) have shifted from initial work testing the feasibility and accuracy of VPS technology (Andrews et al. 2011, Espinoza et al. 2011, Özgül et al. 2015) to those assessing the complementarity of high-resolution spatiotemporal models to support VPS findings (Goulon et al. 2018, Guénard et al. 2020), and testing of new VPS-compatible technology (Guzzo et al. 2018, Leander et al. 2020). It should be noted that the current review only incorporates VPS studies that had directly tagged animals as part of the study. During this search, 9 articles were identified which tested the mechanics of VPS (see the Supplement), including the factors influencing detection performance (Binder et al. 2014, 2016, Roy et al. 2014, Steel et al. 2014, Swadling et al. 2020). One additional article was feasibility-driven and studied the potential application of VPS to track turtle hatchlings (Thums et al. 2013); however, screening criteria identified understanding behavioural ecology as a primary focus. The first feasibility studies demonstrated the ability of VPS to accurately and precisely generate continuous positioning data (Espinoza et al. 2011) and its improved performance relative to existing VEMCO positioning technology (VRAP; Andrews et al. 2011).

Recently developed VEMCO HR equipment uses binary phase shift signalling to facilitate tag transmission rates several orders of magnitude greater than its predecessor and at a higher resolution. Data loss using this technology is less likely than traditional pulse-per-modulation (PPM) acoustic telemetry, which uses a code burst (8- or 10-ping signal that takes 3–5 s to transmit) transmission type. Due to a reduction in the propensity of signal collision, studies can track larger cohorts of animals. Initial testing by Guzzo et al. (2018) in a freshwater lake in Scotland revealed that the higher transmission interval attainable with HR tags (mean = 4 s) could more accurately determine complex path tortuosity as a result of higher data yield. Tortuosity characteristics, including turning angles and speed, are key characteristics for deciphering behavioural modes which drive movement choices (Gurarie et al. 2016). In addition, a comparison between traditional PPM and HR transmissions conducted by Leander et al. (2020) found that the higher transmission rates achieved by HR enabled the generation of 12 times more positions for tagged European eels navigating the Motala River in Sweden using a tag transmitting both signal types (1.1 s nominal HR transmission rate versus 37.5 s with PPM). It should be noted that while HR can generate a significant volume of data, these positions require careful evaluation to assess whether positions are ecologically meaningful, particularly in cases where the error associated with a position exceeds the scale of movement studied (C. H. Fleming et al. preprint; https://doi.org/10.1101/2020.06.12.13019).

3.3.6. Reproductive ecology

VPS articles primarily focussing on reproductive ecology (n articles = 8) have investigated key characteristics, including spawning cues and sex-based differences in behaviour. These studies have incorporated large sample sizes (mean n animals tagged = 147, unique datasets = 7), including the largest cohort of animals tagged within a single VPS study (lake trout, n = 390; Riley et al. 2014, Binder et al. 2018). Often studies addressing this theme incorporate abiotic data streams, including habitat mapping using high-resolution multibeam bathymetric surveys (Riley et al. 2014, Binder et al. 2018, unique datasets = 1) and habitat flow models (Wyman et al. 2018). A novel multifaceted study by Buchinger et al. (2017) used chemical analyses, electro-olfactogram recordings and behavioural assays to evaluate the persistence of fry odours during a spawning season coupled with the installation of a 27-receiver VPS array. While laboratory components of this study supported the theory that lake trout use fry odours as cues of past reproductive success, these results were not replicated in the natural VPS experiment (Buchinger et al. 2017). This example highlights how a multifaceted study design, with both laboratory and in-field components, can identify differences in observed behaviours dependent on the environmental setting.

3.3.7. Other drivers of movement

Aquatic environments are highly dynamic with the scale of movement necessary to acquire essential resources and undertake life history processes in part modulated by abiotic conditions (Jackson et al. 2001). Vast expanses of the aquatic realm are physiologically challenging to occupy, and therefore it is critical to identify environmental and oceanographic conditions which drive movement behaviours and intimately link with individual performance and fitness (Madigan et al. 2021). While only 7 articles focussed primarily on abiotic environmental variables, a large proportion of remaining articles listed this as a secondary (n articles = 23; 21 %) or tertiary (n = 33; 38 %) aim.

Environmental sensors are often deployed alongside VPS to measure temporal and seasonal changes in the ambient environment, including temperature, salinity, dissolved oxygen and photosynthetically active radiation. Aside from using these data to identify environmental drivers of movement, they can also provide indicators of conditions that may impede system performance. For example, weather extremes such as hurricanes can reduce data acquisition due to animal displacement, while increased turbidity and wave action can limit signal propagation (Dahl & Patterson 2020, Bacheler et al. 2021). Ivanova et al. (2018) provided an applied example of using environmental sensors to explore the drivers of movements. To disentangle whether the movements of shorthorn sculpin in Resolute Bay, Nunavut, Canada, were driven by vessel presence and/or abiotic factors, environmental loggers were installed to record salinity, water temperature and dissolved oxygen. Additional environmental covariates, including mean wind speed, air temperature and photoperiod, were retrieved from online archives. Using fine-scale VPS data, trajectories were broken into bursts containing discrete successive VPS positions which were then clustered into 3 movement types. Models were subsequently run to examine the influence of ship traffic and environmental variables on the 3 defined movement behaviours.

Given the forecasted increase in the frequency of extreme weather events with climate change (National Academies of Sciences, Engineering, and Medicine 2016, Knutson et al. 2020), it is likely that future studies will unwittingly capture these events, which will improve our fundamental understanding of behavioural responses and potential plasticity of species' movements. Future work is also required to capture the influence of other environmental extremes, including El Niño, La Niña and flooding, on animal movement (Wilson et al. 2001, Campbell et al. 2012, Briscoe et al. 2021).

3.4. Analytical approaches for VPS data

Increased transmission rates and encoding options (with reduced transmission intervals and multiple steps of programming) have the potential to yield an unprecedented quantity of high-accuracy positions using VPS technology (Espinoza et al. 2011). VPS studies using traditional PPM VEMCO technology typically generate upward of 500 positions a day (n unique species datasets with nominal transmission rate detailed = 109, median nominal transmission rate = 120 s, range of nominal delay = 7.5–4800 s). The new age of enhanced positioning accuracy, precision and tracking resolution offered by VEMCO HR equipment can generate over 20 000 positions d^{-1} for a single animal (n HR-VPS species datasets = 6) with sub-metre accuracy. With this volume of data, there are 2 integral steps to ensure that data integrity is maintained. Firstly, the error associated with a position does not exceed the scale of movement studied. VPS positions include a horizontal positioning error (HPE), a form of dimensionless error analogous to GPS horizontal dilution of precision (C. H. Fleming et al. preprint; https://doi.org/10.1101/2020.06.12.13019). HPE values are unique to each application of VPS, with fixed reference tags used to compare location error with calculated animal positions (Smith 2013). Identifying associated error is key to selecting an appropriate analytical technique. For example, Fleming et al. (2021) identified that a per unit increase in HPE equated to 3–9 m of location error. Given this scale of error, if step lengths (distance between 2 consecutive positions) were calculated at <9 m, subsequent calculations would be contaminated by location error as the error associated exceeds the scale of movement studied. Secondly, it is key that for high-resolution tracking data, analytical techniques that account for autocorrelation are selected (Gurarie et al. 2009). Autocorrelation describes positions that are not independent in time or space, which is the case for consecutive telemetric datapoints (Gurarie et al. 2009).

On a foundational level, consecutive detections can be used to calculate basic metrics, including step length and turning angle (bearing between consecutive positions) (Ironside et al. 2017). Using these foundational units of movement, metrics including tortuosity (degree of turning across the movement path) and total distance travelled (Euclidean distance between first and last points or within a user-determined time frame) can be calculated for a given trajectory. Trajectories are often used to investigate species distribution metrics such as space and habitat use, including home range, site fidelity and residency. By incorporating potential drivers of movement, for example, environmental and oceanographic conditions, these covariates can be used to explore animal movement as a community-level process and identify underlying behavioural patterns (Schick et al. 2008). While VPS-compatible technology advances and user-friendly data handling and modelling techniques are explored in seminal papers and guides (e.g. a continuous-time correlated random walk model, Johnson et al. 2008; state space models, Auger-Méthé et al. 2021), the diversity of analytical techniques used to explore fine-scale movement will continue to diversify.

3.4.1. Home range

A fundamental characteristic of an animal's movement trajectory is its home range. Information on animal home ranges can be used in conjunction with broader ecosystem models to develop and assess conservation strategies such as protected areas (Andrzejaczek et al. 2020). Home range describes the area in which an animal travels to acquire the resources it needs for survival and reproduction (Burt 1943). Despite the simplicity of this definition, defining this statistically is challenging (Dougherty et al. 2017). Common approaches to estimate home range can be grouped in 2 different ways: firstly, those that aim to estimate an animal's range distribution and its long-term area requirements (as per the definition provided by Burt 1943) which commonly include minimum convex polygon (MCP) and kernel-density estimators (KDE) (Fleming et al. 2015); alternatively, techniques that estimate occurrence distributions through interpolation of the observed data during the study period include Brownian bridge density estimators (BBDE) and time local convex hull (T-LoCoh) which do not link to Burt's (1943) conceptualisation of home range. As detailed by Fleming et al. (2015), these approaches can also be viewed in terms of their methods as either (1) geometric (lacking an underlying probabilistic model, includes MCP and T-LoCoh) or (2) statistical (KDE and BBDE). Choice of statistical approach depends on the study question at hand and can differ in its fundamental framework; therefore, comparisons between fine-scale telemetry studies that use different methods should be made with caution.

Early techniques of home-range analysis were devised to quantify 2D (i.e. horizontal) space use, such as 100% MCPs (Blair 1940, Odum & Kuenzler 1955). MCP (also called a convex hull) is a simple technique that draws the smallest possible convex polygon around point locations (x, y). Despite the well-published limitations of this technique (Worton 1987, 1995, Börger et al. 2006), it is still used today in VPS studies (n articles = 14).

Home range is often analysed as the relative frequency (probability) distribution of an animal's location in space, also known as a utilisation distribution (UD) (French et al. 2019). A common form of UD estimation uses a KDE. While initially not intended for telemetric datasets, this technique is very popular (n VPS articles = 41). Kernel UDs often use the 50 and 95% isopleths of the probability distribution of locations to estimate an animal's core and extended home range (see Worton 1989). This technique relies on the assumption that data are independent and identically distributed (Silverman 1983). High-resolution telemetric data do not meet this assumption as they are intrinsically autocorrelated and nonstationary (Fleming et al. 2015). Autocorrelated KDE is a generalisation of KDE which incorporates an autocorrelation function and is derived from a fitted model or directly from the data (see Fleming et al. 2015). The only example of its application to VPS data to date is provided by Bašić et al. (2019), who used this technique to determine the home range and core areas used by tracked European eels.

Three VPS articles used BBDE (for methods, see Horne et al. 2007), an approach originally devised for occurrence distributions that is not a home-range estimator (see Fleming et al. 2015 for further details). This technique uses an underlying movement model to create a smooth bridge between animal relocations (Kranstauber et al. 2012). The driving parameter in Brownian bridge movement models (BBMMs) is the Brownian motion variance, which describes the irregularity of the path of an animal track (Byrne et al. 2014, Kranstauber 2019). Adaptations of BBMMs include dynamic BBMMs, which calculate the Brownian motion variance for each behavioural track segment (Kranstauber et al. 2012, Silva et al. 2018) with the aim of improving estimator accuracy.

The T-LoCoH technique is an occurrence distribution estimator which generalises the MCP method (see Getz et al. 2007, Kie et al. 2010) and incorporates time (Lyons et al. 2013) (n = 1). Whitmore & Litvak (2018) used T-LoCoH to study the space use and aggregation behaviour of juvenile Atlantic sturgeon; and constructed isopleths incorporating point density, directional movement, revisitation and residency time to identify pathways and activity space across 2 seasons.

3.4.2. Habitat selection

Habitat selection describes the process by which an animal chooses a resource, and habitat preference indicates the likelihood that an animal selects a resource given equal availability (Johnson 1980). The ability to identify preferred or critical habitats which support vital life-history stages, including spawning, is central to conservation (Caro 1999). Two common techniques used to quantify microhabitat selection using VPS data include compositional analysis (classification based) and Euclidean distance analysis (EDA) (distance-based; Degregorio et al. 2011).

Compositional analysis classifies animal locations by a single habitat type to determine proportional use (Aebischer et al. 1993). The method relies on several assumptions: (1) each animal provides an independent measure of habitat use within the population, e.g. no gregarious behaviour; (2) all animals select habitat in the same way, i.e. all have equal access to resources and exhibit no territoriality; (3) habitat use by different animals is equally accurate, e.g. not dependent on 'detectability' such as reduced detection likelihoods in complex habitats; and (4) the more available a resource is, the more likely an animal is to use it (Garshelis 2000).

The habitat selection index (HSI), a type of compositional analysis, has been used to estimate the preference or avoidance for a given habitat (n articles = 5), where resultant values >1 indicate preference and <1 indicate avoidance (Manly 1972). To calculate HSI, the proportion of positions within each habitat type is divided by the proportion of available habitat. For example, Özgül et al. (2019) used HSI to evaluate the conservation benefit of artificial reefs, with habitat selection by 2 species of scorpionfish (*Scorpaena*) identified within a 15 m spatial buffer generated around 12 artificial reef sets within a 0.28 km^2 VPS array.

Resource selection functions (RSFs, n articles = 2) are often favoured as they yield statistical rankings among habitats (Garshelis 2000). Data are arranged similar to an ANOVA whereby between-group variation can be tested against within-group variation among individuals. RSFs can also incorporate covariates such as temporal scale (diurnal, seasonal and annual differences) and study areas (such as differing biomass and animal densities) (Garshelis 2000, Boyce et al. 2002, McLoughlin et al. 2010). For example, Freitas et al. (2016) used VPS to identify habitat selection by Atlantic cod within a Norwegian fjord across seasons and temperature ranges. Habitat selected by tagged cod were coded as 1 while an equal number of theoretical random locations were generated and coded as 0 (see the detailed method in Johnson et al. 2006).

In contrast to compositional analysis, EDA (n articles = 15) is a multivariate distance-based approach that computes the distance between each animal position and the nearest occurrence of each habitat type (Conner et al. 2003). Random points are simulated, which present the expected distances to each habitat type (the null distribution). If an individual's habitat use is random, then the distance calculated for the null distribution and animal positions should be equal for a given habitat type (Novak et al. 2020). EDA is preferable in incidences where an area is classified as 2 habitat types simultaneously, whereas compositional analysis requires a single discrete categorisation for each area (Conner & Plowman 2001). Novak et al. (2020) used EDA to investigate fine-scale habitat use by the yellowtail snapper *Ocyurus chrysurus* within a nearshore marine protected area.

Results suggested that EDA is a valuable tool when looking at population-level habitat preference, but differences in individual preference or avoidance in habitat use were masked.

It should be noted that if receivers are unevenly spaced or prone to reduced detection efficiency due to physical barriers, the perceived time spent across different portions of the array (particularly in truncated systems) may be inaccurate. These approaches assume that all habitat is equally available, regardless of distance and animal speed (Forester et al. 2009). Alternate habitat selection methods using telemetry data, but not yet VPS, include step selection functions (SSFs) which are similar mathematically in structure to RSFs (Fortin et al. 2005). The main difference is that SSFs account for distance (defined as step length) and turning angle. In addition, there is potential for the use of non-Euclidean distances to assign a cost to movements across habitats, which is used in metapopulation ecology (Wiens et al. 1993).

Habitat connectivity and use have been studied primarily through the use of multiple installed VPS arrays (n articles = 21) and the integration of additional gates of receivers across broad-scale habitat features (n = 39). For example, Dance & Rooker (2015) examined movements of 2 co-occurring juvenile fishes, southern flounder *Paralichthys lethostigma* and red drum, across a range of spatial scales. Movement was studied at a habitat scale using a VPS (n receivers = 10; coverage = 1 km^2), and bay scale using a grid of receivers with non-overlapping detection ranges (n receivers = 17; coverage = 20 km^2). It was found that environmental factors did not affect red drum movement on a habitat scale, but on a broader bay-wide scale, movement increased in response to decreasing salinity and lower temperatures.

3.4.3. Activity

Animal movements, behaviour and energetics vary across habitats, landscapes and climes. Consequently, quantifying spatiotemporal variation in animal activity is key to understanding energetic budgets (Wilson et al. 2012). The activity of tracked animals within VPS is predominantly determined using basic calculations generated from animal relocations, including the ROM (estimated by dividing the distance between detections by the elapsed time, n articles = 42). Straight-line displacement estimates (typically used for ROM calculations) are susceptible to errors associated with the scale of measurement, sampling frequency, and path tortuosity (Rowcliffe et al. 2012, Noonan et al. 2019).

While not yet applied in VPS studies, continuous-time speed and distance estimation methods may offer greater accuracy for mean speed estimates from fine-scale positioning data (Noonan et al. 2019). This approach uses measurement and process models estimated from tracking and preferably calibration data (from fixed-location tags). A trajectory is then simulated as conditioned by the data, fitted movement model and aforementioned calibrated error model (see Noonan et al. 2019 for further details). The distance/speed of that trajectory is then calculated, and the process is repeated through multiple simulations to create a point estimate and confidence intervals that come directly from the sampling distribution (Noonan et al. 2019).

The integration of an acceleration sensor in tags has allowed the identification of animal behaviours (feeding, foraging, transiting) (Cott et al. 2015) and estimates of energy expenditure (Brownscombe et al. 2017). VEMCO acoustic triaxial accelerometers can either log data at high frequencies (>100 Hz; but require animal recapture) or transmit data less frequently in the form of a summarised activity value (5–10 Hz; SI units). SI units are calculated from measuring acceleration over 2 ('tailbeat algorithm' uses lateral [*x*] and vertical [*z*] axes) or 3 axes ('activity algorithm' uses lateral [*x*], forward [*y*] and vertical axes [*z*]) (InnovaSea Systems Inc. 2018). For the 'activity algorithm', the root mean square of acceleration is calculated and averaged over a given sampling period, e.g. 25 s (Brownscombe et al. 2017). As with positioning data, sampling frequency directly determines the scale of inference, e.g. identification of fast-action feeding events and burst swimming to escape predation (Broell et al. 2013). While these intensive movement events often last seconds, they constitute an important component of an animal's energy budget. Low-frequency accelerometer sampling is often selected due to constraints on battery life and data-archiving and can record for >1 yr. Paired laboratory trials provide a crucial tool to validate assumptions of animal energetics from accelerometers (Broell et al. 2013, Brownscombe et al. 2017, InnovaSea Systems Inc. 2018). While high-frequency sampling is feasible with an acoustic tag, this equates to a larger battery and storage requirement, increasing tag dimensions. Alternatively, developments in tags could allow the recording and transmission of each triaxial axis of acceleration independently. With future advances in microprocessors, battery power and storage or data compression capabilities (Lennox et al. 2017), integrated high-resolution accelerometers offer a tool to identify animal activity rates outside of simplified point-by-point calculations used to estimate the rate of movement or current combined triaxial metrics.

3.4.4. Behavioural patterns

Behavioural states which drive movement choices, such as foraging, feeding and transiting, are often assumed from systematic patterns and structures observed in telemetric data (Gurarie et al. 2016). Enhanced resolution of VPS positions enabled by higher transmission rates and typically lower probable error bounds can equate to a trajectory that better reflects the true path of an animal, and thus its behaviour. There are 4 broad categories of behavioural movement analysis techniques: (1) metric-based, (2) classification and segmentation techniques, (3) phenomenological time-series analysis and (4) mechanistic movement models (Gurarie et al. 2016).

Metric-based analytical techniques use movement path characteristics estimated from variables such as distance, speed, turning angles and residency to classify behaviours or distinct movement trajectories. This method is often paired with classification and segmentation techniques, for example, *k*-means cluster-based analysis (n articles = 3). To conduct *k*-means clustering, '*k*' describes the number of centroids (clusters) to group the data, with each location allocated to the nearest randomly generated centroid in n-dimensional space. The cluster is then recalculated using the mean of all vectors in the group and reiterated until the centroids show minimal change (Zhang et al. 2015). For example, Landry et al. (2019) identified periods of activity of the shorthorn sculpin using the 'adehabitatLT' package in R (Calenge 2006), which groups detections into bursts identified as continuous consecutive detections terminated by 30 min of no consecutive detections. To distinguish between movement trajectory types, metrics including (but not limited to) mean turning angle, mean bearing, mean depth, mean ROM and path linearity were classified using *k*-means cluster analysis (Landry et al. 2019). Using this technique, 3 behavioural types were identified from the shorthorn sculpin data. Feeding behaviour was identified by quick turns within a small area, with foraging classified by a higher sum of distance and mean ROM than the speculated feeding cluster. Transiting was identified by large, straight movements across deeper waters identifiable by a higher cumulative distance travelled, rate of movement and linearity ratios.

Phenomenological time-series models are used to identify relationships observed within time-series data without exploring the underlying drivers of changes in detection sequence indicative of a behavioural change (Hilborn & Mangel 1997, Zhang et al. 2015). An example of this model type used in VPS studies includes behavioural change point analysis (BCPA) (n articles = 1). BCPA uses a likelihood-based method to identify changes in movement parameter values by identifying likely behavioural change-points from abrupt changes in the underlying autocorrelation structure, and then testing if they occurred using the Bayesian inference criterion (Gurarie 2013, Zhang et al. 2015). Cote et al. (2019) used the 'BCPA' package in R (Gurarie 2013) to calculate metrics of snow crab movement behaviour, including velocity and changes in movement direction for each track segment (successive positions) within a state-space modelled track.

Mechanistic movement models used in VPS studies include hierarchical models such as state-space models (SSMs, n articles = 1) and hidden Markov models (HMMs, n articles = 4). These time-series models predict the future 'state' (e.g. location, behavioural state, physiological or energetic condition) based on its previous states in a probabilistic manner using a process model (Patterson et al. 2008). A HMM is a SSM in which the states are discrete rather than continuous (Auger-Méthé et al. 2021). Random walks are a form of process model often used as a foundational step for generating complex, multistate models, such as SSMs. A random walk is a mathematical description that is often a Markov process (a stochastic process in which the probability of a future state is a function of its current and past states, Patterson et al. 2008). For example, Cote et al. (2019) used a one-behavioural first difference correlated random walk SSM to generate movement tracks which were then integrated into a generalised additive mixed model to understand snow crab movement behaviour in a deep offshore environment. A key advantage of using an SSM is that it integrates error correction into the modelling process, rather than relying on pre-processing and subjective data cleaning prior to modelling (Patterson et al. 2008).

A promising technique that has yet to be utilised with VPS data is the time-varying move persistence model (Jonsen et al. 2019). This approach identifies 'move persistence', which describes autocorrelation in both animal speed and duration, by identifying variance in move persistence along a movement trajectory and indexing behaviour from 0 (low movement persistence) to 1 (high movement persistence).

3.4.5. Species interactions

As the resolution and accuracy of positioning multiple individuals and species improves, so does our ability to identify the fine-scale movement behaviours associated with species interactions. Movement behaviour is shaped by intra- and inter-species interactions that directly influence the fates of individuals, from competing for resources to predator avoidance. On a finer scale, species interactions also include symbiotic relationships such as cleaning behaviour, parasitism and cooperative feeding (Henry 1966). Identifying species interactions and testing of classic ecological theory, including coexistence, has been conducted by comparing species overlap using measures of space use (EDA and residency) and movement metrics such as ROM. For example, Moulton et al. (2017) used VPS positioning data to study habitat-scale space use (using EDA, residency and ROM metrics) of 2 teleost species over diel and seasonal scales and subsequently compared within and between species differences using *t*-tests. This study combined stable isotope and VPS data to identify differences in spatial (telemetric) niche and dietary niche, with data-rich mixed effect models used to examine coexistence (Guzzo et al. 2016).

Identifying sociality from tracking data requires careful consideration of an animal's ecology and the positioning accuracy of the system. For example, Armansin et al. (2016) studied the sociality of the spotted wobbegong (n tagged = 23) within a coastal protected reserve with the aim of identifying associations between both juveniles and adults over a 15 mo period. This study used social network analysis which can be used to characterise the social structure of a population by identifying associations and interactions suggested by closely associated positioning data (Godde et al. 2013). The maximum distance at which wobbegongs impact each other's movements and share information socially was defined as the combined value of 1 body length (148 cm, the max recorded total length of all tagged sharks) and the median positional error calculated for VPS positions (280 cm). In this case, a half-weight index was used to estimate the proportion of time individuals spent together over a dyadic scale, whereby '0' represents individuals never observed together and '1' describes continuous individual association. In addition, simple ratio indices were also used to calculate the probability that 2 individuals were observed together, given that one has been detected. Dyadic data were then compiled into symmetric and weighted association matrices for the 15 mo study period to assess how the dynamics of individual associations changed over time (Armansin et al. 2016).

At present, the ability to quantitively describe how a network changes over time is limited. For example, can temporal shifts in network use by an animal be used to understand changes in the navigational abilities of tracked animals under differing environmental conditions or scenarios (Jacoby & Freeman 2016)? Direct comparisons of network analysis conducted across different locations are not feasible, as the network structure itself is dependent on the deployment design of a receiver network. Improvements in the predictive power of social network analysis within VPS have vast potential in understanding sociality, which forms the building blocks of animal societies, and our ability to estimate the resilience of animals to disturbances (Silk et al. 2018).

4. CONCLUSION

VPS allows the study of the fine-scale movements of aquatic animals across size spectra and developmental stages, offering unique behavioural insights into a range of behaviours, including coexistence, sociality and predator–prey interactions. VPS has been used to investigate key ecological themes that shape environmental policy and management across local and regional scales. A plethora of topics within these broad ecological themes remains to be investigated, and this technology could provide unique insights into species under real-world experimental settings. Moreover, such fine-scale positioning systems and current developments (i.e. HR) can generate big data, allowing the use and further development of advanced analytical techniques to characterise the intrinsic (physical state; memory, perception and energetics) and extrinsic drivers of animal behaviour. However, as the volume of data continues to increase, robust ecological grounding is required to determine meaningful data standards, from filtering, cleaning and pre-processing (e.g. position filtering) to modelling positioning data and integrating multiplex data streams. Continued efforts to identify and incorporate error will facilitate the next frontier of ecological inference from high-resolution telemetric data, which has vast potential to improve our understanding of fundamental aspects of animal ecology in the aquatic realm.

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