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REVIEW

Tracking movements of decapod crustaceans: a review of a half-century of telemetry-based studies

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ABSTRACT: Decapod crustaceans are ecologically and economically important invertebrates but are vulnerable to anthropogenic pressures and climate change. Understanding their spatial ecology is essential for their management and conservation, with telemetry emerging as a useful tool to quantify space-use and movements. Here, we synthesized the use of telemetry to study decapods among articles published from 1971 to 2019 (n = 102 studies), by taxonomic group of the study species, study location, objectives, number of animals tagged and their tag recovery rate, types (and trends) of telemetry used, and IUCN conservation status. These studies revealed insight into the behaviours and roles of decapods across habitats and geographic regions. The most common study species were crayfish and lobsters (41%, Astacidea), and these studies also had the highest number of individuals tagged per study (mean = 149 individuals). Most studies (86%) were conducted in the northern hemisphere. Acoustic tags were the most commonly used equipment (66% of studies) and were first employed in 1971, followed by radio-telemetry (mid-1990s), passive integrated transponders (mid-2000s), and data storage tags (late 2000s). Almost half (48%) of studies focused on species that had a conservation status of Least Concern, perhaps reflecting an applied science focus on animals of commercial interest rather than conservation importance. The positive allometric relationship between body length and movement rate (exponent = 0.86) demonstrates the type of broader ecological insight that combining these studies can provide. Tracking decapod movements will likely become increasingly important for managing fisheries, protecting sensitive species, and understanding invasion biology.

KEY WORDS: Animal tracking · Telemetry · Satellite tracking · GPS · Movement ecology · Allometric scaling · Fisheries · Invasive species

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1. INTRODUCTION

Decapod crustaceans are widely distributed across freshwater, estuarine, and marine waters globally and along gradients in habitat types, depths, and water temperatures (Boschi 2000, Crandall & Buhay 2008, De Grave et al. 2008, Cumberlidge et al. 2009, Hall & Thatje 2009, Vereshchaka et al. 2014). Globally, decapods play a variety of important biological and ecological roles (Boudreau & Worm 2012, Rey-

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nolds et al. 2013), including as strong influencers of food webs via predation and omnivory (Creed 1994, Momot 1995, Silliman & Bertness 2002, Dorn & Wojdak 2004), bioindicators (Barros 2001, Key et al. 2006, Reynolds et al. 2013), and bioengineers (Jones et al. 1994, Creed & Reed 2004, Pillay & Branch 2011). Furthermore, decapods are an important component of global food security and socioeconomic well-being (Bondad-Reantaso et al. 2012); worldwide catch of lobsters, crabs, and shrimps have all increased steadily from the 1970s to present day (FAO 2018). These fisheries vary in size, from large scale, such as the intensely researched American lobster *Homarus americanus* of the Northwest Atlantic (Steneck & Whale 2013), to more localized or regionally focused (Lunn & Dearden 2006, Espinosa-Romero et al. 2014).

These ecologically and economically important taxa are of increasing focus for conservation and management in the Anthropocene. In freshwater, an alarming proportion of taxa are imperilled due to threats on their limited distributions, including crayfish (Taylor et al. 1996, Richman et al. 2015), crabs (Cumberlidge et al. 2009), and shrimps (De Grave et al. 2015). In addition to directly affecting populations (Dow 1980, Agnalt et al. 2007), fisheries continue to impact the marine benthic habitats (Sciberras et al. 2018) upon which crustaceans depend. Furthermore, the effects of anthropogenic disturbance (Taormina et al. 2018) and coastal development (e.g. wind turbines, Hardy et al. 2008, Hooper & Austen 2014, Hooper et al. 2015) on the distribution of species and their associated fisheries are not well understood (Wehkamp & Fischer 2013, Roach et al. 2018).

The ability to conserve and manage decapods is complicated by shifts in the functional roles of these taxa; climate change and top-down fishing pressures have elevated the trophic positions of many predatory decapods within ecosystems (Steneck et al. 2004, Lindley et al. 2010). Warming water temperatures due to climate change may also lead to increased incidence of disease (Stentiford et al. 2012, Steneck & Wahle 2013). Lastly, decapods are among the most successful and influential invaders of freshwater and marine ecosystems, exerting measurable influences on biological communities (McCarthy et al. 2006, Snyder & Evans 2006, Twardochleb et al. 2013, Matheson et al. 2016). Addressing these challenges, both old and new, requires information on how decapods interact with other ecosystem components across space and time.

Scales of movements by adult decapods vary widely, from meters to >100 km (Groeneveld & Branch 2002, Allen et al. 2015, Davidson & Hussey 2019), encompassing a variety of complex behaviours and habitats (Pittman & McAlpine 2003). The movement ecology of species also varies among individuals, life history stages, and populations, and a comprehensive understanding of these spatial behaviours is required for effective conservation management. However, decapods are often considered difficult to study due to their benthic habitats (Hunter et al. 2013), use of shelters, and nocturnal and cryptic behaviour (Smith et al. 2000). As a result, research into their behaviour has often taken place in aquaria or mesocosms, which lack realism and can restrict movements (Lees et al. 2018) and normal interactions (Jézéquel et al. 2019, 2020). Traditional attempts to study decapod movements in the field used persistent external tags to uniquely identify recaptured individuals; however, mark−recapture studies provide no information on movement processes between the release site and the location of the subsequent recapture. Moreover, only active animals may be recaptured; those not moving seasonally or for other reasons will not be captured and considered in the movement analyses.

Telemetry has emerged as an important tool for answering questions in ecology and to inform conservation and management (Hussey et al. 2015, Hays et al. 2016), including fisheries (Crossin et al. 2017, Lowerre-Barbieri et al. 2019). Telemetry use has increased for many species, owing to continued technological advancements, tag miniaturization, and the development of regional infrastructure and data exchange networks that allow researchers to leverage resources and maximize collaboration (Block et al. 2016, Taylor et al. 2017, Abecasis et al. 2018, Iverson et al. 2019). The variety of telemetry technologies appropriate for aquatic and marine environments (e.g. data storage tags [DSTs], satellite, acoustic, radio, passive integrated transponder [PIT], and electromagnetic tags, among others) can provide information on animal movements across different spatiotemporal scales to quantify aspects of behaviour, habitat use, and large-scale migrations (Hussey et al. 2015). However, use of telemetry on crustaceans has lagged behind its use on other taxa (e.g. fish: Guerra-Castro et al. 2011, Abecasis et al. 2018), and as such, there are a limited number of studies with information on individual-level movements of crustaceans (Holyoak et al. 2008). The utility of telemetry is species-, system-, and question-specific. Thus, it can be informative to formally assess the use of telemetry to advance the ecological understanding and management of taxa of specific interest.

Over the past years, scientific literature reviews on the use of telemetry within the aquatic environment have focused on specific taxa and/or regions, with most focused on fish (Sundström et al. 2001, Jellyman 2009, Drenner et al. 2012). These reviews documented trends in taxa-specific and geographic foci, identified limitations of the technology, and provided suggestions for future research and areas that were understudied. Guerra-Castro et al. (2011) reviewed the use of telemetry on decapods, but focused on statistical analyses of telemetry data. Therefore, an opportunity exists to update the status of telemetry use on decapods globally to highlight knowledge gaps and guide future research.

Here, we review and quantify the evolution of studies in terms of their geography, habitats of focus (i.e. marine/freshwater), study objectives, and types of telemetry used. We present temporal trends in telemetry equipment used (e.g. radio, acoustic, etc.). We explore the number of individuals tagged (and recovered) in studies on different decapod families to provide insight on family-specific telemetry-use (and recovery rate). We also summarize the IUCN conservation status of the study species among the studies included in our review. We identify opportunities for expanded use of telemetry to study decapods, including types of questions that cannot be answered in traditional laboratory or mesocosm experiments, or using non-telemetry field studies (e.g. mark–recapture or focal observations by divers). Finally, to demonstrate how telemetry studies can provide broader ecological insight, we explore whether decapods display the commonly observed positive allometric relationship between animal body size and metrics of movement (McNab 1963).

2. MATERIALS AND METHODS

2.1. Literature key word searches

English language literature searches were completed on 11 March 2020 in the Web of Science (WoS; Clarivate Analytics) and Scopus (Elsevier). Search terms were entered in WoS as topic terms and could be present in the article title, abstract, author-specified key words, and WoS-assigned key words. Search terms in Scopus had to be present in the article title, abstract, and the author-specified key words. Search terms used were: ('crustacean' OR 'marine invertebrate' OR 'lobster' OR 'crab OR 'decapod' OR 'crayfish') AND (telemetry OR 'acoustic tracking' OR 'ultrasonic tracking' OR 'radio tracking' OR 'PIT tag*') NOT (shark OR turtle OR seal OR bird OR skate OR physics).

The WoS and Scopus searches (201 and 182 articles returned, respectively) were combined and duplicate entries removed to yield 253 published articles and reports. Our focus was on decapods that spend a substantive part of their life-cycle in the aquatic environment, and thus excluded coconut crabs *Birgus latro* that only return briefly to the ocean to spawn, and are generally considered terrestrial (Reese 1968). Studies that were exclusively conducted in a laboratory environment were excluded, as were studies on general telemetry techniques, or studies focused solely on calibrating technologies without consideration of documenting the ecology or behaviour of decapod species. Similarly, review articles were excluded. There were 82 studies that met all inclusion criteria.

These results were further supplemented with articles identified via 2 previous literature searches during 2015 and 2019 conducted in WoS, Science Direct, and Springer. Search terms were 'telemetry', 'acoustic', 'tracking', 'ultrasonic', 'tag', 'crustacean', 'crab', 'lobster', 'crayfish', and 'movement'; combinations of 3 or 4 words were searched at a time. Additionally, articles that were cited within selected studies and met the inclusion criteria were included, and those known to the authors, but that had not been previously identified in any of the previous searches, were also included. These earlier combined searches produced 86 articles, 20 of which were not identified by the 2020 WoS and Scopus searches (and were added to the above 82 articles). In total, 102 unique articles were identified and included as part of the review (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m679p219_supp.pdf).

2.2. Classification of studies

For each article retained, the following information was recorded: (1) species tagged; (2) study location; (3) study habitat (i.e. marine/freshwater); (3) study objectives; (4) type of telemetry used (this usage was summarized by year); (5) number of tagged individuals; (6) tag recovery rate (i.e. number of tags recovered / number of individuals tagged), and (7) the IUCN conservation status of the study species (Table S1). Study locations were grouped into 5 'geographic regions' based on the spatial distribution of studies (Table 1). Each study was classified based on 7 'study objective' categories: movement, behaviour, habitat use, interaction, management, invasive species, and environmental conditions (Table 2). Appropriate categories were assigned using the title, key words (when present), and abstract of each study,

Table 1. Coordinate definitions used when grouping decapod movement studies by region; 102 articles published between 1971 and 2019 were included in our review. Latitude and longitude are expressed in degrees, with negative values representing the Southern and Western hemispheres and positive values representing the Northern and Eastern hemispheres. NA: values were not needed to group studies

Geographic region	Latitude bounds	Longitude bounds
Northeastern Atlantic	>25°	>−50°
Northeastern Pacific	NA	<−100°
Northwestern Atlantic	>42°	>−100° & <50°
Southern Pacific	<0°	NA
Tropical Western Atlantic	<42°	>−100° & <50°

with the potential designation of multiple categories per study; 1 article did not contain an abstract and was categorised using the results section. The type of telemetry tracking used in the study was grouped into 5 categories: acoustic, radio, electromagnetic, PIT tag, and DST (see Lennox et al. 2017 for a description of different tag types). We also recorded the study duration to the nearest day if exact dates were provided; otherwise, the number of days was approximated to the nearest month in a given year. Finally, we recorded the furthest distance moved by a tagged individual that was reported in each study.

2.3. Allometric relationship between body size and movement

As in Rosten et al. (2016), we used a linear model to explore the relationship between the log mean body length of an animal and the log movement speed (furthest distance moved divided by study duration) in R (version 4.1.1., R Core Team 2021). Mean body length was extracted from each study, and was the measure of the carapace length (carapace width for some crab species).

3. RESULTS

The 102 original and peer-reviewed papers that used telemetry to study aquatic decapods included studies on 13 decapod families (Fig. 1; Table S1). Mean ± SD study duration was 134.1 ± 177.7 d (range: 1–950 d; Fig. S1). The mean of the maximum distance of animal movement recorded from each study was 14.3 ± 44.9 km (range: 0.0025–302 km; Fig. S1).

3.1. Spatial, habitat, and taxonomic differences in study purpose

The vast majority of studies were done in the northern hemisphere (86.3%; Fig. S2), mostly in the Northeast Atlantic region (42.2% of all studies) and focused on movement (Table 1, Fig. 2A). Several freshwater studies contributed considerably to the high number of papers on species in the Northeast Atlantic region, whereas marine species were the focus of most studies on decapod movement in all other regions (Tables 1 & 2, Fig. 2A). Across all geographic regions, movement was the most common study purpose (87.3%), followed by behavioural studies (70.3%). Conversely, relatively few studies focused on interactions (9.9%), invasive species (12.9%), or management (24.8%; Table 2; Fig. 2A). Most notably, the majority of studies focused on crayfish and lobsters (40.6%; Infraorder Astacidea) and crabs (34%; Infraorder Brachyura), and only a few studies

Table 2. Classification definitions for 102 articles published on crustacean movement between 1971 and 2019 that were included in our review. The classification was based on 7 basic study objectives

Study objective	Description
Movement	Study reports basic movement components, for example: speed, turning angle, distance, orientation, navigation, dispersal, migration
Behaviour	Study discusses movement related to foraging/feeding, homing, wintering, moulting, survival, diurnal/nocturnal activities, and/or podding/aggregating
Habitat use	Study discusses movement related to site fidelity and/or home range
Interaction	Study reports any interaction within the group, and/or with other species outside of the group
Management	Study relates movement to conservation or management (e.g. influence of marine protected areas), catchability, and/or fisheries management
Invasive species	Studied species is invasive or there is interaction with an invasive species
Environmental condition	Study incorporates or tests movement with environmental covariates

focused on prawns (0.94 %; Infraorder Caridea) or king crabs (5.7 %; Infraorder Anomura, Fig. 2B).

3.2. Tag types and usage

The use of acoustic telemetry tags (66.4 % of studies) far outweighed the use of other telemetry types, and this was consistent across geographic regions (Fig. 3A). Radio tags were frequently used in studies in the Northeast Atlantic (31.1 % of studies there), with a lesser use of PIT technology, and all studies using PIT tags focused on freshwater species. Radio telemetry generally performs well in shallow freshwater sites, but is not suitable for marine studies, as radio signals attenuate in saltwater. Studies on crayfish

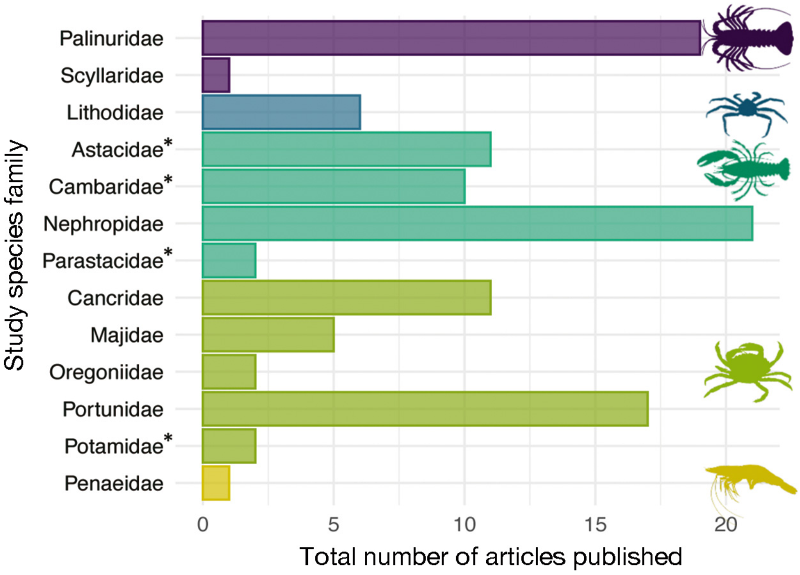

Fig. 1. Summary of the 102 articles published on decapod movement from 1971 to 2019 and included in our review, grouped by family and coloured by infraorder (purple: Achelata; blue: Anomura; emerald green: Astacidea; pea green: Brachyura; yellow: Caridea). Freshwater families are indicated by an asterisk (*)

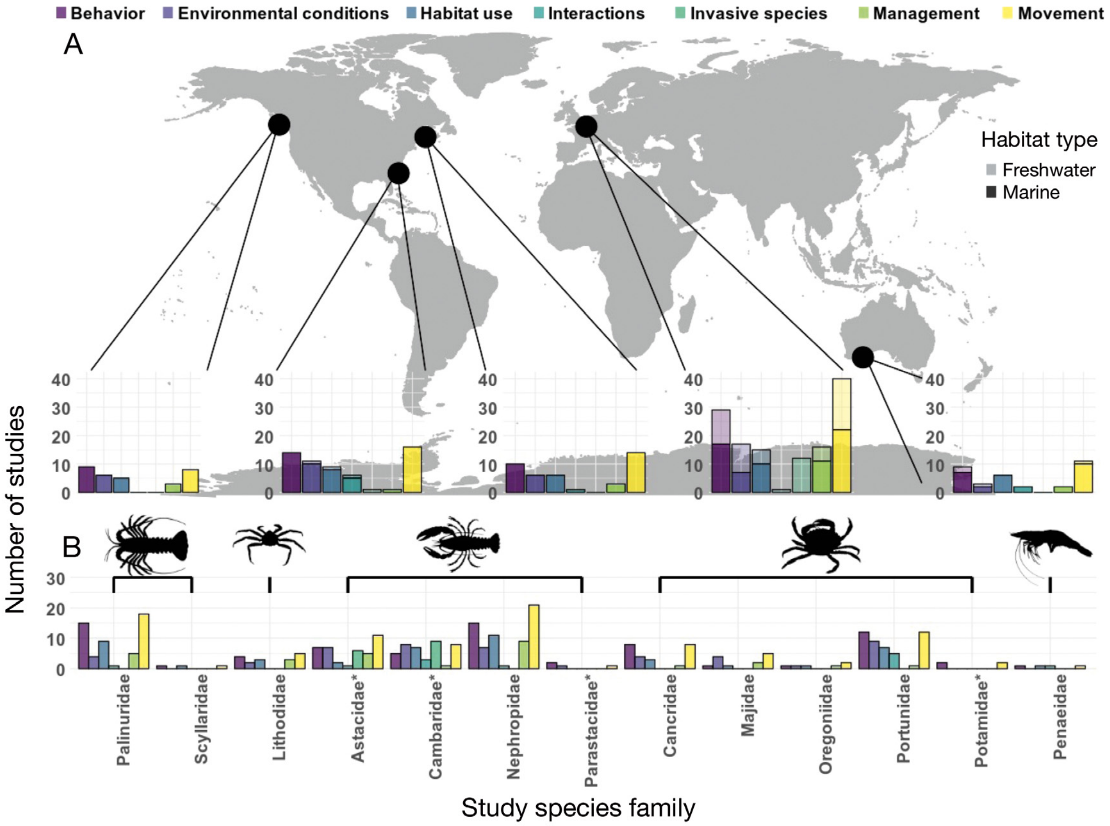

Fig. 2. Summary of the purpose of decapod telemetry studies by (A) geographic region and (B) family. Bars represent the number of studies and are coloured by study purpose. Large circles within the map indicate the centroid of studies within a particular region and the associated lines indicate the relevant graph for that region. Within graphs, habitat type is represented by the transparency of the bar (marine more opaque and freshwater more transparent). In (B), freshwater families are indicated by an asterisk (*) rather than bar transparency. Silhouettes representing the infraorder (see Fig. 1) of studied taxa are shown above representative families; from left to right: Achelata, Anomura, Astacidea, Brachyura, Caridea

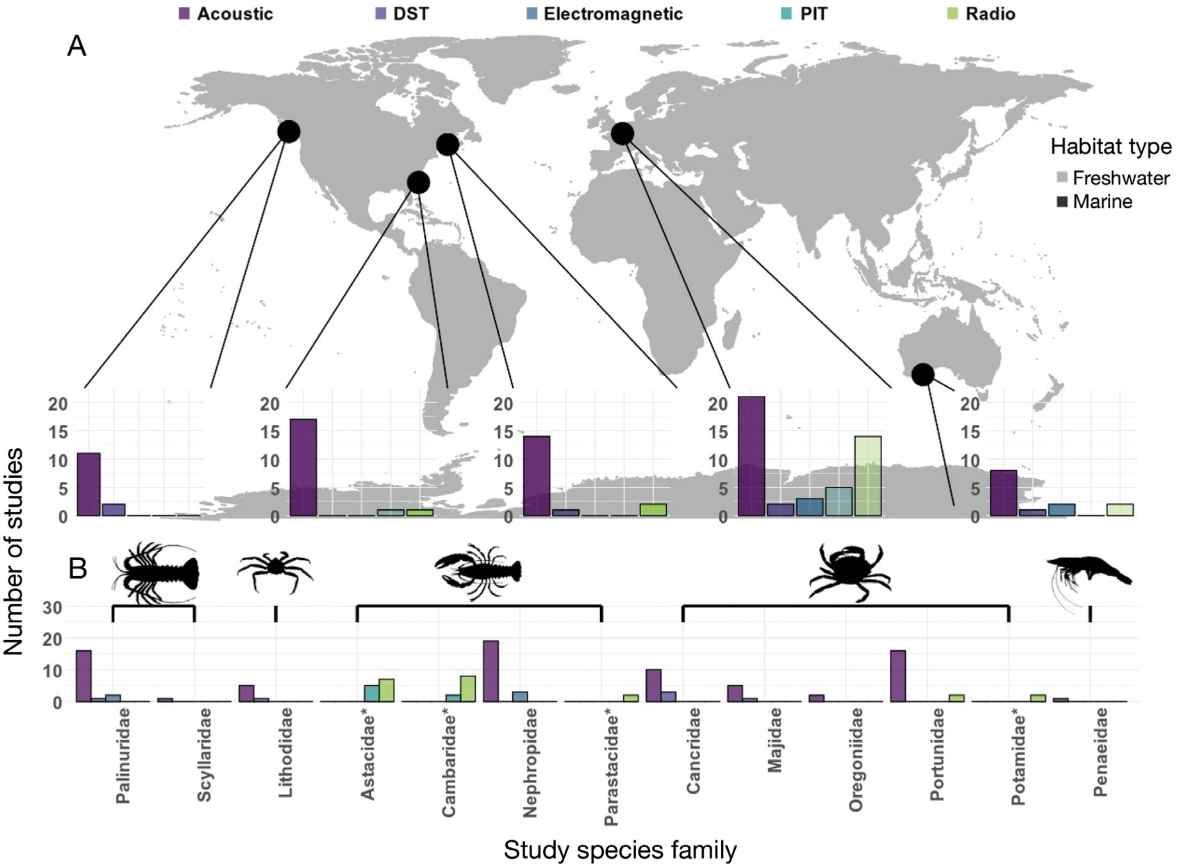

Fig. 3. Summary of the tag types used in decapod telemetry studies by (A) geographic region and (B) family. Bars represent the number of studies and are coloured by tag type. Large circles within the map indicate the centroid of studies within a particular region and the associated lines indicate the relevant graph for that region. Within graphs, habitat type is represented by the transparency of the bar. Radio and PIT tags were the only tag types used in freshwater, although the former were occasionally used in marine systems as well (see Northwest Atlantic & Tropical Atlantic). In (B), freshwater families are indicated by an asterisk (*) rather than bar transparency. Silhouettes representing the infraorder (see Fig. 1) of studied taxa are shown above representative families

(i.e. Families Astacidae, Cambaridae, and Parastacidae) and some freshwater crabs (Family Potamidae) often used radio and PIT tags (Fig. 3B).

Acoustic tags were the first method used to track decapods (Herrnkind & McLean 1971), and they remained the most commonly used tag type through 2019 (Fig. 4). Electromagnetic tags have been used to track decapods since the mid-1980s, radio tags since the mid-1990s, PIT tags since the mid-2000s, and DSTs since the late 2000s (Fig. 4). All of these tag types are still in current use (Fig. 4).

3.3. Sample size

Studies on crayfish and lobsters (Infraorder Astacidea, n = 11 studies) had the highest mean ± SE number of individuals tagged per study (149 ± 56.8 individuals), followed by crayfish in the Infraorder Cambaridae (n = 10 studies) with the second highest mean number of individuals tagged per study (136 ± 83). However, studies on crayfish species in the Infraorder Parastacidae tagged a mean of 12.5 ± 4.5 individuals (Fig. 5A). Studies on species in the Infraorders Achelata (spiny and slipper lobsters), Anomura (king crabs), Brachyura (crabs), and Dendrobrachiata (prawns) involved fewer individuals tagged, although studies (n = 2) on crab species in the Oregoniidae tracked the movement of 97.5 ± 66.5 individuals (Fig. 5A).

Where possible, we recorded the recovery rate of tags for each study as the number of tags recovered divided by the number of individuals reported as tagged. Note that not all studies were able or intended to recover tags. Studies had high tag recovery rates (mean ≥0.9 recovery rate) in most infraorders,

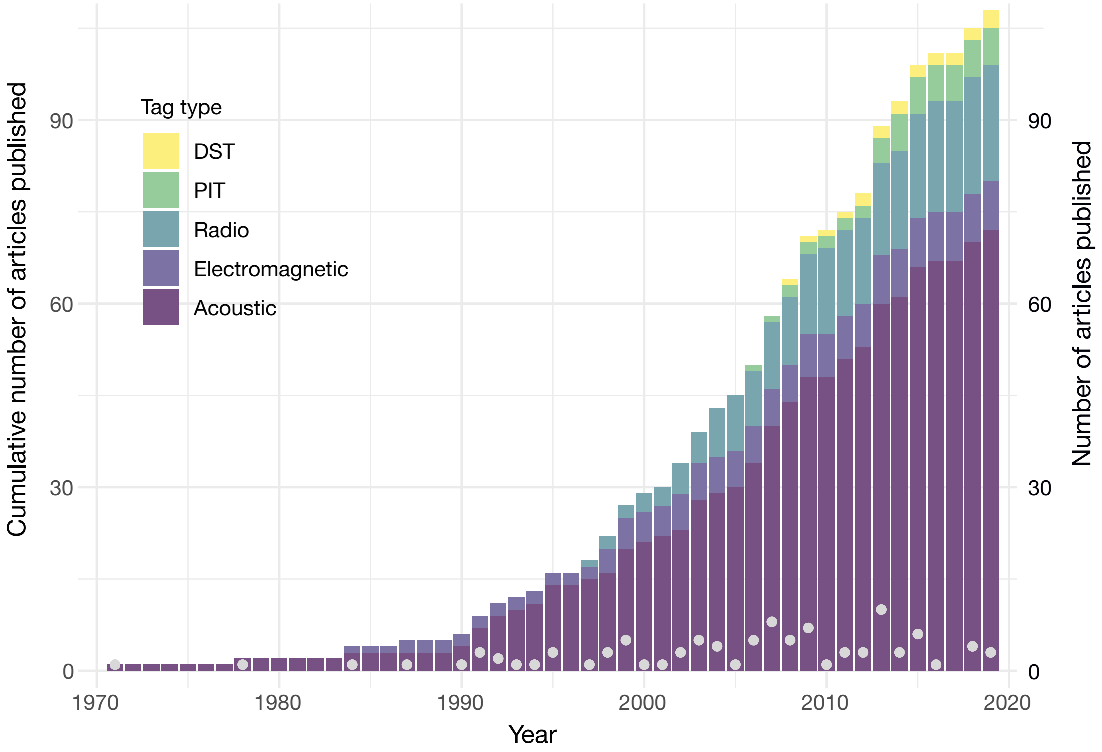

Fig. 4. Cumulative number of articles published from 1971 to 2019 (n = 102), coloured by the tag type used in decapod telemetry studies. Articles were classified as using data storage tags (DSTs), passive integrated transponder (PIT), radio, electromagnetic, or acoustic tags. Note: some studies used 2 methods, and for the purpose of this figure, were double counted to represent using both technologies. Grey circles represent the number of articles published each year for all tag types summed

and relatively lower recovery rates (mean ≥0.8) in the Infraorders Cancridae (crabs) and Nephropidae (lobsters) (Fig. 5B). The mean study tag recovery rate was lowest in lobster species in the Infraorder Nephropidae (0.8 ± 0.04) and crab species in the Infraorder Cancridae (0.8 ± 0.1) (Fig. 5B).

3.4. IUCN conservation status of study species

The greatest proportion of studies (49%) focused on species the IUCN has designated as Least Concern, followed by those that were either Not Evaluated (26.5%) or Data Deficient (15.7%). Few studies focused on species the IUCN designated as Endangered (3.9%) or Vulnerable (2.9%), and only 2 studies (2%) in our review focused on Near Threatened species.

3.5. Allometric relationship between body size and movement

We found that the log mean length of an animal was positively related to the log movement speed (Fig. 6; exponent = 0.858, R^2 = 0.160, df = 21, p = 0.034).

4. DISCUSSION

Our review revealed that tracking the movements and behaviour of decapods with telemetry has occurred across a wide geographic and taxonomic distribution since the development of a suite of technologies suitable for decapods over the past half-century (Lund & Lockwood 1970). These studies showed that decapods could be tracked for >1 yr (e.g. Rosewarne et al. 2013, Goldstein & Watson 2015) and over distances up to 302 km (Hunter et al. 2013) from the release point, and revealed a broad range of ecological insight (e.g. behavioural cascades between 3 trophic levels; Geraldi & Powers 2011). However, our review identified many opportunities for future telemetry research to advance knowledge and support the sustainable management and conservation of these ecologically and commercially valuable invertebrates. In particular, this is due to technological ad-

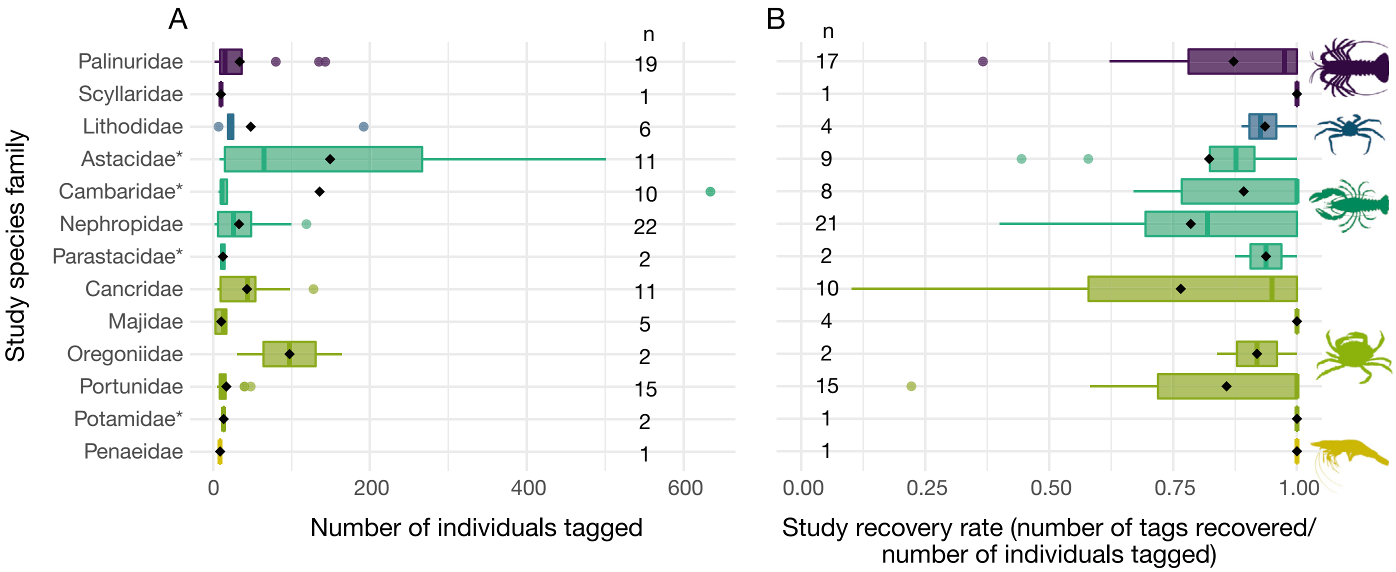

Fig. 5. Summary of (A) number of individuals tagged per article, and (B) study recovery rate (number of tags recovered/number of individuals tagged) from articles published using decapod telemetry data, from 1971 to 2019. Results are presented as boxplots showing the 25th, median, and 75th percentiles and circles represent outliers. The lower and upper whisker extends to the smallest and largest (respectively) value no further than 1.5 times the interquartile range (distance between 25th and 75th percentiles). Black diamonds represent means. Sample sizes (n; number of articles published) are indicated for each family; note that not all studies reported the number of individuals tagged and recovered and thus, n in (B) is lower than the total number of studies in (A). Study species are grouped by family (freshwater families are indicated by an asterisk [*]) and coloured by infraorder (see Fig. 1)

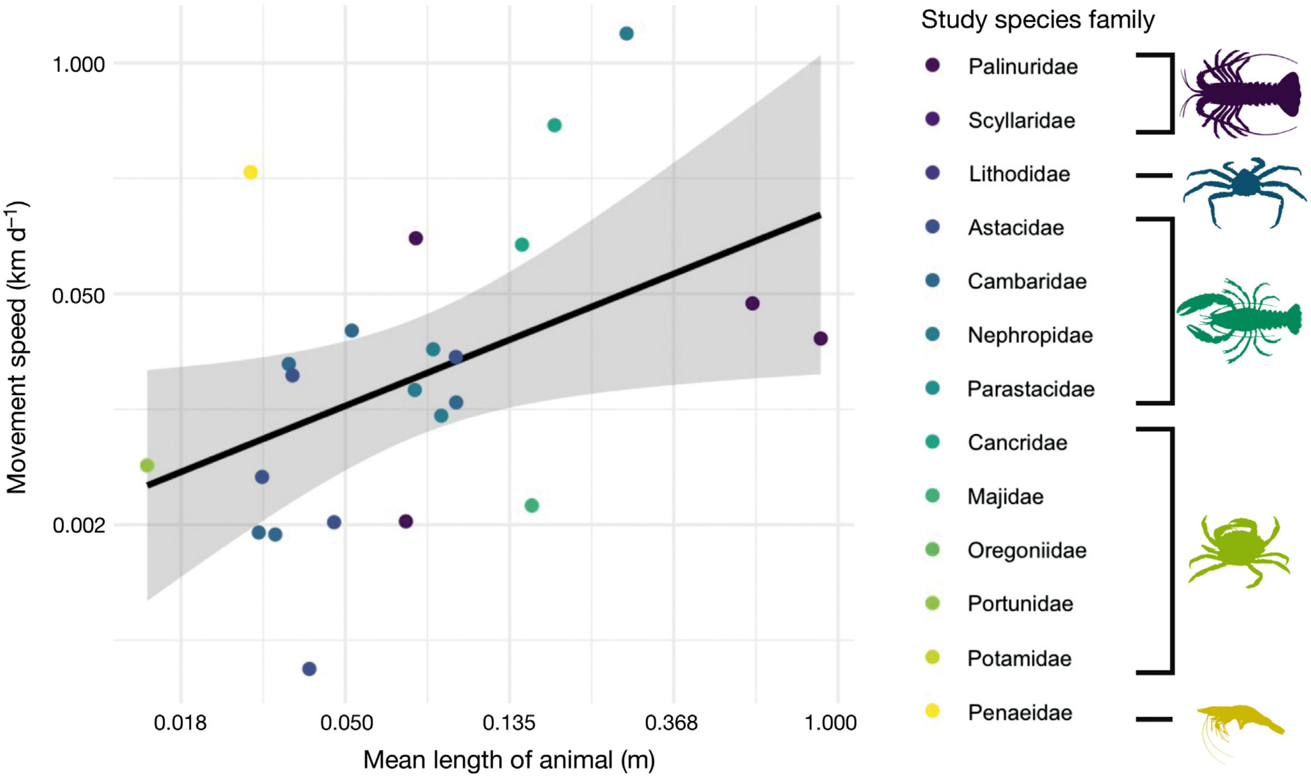

Fig. 6. Allometric relationship between mean length of the animal and the movement speed (presented as furthest distance moved divided by study duration). Shaded areas present the 95% confidence intervals

vances decreasing tag sizes, tagging methods for decapods becoming more established, and the development of new sensors to address challenging topics related to decapod ecology. Our analysis found a positive allometric relationship between body lengthand movement rate, demonstrating the type of broader ecological insight that combining these studies can provide.

4.1. Opportunities in a variety of habitats

There has been a preponderance of telemetry-based decapod movement studies in coastal marine and riverine habitats (~70% of studies; Fig. S2). Decapods occupy a variety of aquatic environments across the globe in habitats such as brackish waters, intertidal zones (including semi-terrestrial), lakes, continental shelf, and the deep-sea. These habitats are important to decapods for food, shelter, and reproduction, and in turn, decapods play key roles in these habitats by predating or scavenging, bioturbating, transporting nutrients, acting as prey for higher trophic level species, or by augmenting the physical habitat (e.g. ecosystem engineering; Jones et al. 1994, Creed & Reed 2004). Telemetry could be used to further understand decapod ecology across these less studied habitats. For example, Barbaresi et al. (2004) used telemetry to show how invasive crayfish *Procambarus clarkii* disperse in an irrigation ditch system. Tracking movements is a useful tool to increase knowledge of decapod behaviour and roles in these understudied habitats to determine how effectively they move nutrients through food webs in different ecosystems and contribute to ecological connectivity (Nemeth 2009).

We also found an uneven distribution of decapod telemetry studies globally, with a focus in the Northeast Atlantic and a complete or nearly complete lack of telemetry studies (published in English) in South America, the Indo-Pacific, Africa (1 study in South Africa), Northwestern Pacific, and Antarctic. As our search terms only generated articles published in English, we may have underestimated the true prevalence of telemetry studies in some regions. Likewise, theses/dissertations and other published work (non-scientific articles) were not considered due to the difficulty in accessing them in many cases. Similar geographic biases occurred for research on topics highly relevant to decapods, including invasion ecology (Pyšek et al. 2008) and conservation biology (Di Marco et al. 2017). Increased information on decapod movement in these understudied areas would fill gaps in biological and ecological knowledge that could be useful for conservation. For example, in the Northeast Atlantic, Rotllant et al. (2015) used telemetry to evaluate the success of artificial reefs for restocking overfished decapods in the Mediterranean and found these reefs may be suitable for spiny lobsters *Palinurus mauritanicus* but not spider crabs *Maja squinado*. Further, climate change is causing range shifts in many marine species, including decapods (Neumann et al. 2013, Aronson et al. 2015, Scott et al. 2015). These range shifts are affecting a diverse array of ecosystems, for example by making polar regions more susceptible to invasion by temperate decapod species (Goldsmit et al. 2019, 2020). Furthermore, the underrepresentation of species from tropical and Arctic regions in telemetry studies means we have limited baseline information against which we can evaluate how crustaceans in general are affected by climate change.

4.2. Taxonomic coverage

Telemetry has been used to study a range of decapod taxa, from porcupine crabs *Neolithodes grimaldii* to Mediterranean slipper lobsters *Scyllarides latus*. Taylor & Ko (2011) successfully tagged eastern king prawn *Penaeus plebejus* and provided insight on the diel activity patterns of prawns in different habitats. Despite the number of studies discussed in this review, the movements of only 13 among ~300 families of decapods have been examined using telemetry-based methods, perhaps due to the focus on species of commercial value. Expanding the use of telemetry to other decapods could first be accomplished for those groups with similar body types to those that are readily studied with telemetry, for example, adult squat lobsters (Agelidae, Galatheidae) due to their similar body shape to true lobsters (Nephropidae). The successful application of acoustic telemetry to penaeid prawns (Penaeidae; Taylor & Ko 2011) presents an opportunity to expand efforts to similar prawn families. Complementary work on gastropods such as conches, abalone, and tritons (Coates et al. 2013, Stieglitz & Dujon 2017, Schlaff et al. 2020) could provide insight into the suitability of telemetry for decapods that appropriate shells as protective coverings (e.g. Paguridae). However, factors limiting the overall diversity of decapod species studied with telemetry in the wild are surely closely linked to gaps in knowledge of basic life history and development, particularly characteristics such as timing of moult cycles, use of shelters, and occurrence of burrowing behaviour, which impacts the use of telemetry equipment (addressed further in Section 4.5).

4.3. Study purpose

Understanding movement and related behaviour were the primary purposes for the majority of decapod telemetry studies. This focus was not surprising given that telemetry was developed to characterize individual-level movements and is effective for estimating important metrics such as home range size (e.g. Scopel et al. 2009, Moland et al. 2011a), movement rates (e.g. Hines et al. 1995, Cote et al. 2019), and the temporal and spatial scales of migrations (e.g. González-Gurriarán et al. 2002). Telemetry is particularly useful for relating movement to aspects of species life histories and has identified differences in movement patterns between sexes relating to the timing of reproduction for a number of species including red swamp crayfish *Procambarus clarkii* (Barbaresi et al. 2004), American lobster (Goldstein & Watson 2015), and brown crabs *Cancer pagurus* (Ungfors et al. 2007). Kelly (2001) found that spiny rock lobsters *Jasus edwardsii* could travel up to 12 km in a year, females are most active near the end of the egg-bearing season (austral autumn), and males have 2 activity peaks: at the beginning of the moult cycle (austral summer) and after the mating season (austral winter). Further, Moland et al. (2019) used simple movement metrics derived from telemetry data to identify consistent individual behavioural patterns and traits such as ‘boldness’ in European lobsters *Homarus gammarus*. Advancing our basic understanding of decapod movement ecology and life history is important for many aspects of species conservation and management. However, further opportunities exist to expand the role of telemetry in quantifying group movement and behavioural interactions in decapods.

Similarly, decapod telemetry studies often assessed habitat use (e.g. Bertelsen 2013) and its associations with environmental conditions (e.g. Moland et al. 2011b), linking space use and movement with spatiotemporal characteristics. For example, Lynch & Rochette (2007) documented the movement of European green crab *Carcinus maenas* in relation to tidal phases and found that crab activity increased and decreased with rising and falling tides, respectively. A few papers (~10% of total) focused on the interactions between tagged individuals of the same or different species and other animals. For example, Geraldi & Powers (2011) tagged blue crabs *Callinectes sapidus* and showed that when predators (red drum *Sciaenops ocellatus*) were present, their movement was not affected but their ability to forage on their prey (hard clam *Mercenaria mercenaria*) was reduced, providing insight on behavioural cascades and trait-mediated indirect effects of trophic interactions. Telemetry studies can further quantify spatial overlap among individuals or species, including overlap of home ranges where animals use the same habitats (e.g. Silverman 1986, Fieberg & Kochanny 2005), or co-occurrence in time and space (e.g. contact rates between individuals, Bertrand et al. 1996). However, telemetry studies can only infer behaviours from the tagged portion of the population, and limited sample sizes in such studies result in tagged individuals most likely interacting with untagged individuals. Further, decapods, such as lobsters, can exhibit a range of behaviours relating to mate choice and dominance hierarchies (Scrivener 1971). However, the scale of movements in these behaviours can be small compared to the measurement error of many telemetry systems, which currently limits the study of interactions among individuals (Lees et al. 2020). Individuals can exhibit highly variable movement patterns, with periods of sedentary behaviour interspersed with infrequent long-range movements (Hines et al. 1995, Skerritt et al. 2015, Lees et al. 2018). Thus, studies should be long enough in duration to capture these rarer behaviours and accurately reflect space use. Understanding the distribution of individuals in relation to habitat availability, mate choice, fishing pressure, and other features of the landscape is relevant to disease management, stock assessment, fisheries management, conservation actions, and protected areas designation. As a consequence of interspecies spatial co-occurrence, decapods may be harvested as part of a mixed fishery (e.g. brown crab and European lobster), where behavioural interactions between target species can affect their catchability, potentially affecting estimates of abundance (Miller & Addison 1995, Skerritt et al. 2020).

Decapods occupy a broad range of ecological niches and trophic positions such that interactions with other species are key to understanding their biology as predators, scavengers, and prey in different ecosystems. A few studies have used telemetry to study predator–prey interactions between crustaceans and non-crustaceans. For example, the predator response of tracked blue crabs was found to vary with patterns in bivalve prey distribution (Clark et al. 1999b). Similarly, American lobsters decreased total distances moved from their shelter and contracted their maximum home range size in the presence of a predator, Atlantic cod *Gadus morhua* (McMahan et al. 2013). We encourage the use of telemetry to advance understanding of crustacean–non-crustacean interactions, expanding to other types of interactions such as territoriality or spatial competition. Acoustic transmitters with predation sensors are increasingly used to identify predator–prey interactions; these tags alert an analyst to a predation event by changing the tag ID code when a predation sensor is triggered by stomach acid (Halfyard et al. 2017) or changes in tag orientation (R. J. Lennox unpublished). Depth and temperature sensors may equally be able to help identify predation events, with rapid changes in either condition indicating that a tagged animal has been eaten (Béguer-Pon et al. 2012, Seitz et al. 2019, Strøm et al. 2019); given that decapods are benthic, rapid changes (reductions) in depth may be especially informative.

Telemetry is also well-suited for studying group movement in natural settings (Heupel et al. 2006). Tracking numerous individuals simultaneously allows for the collection of basic information such as onset, duration, preference for or fidelity to aggregation sites, inter-individual variation in behaviour, and aggregative behaviours (e.g. Sumpter 2006, Couzin et al. 2005, Torney et al. 2018). For example, Clark et al. (1999a) showed that the high densities of blue crabs during feeding aggregations led to crabs becoming more aggressive with increased frequency of intraspecific injury and cannibalism, and subsequently, interference with foraging behaviour. Environmental variables that likely cue group movements (e.g. water temperature, current speed, and light) (Dew 1990, Forward et al. 2003) can be collected at similar spatial scales, and integrated with telemetry-based movement data. Telemetry has been more extensively used to examine aggregation behaviour for highly mobile species (e.g. juvenile blacktip sharks *Carcharhinus limbatus*) (Heupel & Simpfendorfer 2005) including the use of combined transmitter–receiver tags for examining movement behaviour between individuals of other taxa (Guttridge et al. 2010), although these tags are large and may be unsuitable for many decapods.

4.4. Technology and opportunities

Advances in aquatic movement ecology have been enabled by developments in animal tracking technology (Hussey et al. 2015). Acoustic telemetry, a tool exclusively suitable for aquatic environments, is the most common tool for studying crustacean movement, and its use dates back to the early 1970s (Herrnkind & McLean 1971). Electromagnetic tags have been used since the mid-1980s (Phillips et al. 1984); spiny (rock) lobsters (Palinuridae) were the study species for both of these initial studies using acoustic and electromagnetic tags. With regards to acoustic telemetry, acoustic tags generally can be detected by a receiver at a distance of up to 1 km. Thus, strategic placement of a limited number of receivers to document animal movements at desired spatial and temporal scales is needed. The global telemetry community is working to establish sustained networks of fixed receivers and associated data systems to get detection information from the receivers back to investigators tagging animals (Abecasis et al. 2018, Iverson et al. 2019). In addition, slow-moving decapods can also be effectively monitored by mobile receivers placed on marine autonomous vehicles (Cote et al. 2019). These vehicles have the potential to replace the needs for hundreds of fixed receivers, depending on the study, and have the advantage of not interfering with or being vulnerable to fishing practices like dragging. In freshwater, PIT tagging and radio telemetry have been used to track upstream and downstream decapod movements in rivers (e.g. Bubb et al. 2002a,b, 2008, Webb & Richardson 2004). Barbaresi et al. (1997) first used radio telemetry to track river crabs (Potamoidea), and Bubb et al. (2006) first used PIT tags to track invasive signal crayfish *Pacifastacus leniusculus* (Astacidae). More recently, DSTs have allowed for more fine-scale tracking of decapods, as first used by Curtis & McGaw (2008) on Dungeness crab *Metacarcinus magister* (Cancridae).

Biologging allows for high-resolution recording of environmental conditions (e.g. temperature, depth) or biological characteristics (e.g. acceleration, heart rate) (Wilmers et al. 2015, Jury et al. 2018, McGaw et al. 2018, Steell et al. 2020) but do not transmit such high-quality data and thus require recapture. Many decapods have relatively small home ranges but still may not be easily recaptured and thus are generally not conducive to study using biologging techniques (i.e. using tags that log rather than transmit data; but see Jury et al. 2018). However, environmental conditions and sensors can be integrated into acoustic telemetry packages to measure the environmental niche or physiology of free-ranging crustaceans in the wild, such as electromyographic sensors used to measure feeding activity of blue crabs (Wolcott & Hines 1989). Either paired use of biologgers and telemetry packages or improved performance of hybrid telemetry technologies would better allow for integration of environmental conditions, biological responses, and movement behaviours across space and time. Such approaches would facilitate integrating physiology with telemetry to enhance our understanding of animal behaviour (Madliger et al. 2018). This approach has been applied to marine fish (e.g. Metcalfe et al. 2012) and could be applied to decapods. Combining physiology measures alongside movement in natural settings could also benefit the conservation of vulnerable crustacean species (see Cooke 2008).

Fine-scale positioning systems (e.g. VEMCO Positioning Systems [VPS], Innovasea; and Lotek UMAP) could be used effectively in future decapod movement work by increasing the resolution of movement data collected. With fine-scale positioning systems, researchers are able to increase knowledge of space use and movement ecology through calculating metrics such as home range size, step length, tortuosity of movement, and displacement of individuals. To adequately capture the fine-scale spatial behaviours that characterize species interactions, movement should be studied using such 3-dimensional positioning system technologies to locate animals with low positional error and describe trajectories of movement rather than point locations (e.g. Skerritt et al. 2015, Lees et al. 2018, Cote et al. 2019). This technique has been used with lobsters (Lees et al. 2018) and crabs (Cote et al. 2019) and other mobile benthic invertebrates, such as abalone (Coates et al. 2013), queen conch (Stieglitz & Dujon 2017), sea stars (Miyoshi et al. 2018), and giant tritons (Schlaff et al. 2020). A major drawback of these approaches can be their expense and often relatively small spatial coverage; if animals leave the receiver array, they are no longer detected. To compensate for this, surrounding areas can be surveyed using mobile tracking where receivers can be mounted on a boat or an autonomous underwater glider (e.g. Vemco Mobile Transceiver receivers; Cote et al. 2019). These systems are suitable for complex analyses such as state space or hidden Markov models that are used to reveal different behaviours from movement paths, such as area-restricted movement indicative of foraging (Whoriskey et al. 2017). However, positioning systems must cover a suitably large geographic area to fully capture individual movements and can therefore be financially prohibitive to purchase and resource-intensive to maintain. These systems are well suited to whole-basin experiments, for example tracking crayfish in lakes or ponds, or crabs in estuaries or embayments, although some animals may still leave the study area despite good coverage. When positioning arrays are established with overlapping detection range, precise coordinates can be derived to reconstruct paths using open source software such as Yet Another Positioning System (YAPS; Baktoft et al. 2017). YAPS synchronizes the detection times on receivers (i.e. due to clock drift on each unit) based on pings from synchronization tags deployed within the array and estimates a movement path that minimises positional error by triangulating the location based on the known locations of receivers and the speed of sound in water (Baktoft et al. 2017). Approaches using YAPS can provide equivalent results to existing proprietor algorithms (Baktoft et al. 2017), and in some cases may perform better than VPS, for example in highly reflective environments where diffraction contributes to large positional error (Vergeynst et al. 2020).

Satellite telemetry is not often used on decapods and has typically been applied to terrestrial animals or marine animals that frequent the surface of the water (Hussey et al. 2015). However, estimates of marine decapod movement, especially presumed long-distance migrants, could be obtained through pop-off satellite telemetry. Pop-off tags use light-based geolocation to determine the latitude and longitude of an animal at preset time intervals and can carry a variety of environmental sensors for variables including temperature and salinity. The tags record these observations on board until, on a predetermined date (or when the animal dies), the tag releases, floats to the surface, and broadcasts its data back to the investigator via satellite. In instances where light-based geolocation is not possible (e.g. the deep sea, or high latitudes during winter) multiple tags can be fixed to an animal, if it is big enough, and be programmed to release on different dates. When the tag releases and reaches the surface, the location is recorded via satellite, allowing for the creation of a movement pathway. We see potential for this method, in particular for deep-sea decapods (as in Davidson & Hussey 2019), where other telemetry methods may not be as feasible. This is particularly true as light-based geolocation will not perform at depths where sunlight is unavailable to the tags for estimating position.

4.5. Tag attachment

A variety of methods have been employed to attach tags to decapods (Fig. 7), and there is an opportunity to incorporate further information about their biology and behaviour to increase tracking success and facilitate the evolution of telemetry methodology. The hard decapod exoskeleton makes external attach-

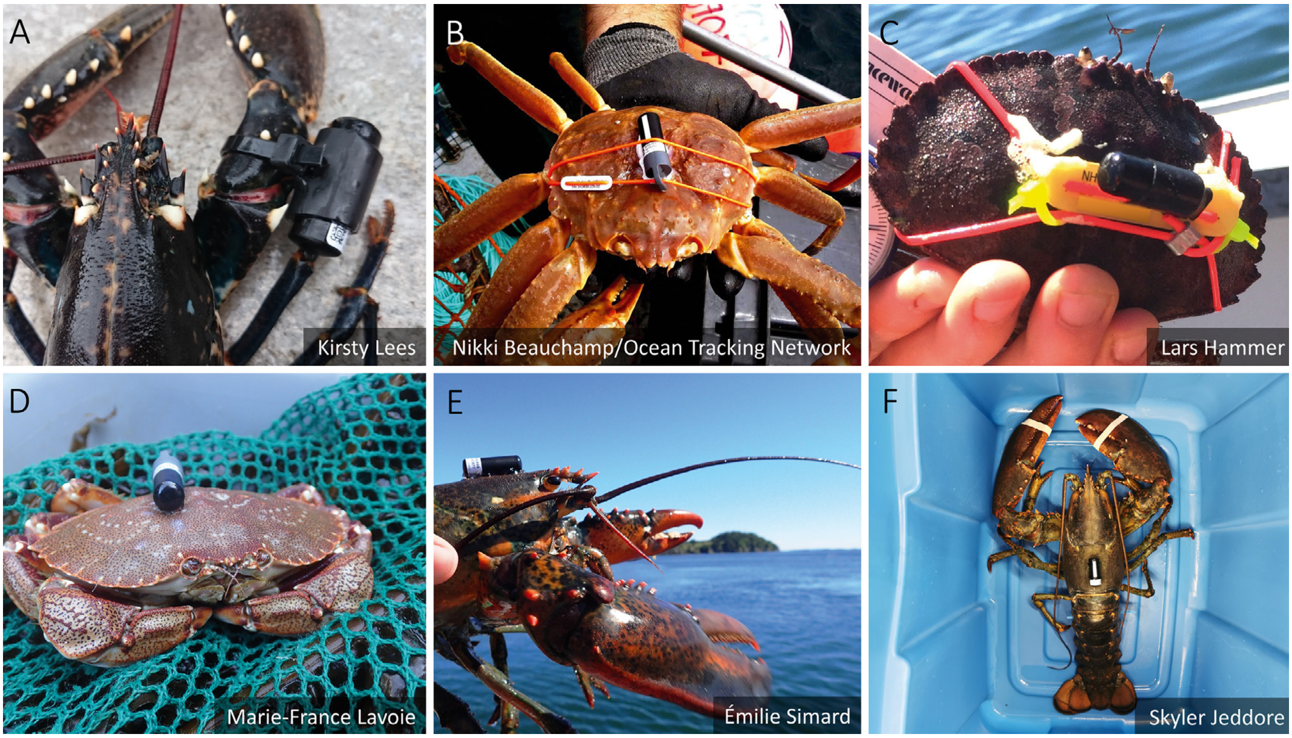

Fig. 7. Examples of different telemetry tag attachments. (A) American lobster *Homarus americanus* with a cable attachment; (B) snow crab *Chionoecetes opilio* and (C) Jonah crab *Cancer borealis* with harness attachments; (D) rock crab *Callinectes sapidus* and (E,F) American lobster with glued adhesive attachments. Photos used with permission from (A) Kirsty Lees, (B) Nikki Beauchamp/Ocean Tracking Network, (C) Lars Hammer, (D) Marie-France Lavoie, (E) Émilie Simard, and (F) Skyler Jeddore

ment of tags using glue or a harnesses relatively easy, reducing handling time and the associated physiological stress (Fig. 7). Cote et al. (2019) described the use of a rotary tool to roughen the carapace of snow crabs and attach an acoustic transmitter with an aluminum sleeve, spaghetti tag, and pipe cleaner. Moland et al. (2011a) used cable ties to strap acoustic transmitters to the left cheliped of European lobsters, anchored between denticles to prevent slipping (Fig. 2 in Moland et al. 2011a). For Dungeness crabs *Cancer magister* (also known as *Metacarcinus magister*), Burns et al. (2020) drilled holes in the carapace and threaded monofilament to secure the tag with a crimp to secure the loop. Davidson & Hussey (2019) compared epoxy, looping leader through drilled holes, and tying a harness around the body axis for securing pop-up archival satellite telemetry tags and suggested the latter to be most appropriate for porcupine crabs.

While strategically placed holes drilled through the carapace may avoid direct damage to internal structures, damage to the carapace may leave an individual susceptible to infection by an opportunistic pathogen leading to shell disease (Getchell 1989). Some species appear more affected than others, in particular brachyuran crabs (Joseph & Ravichandran 2012) and *Homarus* spp. lobsters (Davies et al. 2014). Severe disease is considered rare in wild populations, but can result in death due to incomplete separation of the old and new exoskeleton when moulting (Smolowitz et al. 1992). Mild to moderate disease can cause behavioural changes in moult patterns; for example, infected ovigerous lobsters may moult, resulting in total egg loss (Laufer et al. 2005). Although external attachment is the most common attachment method, if the animal has not reached, or does not have, a terminal moult, externally mounted tags will be shed as the animal grows. Intramuscular attachment of acoustic tags in king crabs via piercing of the isthmus, the fleshy connective tissue that joins the ventral surface of the carapace to the abdomen, allows tags to be retrained during moult, potentially facilitating multiple years of data collection (Zacher 2019). Although a common method for the attachment of persistent plastic tags (Huizer 1954), this method has not been widely used for acoustic tags.

Regardless of tag placement, attachment should not impede behaviours such as moulting and mating, or create disproportional drag that will impede movement, and all novel attachment methods should be assessed prior to deployment. Similarly, potential entanglement risk should be assessed prior to deployment; for example, whip antennae associated with radio telemetry tags can become tangled in underwater vegetation (Daněk et al. 2018). Non-cephalopod invertebrates are not subject to animal welfare legislation, and as a consequence there are few published studies that include details on how potential tagging effects were assessed prior to deployment (e.g. aquarium or cage studies; Maynard & Conan 1984, Schmiing & Afonso 2009, Taylor & Ko 2011) or additional details such as the weight of the tag relative to the body weight of the animal (Skerritt et al. 2015). It is possible to minimize the likelihood that a tagged animal will moult before the end of a study by only tagging animals with hard, clean, and undamaged shells. However, selecting undamaged individuals within an active fishery may prove difficult due to high rates of shell damage and limb loss (Scarratt 1973). Selectively tagging may also bias records of movement by under-representing the ecology of damaged individuals. Therefore, the tag attachment method, including external attachment methods (i.e. gluing directly to the carapace or securing around carapace with tubing; Maynard & Conan 1984, Davidson & Hussey 2019) or intramuscular attachment methods (Zacher 2019), as well as length of study period (i.e. avoiding temporal overlap with moulting as tested by Schmiing & Afonso 2009) are important considerations and should be reported by researchers.

Regardless of how the tag is attached, tag burden (the weight of the tag relative to the individual animal) is an important consideration to minimize potential loading on the animal (Wolcott 1995). General ‘rules of thumb’ exist in telemetry studies (Wolcott 1995, Smircich & Kelly 2014), but the impacts of tag burden appear taxa-specific at least in fishes (Brown et al. 1999, Liss et al. 2021). Due to their general reliance on crawling or walking on substrate, it is sometimes suggested that decapods can withstand higher tag burdens (Krieger et al. 2012). External tagging can also facilitate the use of larger tags that would not fit within the body cavity, but the impacts of tagging should continue to be studied and tag burdens be reported by researchers. Although it is difficult to assess tag burden impacts on behaviour *in situ* (but see Bass et al. 2020 for an example in salmonids), experiments can elucidate effects on growth and survival (Bubb et al. 2002a, Westhoff & Sievert 2013, McFarlane et al. 2019) to help set taxa-specific guidelines (Westhoff & Sievert 2013). Further, some decapods exhibit burrowing behaviour, which could directly impact detection (as Grothues et al. 2012 found in burying flounder) and tag retention success, but also interact with tag burden (larger tags could affect ability to burrow or use shelter). Tag performance could be tested during burrowing behaviour in a controlled setting prior to in-field tagging (as in Taylor & Ko 2011, who did not observe an impact of tagging on burying), and those results could be integrated with telemetry-collected movement data; for example, if there are patterns in non-detection associated with diurnal burrowing patterns that could allow interpolation of positions during burrowing hours.

4.6. Management applications

Our review highlights a focus on large-bodied and economically valuable species of king crabs and lobsters (Lithodidae, Palinuridae, and Nephropidae). Telemetry can also be used to track decapod movement across management jurisdictions and within or among protected areas (Giacalone et al. 2006, Moland et al. 2011a, Withy-Allen & Hovel 2013) and to estimate abundance or survival when integrated into a mark–recapture framework (Shepherd et al. 2011, Wiig et al. 2013). For example, acoustic telemetry has revealed home ranges of American lobster (Morse & Rochette 2016), demonstrating that the methods can directly contribute to fisheries conservation and management (Crossin et al. 2017). Further, Lees et al. (2018) investigated the movement of commercially valuable European lobsters relative to the presence of baited traps and found individual variation in response to traps but no overall differences in movement pre- and post-trapping. Overall, our review highlights that studies have rarely focused directly on conservation and management aims.

Telemetry can play a role in understanding invasion processes by identifying important habitats and interactions between native and non-native species. Studies that focused on invasive species researched movements of non-native crayfishes using PIT tags and radio telemetry. For example, Bubb et al. (2004) radio-tracked American signal crayfish in England and found that the invasive potential was negatively related to stream flow. Bubb et al. (2006) found greater movement and dispersal in the invasive signal crayfish than the native white-clawed crayfish *Austropotamobius pallipes*, explaining, at least in part, their relatively fast colonization. However, only a small number of studies (n = 13, spanning 5 invasive species) focused on invasive species, even though several decapod species are highly invasive and have established in new areas. Given the immense impact of invasive species, and invasive decapods specifically, in aquatic systems worldwide (McCarthy et al. 2006, Galil et al. 2011, Twardochleb et al. 2013), additional opportunities exist to use telemetry to quantify the spatial behaviour and interactions of these species in novel environments. For example, Chinese mitten crab *Eriocheir sinensis* has invaded estuarine and coastal regions around New York and San Francisco (USA) and throughout Europe with the potential to damage lucrative native species fisheries and habitats (Therriault et al. 2008). Similarly, green crabs have invaded both Atlantic and Pacific coasts of North America, with impacts on habitat (Matheson et al. 2016, Howard et al. 2019) and native species (Pickering et al. 2017). Other decapods, including king crab *Paralithodes camtschaticus*, have appeared in regions of northern Europe to yield new economic opportunities for local fishers (Sundet & Hoel 2016) as well as impacting indigenous species and habitats (Fuhrmann 2016, Pedersen et al. 2018).

Additional research could support mitigation efforts and better quantify their ecological impacts. Although the pelagic larval phase is assumed to be the dominant mode of dispersal in the marine environment, often little is known about the scale and connectivity of post-settlement benthic movements. The cumulative distance moved by individuals across years can contribute to population connectivity and potential range expansion if the direction of movement is counter to the prevailing current (e.g. Morse et al. 2018). Greater understanding of population connectivity post-settlement could inform management of the potential impact of invasive species. Telemetry may also identify aggregation sites where high densities of invasive species could be removed (i.e. 'Judas technique', Taylor & Katahira 1988). However, there are ethical quandaries associated with releasing invasive or non-native species with tags rather than removing the animals from the invaded habitat (Lennox et al. 2016).

4.7. Allometric relationship between body size and movement

Our synthesis highlights how combining decapod movement studies can provide broad ecological insight. Allometric relationships, where animal movement increases with body size, have been observed in many animals including insects (Kalinkat et al. 2015) and mammals (Noonan et al. 2020). The power law of metabolic scaling has been suggested to be 0.75 (McNab 1963), although recent studies have found this to be far from universal (Glazier 2010). We found the expected positive relationship between body size and movement in decapods with an exponent of 0.86, demonstrating that movement rate increases more rapidly with body size for decapods. This exponent may increase as technology improvement allows for detection at greater distances (see Section 4.4) and seasonal migrations are taken into account. Allometric scaling with movement rate may be influenced by variety of factors, including habitat quality or intraspecific relationships (Rosten et al. 2016). Continued decapod movement research will contribute data to synthetic studies examining allometric relationships, as well as community connectivity, plasticity to changing pressures, food web dynamics, and habitat selection.

4.8. Conclusion

Telemetry has successfully addressed knowledge gaps that have historically impeded the management of decapod fisheries. It has also provided insights into aspects of decapod ecology that were previously unobservable, such as the spawning behaviour of cryptic species, movement and interactions associated with group behaviour, and mechanisms of trophic cascades. Although much of the literature in aquatic telemetry has focused on fishes, decapods have long been a focus of telemetry-based research and we foresee an increase in the number of studies that use this approach. Future studies that use a combination of telemetry approaches are likely to provide the most insight; for example, using a 3D-positioning system in combination with an autonomous glider allows movement to be studied at multiple spatial scales. Likewise, the collection of additional individual-level data such as genetic markers from tagged individuals could provide novel insight into how benthic movement impacts population connectivity. Telemetry research could contribute to the equitable and evidence-based management of high-value fisheries species by, for example, providing a greater understanding of catchability, or a greater understanding of the behaviour of non-target juveniles and females. Comparing the movement and behaviour of species between their native and non-native ranges could also prove informative for emerging fisheries such as non-native snow crab and red king crab that have expanded into Norwegian waters from the Barents Sea. Climate change scenarios will likely facilitate the further spread of marine non-native species, and comparative movement studies between native and non-native ranges can improve our understanding of the important biological mechanisms that facilitate species range expansions. However, decapods are a highly diverse taxon, and it is necessary to expand our focus beyond that of the established commercial species to gain a fuller understanding of decapod movement ecology. Future technological advancements and miniaturization will enable additional species to be studied, and we hope that the collaborative network approach, common within finfish research, will be more widely adopted by researchers, thus facilitating research across multiple study sites within the range of a species and providing a more holistic understanding of decapod movement ecology.

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