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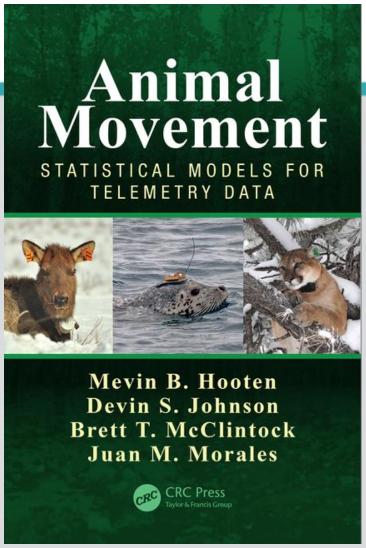
INTRODUCTION



This chapter is excerpted from

Animal Movement: Statistical Models for Telemetry Data

by Mevin B. Hooten, Devin S. Johnson, Brett T. McClintock, Juan M. Morales.

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1 Introduction

The movement of organisms is a fundamentally important ecological process. Voluntary movement is a critical aspect of animal biology and ecology. Humans have been keenly interested in the movement of individual animals and populations for millennia. Over 2000 years ago, Aristotle wrote about the motion of animals, and the associated philosophical and mathematical concepts, in his book, *De Motu Animalium* (Nussbaum 1978). Historically, it was critical to understand how and where wild food sources could be obtained. Thus, early humans were natural animal movement modelers. In modern times, we are interested in the movement of animals for scientific reasons and for making decisions regarding the management and conservation of natural resources (Cagnacci et al. 2010).

The study of wild animals can be challenging. Animals are often elusive and reside in remote or challenging terrain. Many animals have learned to minimize exposure to perceived threats, which, unfortunately for us, include the well-intentioned biologist approaching them with binoculars or a capture net. Therefore, it is no surprise that the development of animal-borne telemetry devices has revolutionized our ability to study animals in the wild (Cagnacci et al. 2010; Kays et al. 2015). Animal telemetry has helped us overcome many of the practical, logistical, and financial challenges of direct field observation. Telemetry data have opened windows that allow us to address some of the most fundamental ecological hypotheses about space use ("Where is the animal?"), movement ("How did the animal get there?," "Where could it go?"), resource selection ("Where does the animal like to be?"), and behavior ("What is the animal doing?") (Figure 1.1).

1.1 BACKGROUND ON ANIMAL MOVEMENT

Animal movement plays important roles in the fitness and evolution of species (e.g., Nathan et al. 2008), the structuring of populations and communities (e.g., Turchin 1998), ecosystem function (Lundberg and Moberg 2003), and responses to environmental change (e.g., Thomas et al. 2004; Trakhtenbrot et al. 2005; Jønsson et al. 2016). The scientific study of animal movement has a deep history, and we are unable to explore all of the ecological implications and methodological developments in a single volume. Instead, we focus on several specific inferential methods that can provide valuable ecological insights about animal movement and behavior from telemetry data.

The importance of animal movement in larger-scale ecosystem function probably inspired the Craighead brothers to develop and deploy the first radio collars on grizzly bears (*Ursus arctos*) from Yellowstone National Park in the 1960s (Craighead and Craighead 1972). Satellite tracking devices are now capable of pinpointing animal locations at any moment, remote sensing provides ever refined environmental

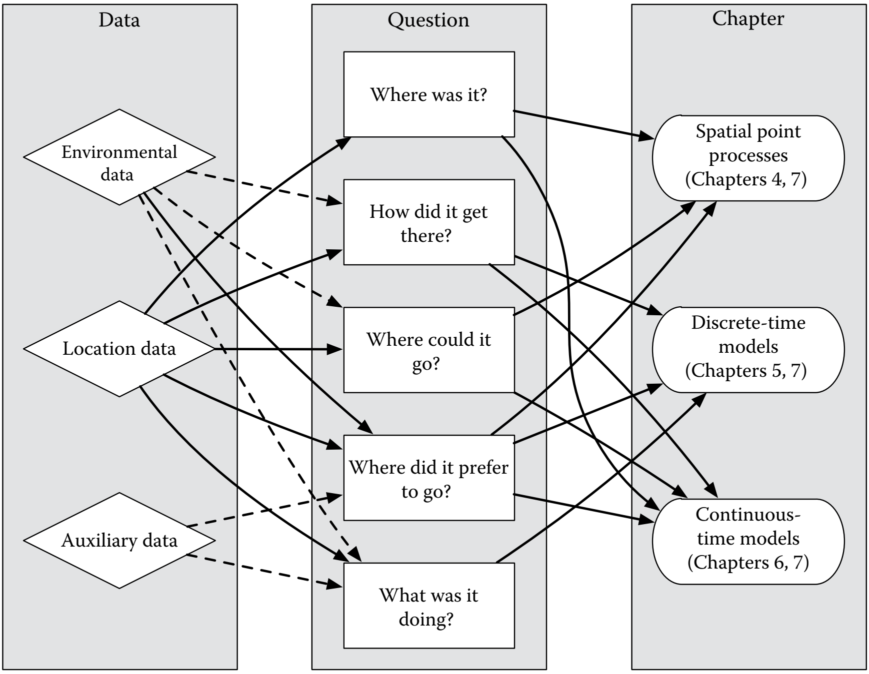

FIGURE 1.1 Relationships among data types, analytical methods, and some fundamental questions of movement ecology. Location data are the cornerstone of all of the analysis methods described in this book. Environmental data, such as those acquired from remote sensing, are useful in drawing connections between animals and their surroundings. Auxiliary biotelemetry data, such as accelerometer or dive profile data, can help address questions about animal behavior. Dashed lines indicate where data can be helpful for addressing particular questions, but are not essential.

data, and biotelemetry tags allow for the simultaneous collection of important physiological and behavioral information from wild animals. These technological advances will lead to a better understanding of how individual decisions affect demographic parameters and ultimately translate into population dynamics. In this sense, animal movement can provide the long-sought bridge between behavior, landscape ecology, and population dynamics (Lima and Zollner 1996; Wiens 1997; Morales et al. 2010; Kays et al. 2015).

In what follows, we provide a brief summary of research findings, existing knowledge, and analytic approaches for important aspects of animal movement ecology. We organized these topics into 10 sections:

1. Population dynamics
2. Spatial redistribution
3. Home ranges, territories, and groups
4. Group movement and dynamics
5. Informed dispersal and prospecting

6. Memory
7. Individual condition
8. Energy balance
9. Food provision
10. Encounter rates and patterns

1.1.1 POPULATION DYNAMICS

In classical models of population dynamics, predators and prey encounter each other in proportion to their overall abundance over space and reproductive rates decrease as the global population density increases. This is because traditional models of population and community dynamics assume we are dealing with many individuals that are well mixed (Turchin 2003). Such "mean field" representations of population dynamics can provide good approximations when the physical environment is relatively homogeneous and organisms are highly mobile, or when organisms interact over large distances. However, when the external environment or the limited mobility of organisms results in lack of mixing, the conditions experienced by a particular member of a population or community can be quite different from the mean (Lloyd 1967; Ovaskainen et al. 2014; Matthiopoulos et al. 2015). That is, when *per capita* vital rates are affected by varying local conditions, the observed population and community dynamics can differ markedly from mean field predictions.

Population dynamics involve births, deaths, immigration, and emigration; modern tracking technology, together with new statistical models, can greatly improve our understanding of these processes. The individuals that comprise a population can vary in several traits and individual behavior can change in response to internal and external stimuli. Individual traits and behavior determine the way they interact with the environment and other organisms while the conditions that individuals experience ultimately translate to their performance (i.e., growth, survival, and reproduction).

Survival analysis can be used to model changes in hazard with time and in relation to covariates such as location, age, body condition, and habitat type. Detailed tracking through satellite telemetry enables spatial information and survival data to be combined at small temporal scales, leading to an increasingly sophisticated understanding of the determinants of survival (Murray 2006; Haydon et al. 2008; Schick et al. 2013). Likewise, changes in movement behavior can be used to infer reproductive events in some species (Long et al. 2009). However, to take full advantage of these data, new analytic techniques should take into account the sequential nature of individual survival and reproduction. For example, the chance of an animal dying of starvation depends on its history of encounters with food items and foraging decisions.

Coupling demographic data with movement models is an area of active research, but is still somewhat nascent. Spatial capture–recapture (SCR) models provide a way to formally connect animal encounter data with movement processes; we refer the interested reader to Royle et al. (2013) and references therein for additional details. The methods presented in this book will be critical for formally integrating location data and demographic data in future SCR modeling efforts.

1.1.2 SPATIAL REDISTRIBUTION

Classical reaction–diffusion models, such as those used by Fisher (1937) to describe the spread of an advantageous mutation within a population assume that mortality and recruitment rates depend linearly on local population density and that individuals move at random over a large and homogeneous area. Early implementations of these models were also used to describe the dynamics of population invasion and range expansion (e.g., Skellam 1951; Andow et al. 1990; Shigesada and Kawasaki 1997), and later, were embedded in a hierarchical statistical modeling framework (e.g., Wikle 2003; Hooten and Wikle 2008; Hooten et al. 2013a) to provide inference about spreading populations.

Diffusion equations have been justified as a good approximation to the displacement of individuals performing a "random walk."* Although we know that animals do not move at random, the diffusion approximation can still be sufficient at certain (usually large) scales and also serves as a null model to compare with more complex models (Turchin 1998).

More general forms of movement can be taken into account by formulating spatial population models as integral equations. These have commonly been formulated in discrete time, yielding integro-difference equations where local population growth is combined with a "redistribution kernel" that describes the probability that an individual moves from its current location to another one in a given time-step.† The temporal scale of these models is usually set to match reproductive events so that the redistribution kernel represents successful dispersal rather than regular movement. A great deal of theoretical and empirical work has explored the consequences of kernel shape, particularly in the tail of the distribution, on invasion speed (Kot et al. 1996; Powell and Zimmermann 2004).

There are many ways to make spatial population models more realistic and appropriate for particular species, places, and scales of interest. A good starting point is to consider the spatial structure of the population, which is generally accepted as an important prerequisite for more accurate ecological predictions (Durrett and Levin 1994; Hanski and Gaggiotti 2004).‡ The spatial structure of populations can range from classical closed populations to a set of subpopulations with different degrees of interaction (Thomas and Kunin 1999). As different degrees of connectivity among subpopulations can have important dynamical consequences, researchers are increasingly interested in understanding how connectivity arises from the interaction among individual phenotypes, behaviors, and the structure of landscapes.

One particular feature of the models described thus far is that every individual is assumed to move according to the same kernel (whether Gaussian or otherwise). However, detailed tracking of individual movements consistently reveals differences among individuals. Theoretical and empirical studies have shown how the characteristics of redistribution kernels can depend on differences among individuals (Skalski and Gilliam 2000; Fraser et al. 2001; Morales and Ellner 2002; Delgado

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[*] We describe random walks in discrete and continuous time in Chapters 5 and 6.

[†] We describe redistribution kernels and integral equation models for movement in Chapters 4 and 6.

[‡] See Chapter 2 for a brief primer on spatial statistics.

and Penteriani 2008), and on the interplay between individual behavior and features of the underlying landscape (Johnson et al. 1992; McIntyre and Wiens 1999; Fahrig 2001; Ricketts 2001; Morales et al. 2004; Mueller and Fagan 2008), including reactions to habitat boundaries (Schultz and Crone 2001; Morales 2002; Schtickzelle and Baguette 2003; Ovaskainen 2004; Haynes and Cronin 2006). In particular, population heterogeneity produces leptokurtic (i.e., heavy tailed) redistribution kernels when a subset of individuals consistently moves longer distances than others (Skalski and Gilliam 2000; Fraser et al. 2001).

Several factors can explain why two individuals belonging to the same population move differently. They may be experiencing different environments of heterogeneous landscapes; they can also have different phenotypes or condition, different past experiences (e.g., Frair et al. 2007), or even different "personalities" (Fraser et al. 2001; Dall et al. 2004). In a theoretical study, Skalski and Gilliam (2003) modeled animals switching between fast and slow random walk movement states and found that the resulting redistribution kernel depended on the total time spent in each of the states and not on the particular sequence of changes. This theoretical result highlights the importance of animals' time budgets for scaling movement processes (Figure 1.2).

It is common to consider that individuals have a small set of movement strategies (Blackwell 1997; Nathan et al. 2008), and the time allocation to these different behaviors (or "activity budgets") can depend on the interaction between their motivation and the structure of the landscape they occupy (Morales et al. 2004, 2005). The results

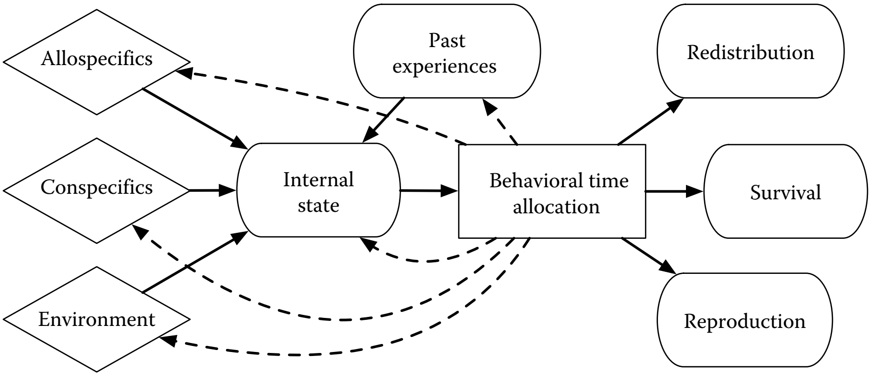

FIGURE 1.2 Mechanistic links between animal movement and population dynamics adapted from Morales et al. (2010). We consider an unobserved individual internal state that integrates body condition (e.g., energy reserves, reproductive status). Several factors affect the dynamics of this internal state, including social interactions with conspecifics, trophic or other interaction with allospecifics (other species), and abiotic environmental effects and dynamics. Internal state dynamics determine the organism's time allocation to different behaviors (e.g., food acquisition, predator avoidance, homing, and landscape exploration) but is also modulated by past experiences and phenotypic trails such as behavioral predispositions. As different behaviors imply different movement strategies, the time budget determines the properties of the spatial redistribution that describes space use. Time allocation to different behaviors also affects individual survival and reproduction, and hence, overall population dynamics.

of Skalski and Gilliam (2003) imply that knowing the fraction of time allocated to each behavior makes it possible to derive suitable redistribution kernels.

A common reaction in the visual inspection of movement data is to intuit that individuals are moving differently at different times. As a result, several techniques (including many *ad hoc* procedures) have been developed to identify and model changes in movement behavior from trajectory data (reviewed in Patterson et al. 2008; Schick et al. 2008; Gurarie et al. 2016). Clustering models, such as those we describe in Chapter 5, can be difficult to reliably implement because biologically different movement behaviors can lead to very similar trajectories. For example, it may be difficult to distinguish relative inactivity (e.g., resting) from intense foraging, within a small patch, based on horizontal trajectory alone. However, as physiological and other information becomes available through biotelemetry devices, we may gain greater insight into how animals allocate time to different tasks and how this allocation changes in different environments (McClintock et al. 2013), thus providing a mechanistic way to model redistribution kernels conditional on individual state.

Another result from Skalski and Gilliam (2003) is that a mixture of movement states converges to simple diffusion if given enough time. The sum of n independent and identically distributed random variables with finite variance will be Gaussian distributed as n increases. Thus, if all individuals in a population move according to the same stochastic process, we would expect that, at some time after the initiation of movement, the distribution of distance moved becomes Gaussian because the distance traveled is the sum of movement vectors. However, this depends on the rate of convergence and independence assumption. Still, similar results may relate to the interaction between individual behavior and landscape structure (Morales 2002; Levey et al. 2005) and are the focus of ongoing research.

We return to redistribution kernels for animal movement in Chapters 4 through 6. In particular, we consider spatial redistribution from three different perspectives (i.e., point processes, discrete-time processes, and continuous-time processes) and highlight the relevant literature associated with each. We also show how to scale up from Lagrangian to Eulerian models for movement in Chapter 6.

1.1.3 HOME RANGES, TERRITORIES, AND GROUPS

Many animals have clearly defined home ranges or territories (Borger et al. 2008). If not, they usually exhibit some form of site fidelity and revisitation patterns that are not captured by simple random walks. Most likely, these animals will spend their reproductive life in a region that is small compared to their movement capabilities. Substantial progress has been made in developing mechanistic models of animal movement with territorial behavior (e.g., Moorcroft et al. 1999; Smouse et al. 2010; Moorcroft and Lewis 2013; Giuggioli and Kenkre 2014). However, territoriality models typically describe the space use by particular individuals (or members of a wolf pack, for example) rather than an entire population. As a result, they have not yet been linked to models of population demography.

For territorial animals, the carrying capacity of a particular region or landscape can be determined by competition for space. When the environment provides a limited number of essential items, such as nest cavities, the maximum number of breeders is bounded and surplus individuals form a population of nonbreeders referred to as "floaters" (Brown 1969; Penteriani and Delgado 2009). When dispersal or mortality create vacancies in previously occupied territories, floaters may become a crucial population reserve for filling these empty territories. Floaters can also have a negative effect on population growth through interference, conflict, or disturbance. Furthermore, the aggressive behavior of breeders can also decrease the carrying capacity of the population.

We describe basic methods for estimating home ranges and core areas in Chapter 4, and discuss methods for modeling interactions among individuals at the end of Chapter 5. However, the formal statistical modeling of floaters, together with individual-level behavior and territoriality is still developing and an open area of research.

1.1.4 GROUP MOVEMENT AND DYNAMICS

Understanding the distribution of social animals over landscapes requires scaling up from individual movement patterns to groups of individuals and populations (Okubo et al. 2001). Most models of group dynamics focus on relatively short temporal scales (Couzin et al. 2005; Eftimie et al. 2007; Strandburg-Peshkin et al. 2015). However, the interaction between the group structure of a population and the movement of individuals is also relevant at longer time scales (e.g., Fryxell et al. 2007). Long time scales in group dynamics are particularly relevant for reintroduced species, where a balance of spread and coalescence processes will determine how individuals distribute themselves over the landscape. Often, individual survival and fecundity are higher in groups, so that the successful persistence of the introduced population may depend on coalescence dominating and limiting the spreading process, thereby enabling the establishment of a natural group structure within the release area. Haydon et al. (2008) developed movement models for North American elk (*Cervus canadensis*), reintroduced to Ontario, where, as in Morales et al. (2004), animals can switch between exploratory (large daily displacements and small turning angles) and encamped behavior (small daily displacements and frequent reversals in direction). The rate of switching among these movement modes depended on whether individuals were part of a group or not. Haydon et al. (2008) combined their movement models with analysis of mortality and fecundity to build a spatially explicit, individual-based model for the dynamics of the reintroduced elk population. Their analysis showed that elk moved farther when they were solitary than when they were in a group, and that mortality risk increased for individuals that moved progressively away from the release location. The simulation model showed how the population rate of increase and the spatial distribution of individuals depended on the balance of fission and fusion processes governing group structure.

New approaches for studying the interaction among individuals in groups are appearing regularly in the literature. For example, Scharf et al. (In Press) developed a discrete-time model that captures the alignment and attraction of killer whales (*Orcinus orca*) in Antarctica, and Russell et al. (2016b) used point processes to model interactions among individual guppies (*Poecilia reticulata*). Using high temporal resolution telemetry data from a group of baboons (*Papio anubis*) in Kenya, Strandburg-Peshkin et al. (2015) analyzed individual movement in relation to one another. They found that, rather than following dominant individuals, baboons are more likely to follow others when multiple initiators of movement agree, suggesting a democratic collective action emerging from simple rules. In a study of fission–fusion dynamics of spider monkeys (*Ateles geoffroyi*), Ramos-Fernández and Morales (2014) found that group composition and cohesion affected the chance that a particular individual will leave or join a group. As another example, Delgado et al. (2014) found that dispersing juveniles of eagle owl (*Bubo bubo*) were generally attracted to conspecifics, but the strength of attraction decreased with decreasing proximity to other individuals. However, despite this progress, models for animals that decide to leave their territory or abandon a group, and how they explore and choose where to establish new territories or home ranges, have yet to appear in the literature.

1.1.5 INFORMED DISPERSAL AND PROSPECTING

Dispersal involves the attempt to move from a natal or breeding site to another breeding site (Clobert 2000), and is essential for species to persist in changing environments (Ronce 2007). The redistribution modeling ideas we introduced in the previous sections represent dispersal as a random process that may be sensitive to the spatial structure of the landscape or the presence of conspecifics. However, there is a great deal of evidence indicating that individuals are capable of sophisticated and informed decision-making when choosing a new place to live (Bowler and Benton 2005; Stamps et al. 2005, 2009). Clobert et al. (2009) proposed the concept of "informed dispersal" to convey the idea that individuals gather and exchange information at all three stages of dispersal (i.e., departure, transience, and settlement). Thus, movement involves not only the exchange of individuals among habitat patches but also information transfer across the landscape. Animals can acquire information about the environment by "looking" at others' morphology, behavior, or reproductive success (Danchin et al. 2004; Dall et al. 2005). For example, in an experiment with the common lizard (*Lacerta vivipara*), Cote and Clobert (2007) quantified emigration rate from artificial enclosures that received immigrants. They found that when local populations received immigrants that were reared under low population density, the emigration rate of the local population increased, providing evidence that immigrants supplied information about the density of surrounding populations, probably via their phenotype.

We only have a rudimentary understanding of how individuals integrate different sources of information to make movement and dispersal decisions. Long-term tracking is needed to study how animals adjust to the changing characteristics of their home ranges or territories, and under what conditions they are likely to search for a new home. Detailed tracking of juveniles may shed light on the processes of exploration (i.e., transience) and settlement. In particular, movement data can be used to test ideas about search strategies, landscape exploration, and the importance of past experience in biasing where animals decide to attempt breeding.

1.1.6 MEMORY

The importance of previous experiences and memory is increasingly being recognized and explicitly considered in the analysis of telemetry data (e.g., Dalziel et al. 2008; McClintock et al. 2012; Avgar et al. 2013; Fagan et al. 2013; Merkle et al.

2014). Smouse et al. (2010) provide a summary of the approaches used to include memory in movement models. Formulating memory models has largely been a theoretical exercise but the formal connection with data is possible. For example, the approach used to model the effect of scent marking in mechanistic home range models (Moorcroft and Lewis 2013) could be easily adapted to model memory processes. Avgar et al. (2015) fit a movement model that included perceived quality of visited areas and memory decays to telemetry data from migrating Caribou. It is less clear what role memory plays in population dynamics.

Forester et al. (2007) describe how certain discrete-time movement models can be reformulated to provide inference about memory. We explain these ideas in Chapter 5. In continuous-time models, Hooten and Johnson (2016) show how to utilize basis function specifications for smooth stochastic processes to represent different types of memory and perception processes. We discuss these functional movement modeling approaches in Chapter 6.

1.1.7 INDIVIDUAL CONDITION

Recognizing that the contribution of a particular individual to the population is a function of its fitness has historically promoted the development of physiological-, age-, and stage-structured population models (Caswell 2001; Ellner and Rees 2006; Metz and Diekmann 2014). Body condition integrates nutritional intake and demands, affecting both survival and reproduction. For example, studies of ungulates living in seasonal environments have found that percent body fat in early winter is a very good predictor for whether animals die, live without reproducing, or live and reproduce (Coulson et al. 2001; Parker et al. 2009). Also, many populations show "carryover effects" where conditions experienced during a time period influence vital rates in future periods, which has the potential to generate many different population responses (Ratikainena et al. 2008; Harrison et al. 2011). Movement decisions and habitat use affect energy balance and body condition in animals. Linking individual condition to movement and space use is challenging because we usually need to recapture individuals to assess percent body fat, for example. However, some marine mammals perform "drift dives," using their buoyancy to change depth without active propulsion and with their rate of drift determined largely by their lipid-to-lean-mass ratio Biuw et al. (2003). Working with Southern elephant seals (*Mirounga leonina*), Schick et al. (2013) modeled changes in individual condition as a function of travel distance and foraging events. They also linked changes in behavior due to human disturbances to population-level effects.

The animal movement models we describe in Chapters 4 through 6 are mostly focused on modeling individuals. However, when scaling up inference to the population level (using random effects for parameters or other hierarchical modeling approaches), it may be important to account for variation in body condition among individuals to help describe differences in movement parameters. See Sections 4.5 and 5.2 for examples of accounting for individual-level differences when obtaining inference at the population level.

1.1.8 ENERGY BALANCE

Many aspects of life history evolution, behavioral ecology, and population dynamics depend on how individuals consume resources and on how they allocate energy to growth and reproduction. Food acquisition is an important driver of animal movement to the point that relationships between scaling of space use and daily distance traveled in relation to body mass and trophic requirements has been hypothesized (Jetz et al. 2004; Carbone et al. 2005).

Technological developments in biotelemetry allows the possibility of observing a suite of relevant physiological data such as heart rate and core temperature, in addition to individual location (Cooke et al. 2004; Rutz and Hays 2009). Furthermore, accelerometers can be used for detailed movement path reconstruction and for recording energy expenditure, activity budgets (i.e., ethograms), and rare behavioral events such as prey captures (Wilson et al. 2007, 2008; Williams et al. 2014; Bidder et al. 2015). Combined with detailed environmental maps, these data could lead to empirically based models of animal performance in the wild, linking behavioral decisions with space use, survival, and reproduction (Figure 1.2).

The formal integration of energy balance information into dynamic statistical animal movement models is still in early development stages (Shepard et al. 2013). However, many approaches we describe in Chapters 4 through 6 allow for the use of auxiliary data pertaining to energy-intensive behavior. For example, Section 5.2.5 describes how to integrate dive data for marine mammals into discrete-time movement models.

1.1.9 FOOD PROVISION

Food acquisition in poor habitats (or in good habitats that have been depleted) demands more searching time and energy, which is reflected in their movement patterns (e.g., Powell 1994). These effects are best documented in central place foragers such as nesting birds or pinnipeds that forage at sea but breed on land. Many of these animals forage at particular oceanographic features (Boersma and Rebstock 2009) that change in location and quality from year to year. Magellanic penguins (*Spheniscus magellanicus*) breeding at Punta Tombo, Argentina showed a decrease in reproductive success with increasing average foraging trip duration (Boersma and Rebstock 2009). Also, penguins stayed longer at feeding sites in more distant foraging areas, presumably to feed themselves and recover from the increased cost of swimming (Boersma and Rebstock 2009). Thus, satellite telemetry technology has allowed a better understanding of the interplay between landscape or seascape variability and breeding success.

In Chapter 5, we show how to use discrete-time movement models to cluster animal paths into different behavioral types, which can help identify food acquisition modes based on telemetry data. We also demonstrate how to account for food-related aspects of movement in the continuous-time setting discussed in Chapter 6.

1.1.10 ENCOUNTER RATES AND PATTERNS

The “functional response” is a key component of population models that include trophic interactions; it describes the rate of prey consumption by individual predators as a function of prey density (Holling 1959a,b). The dynamics and persistence of interacting populations usually depend on the shape and dimensionality of functional responses (Turchin 2003). Mechanistically, the functional response depends on encounter rates. Thus, a useful null model for encounter rates is one where individuals move randomly and independently of each other. More than 150 years ago, Maxwell (1860) calculated the expected rates of molecular collisions of an ideal gas as a function of density, particle size, and speed.* The ideal gas model has been used and rediscovered in many ways, including Lotka's justification of predator-prey encounters being proportional to predator speed and size and to predator and prey densities. As a recent example, the scaling of home ranges with body size derived by Jetz et al. (2004) assumes that the proportion of resources lost to neighbors is related to encounter rates as calculated from the ideal gas model for known scaling relationships of speed, population density, and detection distance.

The thorough review by Hutchinson and Waser (2007) shows many more examples of the application of Maxwell's model plus several refinements, including different assumptions about detection, speed, and density. Recently, Gurarie and Ovaskainen (2013) presented analytical results and a taxonomy for a broad class of encounter processes in ecology. The movement of animals almost certainly deviates from the assumptions of Maxwell's model and we can use information about the characteristics of movement paths from real animals to derive better predictions of encounter rates, or in the case of carnivores, kill rates (e.g., Merrill et al. 2010).

Environmental heterogeneity can also be an important determinant in encounter rates and group dynamics. For example, Flierl et al. (1999) used individual-based models of fish groups to study the interplay among the forces acting on the individuals and the transport induced by water motion. They found that flows often enhanced grouping by increasing the encounter rate among groups and thereby promoting merger into larger groups.† In general, habitat structure will affect encounter rates among individuals of the same species but also among predators and prey.

Encounter rates and population dynamics are also altered when predators or prey form social groups. Fryxell et al. (2007) developed simple models of group-dependent functional responses and applied them to the Serengeti ecosystem. They found that grouping strongly stabilizes interactions between lions and wildebeest, suggesting that social groups, rather than individuals, were the basic building blocks for these predator–prey systems.

As satellite tracking devices become more affordable, and larger numbers of individuals can be tracked in the same study areas, we can expect to learn more about interactions among individuals. Furthermore, the use of additional telemetry technologies can make this more feasible. For example, Prange et al. (2006) used proximity detectors in collars fitted to free-living raccoons and were able to obtain accurate information in terms of detection range, and duration of contact. Animal-borne video systems also may help identify social interactions and foraging events for a focal individual (Hooker et al. 2008; Moll et al. 2009). Hence, the study of encounters offers great opportunities for marrying theory with data and to greatly improve our understanding of spatial dynamics.

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[*] Assuming independent movements in any direction and with normally distributed velocities.

[†] Although the grouping effect breaks down for strong flows.

As animals face similar constraints and environmental heterogeneity, it is expected that they will exhibit similar movement rules and patterns. Early enthusiasm surrounding Levy flights and walks is now being taken with a bit more caution (e.g., Pyke 2015), but it is valuable to identify common movement rules based on individual animal's morphology, physiology, and cognitive capacity. There is also much theoretical and empirical work needed to better understand the costs and benefits of different movement strategies. Scharf et al. (In Press) described a method for inferring time-varying social networks in animals based on telemetry data. Using data from killer whales, Scharf et al. (In Press) developed a model that was motivated by encounter rate approaches that clustered similarities in movement patterns to learn about underlying binary networks that identified groups of individuals and how they change over time. We discuss these ideas more at the end of Chapter 5.

1.2 TELEMETRY DATA

Animal telemetry data are varied. This variation is an advantage because different field studies often have very different objectives and logistical (or financial) constraints. At a minimum, most animal-borne telemetry devices provide information about animal location. The earliest devices were very high frequency (VHF) radio tags designed for large carnivores and ungulates.* VHF tags emit a regular radio wave signal (or pulse) at a specific frequency. A beeping sound (or ping) is heard whenever the signal is picked up by a nearby receiver that is tuned to this frequency, and the pings get louder as the receiver approaches the tag. As one hones in on the pings, the location of an animal with a VHF tag can be either closely approximated or confirmed by visual sighting. Accurate radio telemetry data acquisition requires practice and, often, triangulation. Radio tracking can sometimes be very challenging from the ground; thus, radio relocation surveys are often performed from small aircraft. Many VHF tags include a sensor that triggers a faster pulse rate after a prespecified length of inactivity that is believed to be indicative of mortality or other events (e.g., hibernation). The analysis of radio telemetry data has historically been limited to descriptive statistical models of space use, home range delineation, survival, and abundance (e.g., White and Garrott 1990; Millspaugh and Marzluff 2001; Manly et al. 2007), but more sophisticated movement models have also been applied to radio telemetry data (e.g., Dunn and Gipson 1977; Moorcroft et al. 1999). Early VHF tags were too large for many smaller species, but improvements in battery technology now permit tags that are small enough for birds and even insects. The primary limitations of VHF tags are the limited range of radio signals and the cost and effort required to reliably locate animals via radio tracking. Radio tracking technology may seem archaic in the age of smart phones, but it still offers a relatively inexpensive and long battery-lived alternative to modern telemetry devices.

Since the mid-1990s, modern telemetry devices have been capable of storing and transmitting information about an individual animal's location as well as internal and

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* We refer to "tags" generically here; for most terrestrial mammals, the telemetry devices are attached to neck collars and fitted to the individual animals. Telemetry devices have been fitted to animals in a variety of other ways.

external characteristics (e.g., heart rate, temperature, depth/altitude). Because modern telemetry devices can include additional sensors unrelated to location acquisition, the terms “biotelemetry” and “biologging” are increasingly used for describing modern animal telemetry techniques and devices (e.g., Cooke et al. 2004). There are two main types of modern (non-VHF) animal telemetry tags. These are often called storing (or “archival”) and sending (or “transmitting”) tags. Archival tags can be smaller than transmitting tags and store vast amounts of biotelemetry information, such as high-resolution accelerometer data, but they possess no mechanism for data transmission. Therefore, archival tags must be recovered from the animal before any data can be accessed. Transmitting tags send data in the form of electromagnetic waves to nearby receivers (similar to VHF tags) or to orbiting communications satellites. Satellite transmitting tags allow researchers to retrieve biotelemetry data without needing to recover or be close to the tag. Similar to archival tags, transmitting tags can store vast amounts of data. However, satellite tags require line of sight for transmission, and this limitation often necessitates careful consideration when designing and programming satellite tags. For example, marine animals do not surface long or frequently enough to transmit large quantities of biotelemetry data, so researchers must often make difficult trade-offs between data quality and quantity based on the specific objectives of their study (e.g., Breed et al. 2011).

Whether of the archival or transmitting type, most modern biotelemetry tags rely on satellites for determining an animal’s location. Tags that are equipped with an internal global positioning system (GPS) usually provide the most accurate locations currently available. GPS location errors (i.e., the distance between the observed and true location of the individual) tend to be less than 50 m, but GPS tags need to transmit larger data payloads and tend to be larger in size. Therefore, GPS tags are ideal for larger, terrestrial species in open habitat, but they are typically unsuitable for aquatic species such as marine mammals and fish.

Although not as accurate as GPS, Argos tags are a popular option for marine and small terrestrial species. Argos tags rely on a system of polar-orbiting satellites to decode the animal’s location from a relatively tiny packet of transmitted information. Argos tags can quickly transmit data to satellites within the brief intervals that marine mammals surface to breathe because the transmission packets are small. The main drawback of Argos tags is the limited size and duration of transmissions; this limits the quantity and quality of onboard biotelemetry data that can be recovered. Argos tags tend to perform best at higher latitudes (due to the polar orbits of the satellites), but location errors can typically range from hundreds to thousands of meters (e.g., Costa et al. 2010; Brost et al. 2015).*

As a compromise between GPS and Argos, Fastloc-GPS (Wildtrack Telemetry System Limited, Leeds, UK) tags compress a snapshot of GPS data and quickly transmit via the Argos satellite system. With location errors typically between 50 and 1000 m, Fastloc-GPS is considerably more accurate than Argos overall.

Biotelemetry technology is rapidly improving,† and there are many tag designs and data collection capabilities that we have not covered in this brief introduction. These

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* We describe specific aspects of Argos data and potential remedies in Chapters 4 and 5.

† See Kays et al. (2015) for a recent overview of tag technology.

include light-sensing “geologgers” for smaller species (e.g., Bridge et al. 2011), archival “pop-up” tags popular in fisheries (e.g., Patterson et al. 2008), proximity detectors (e.g., Ji et al. 2005), acoustic tags (e.g., McMichael et al. 2010), “life history” tags (Horning and Hill 2005), accelerometer tags (e.g., Lapanche et al. 2015), and automatic trajectory representation from video recordings (Pérez-Escudero et al. 2014). In what follows, we primarily focus on the analysis of location data such as those obtained from VHF, GPS, and Argos tags. However, many of the methods we present can utilize location information arising from other sources, as well as incorporate auxiliary information about the individual animal’s internal and external environment that is now regularly being collected from modern biotelemetry tags. Winship et al. (2012) provide a comparison of the fitted movement of several different marine animals when using GPS, Argos, and light-based geolocation tags.

1.3 NOTATION

A wide variety of notation has been used in the literature on animal movement data and modeling. This variation in statistical notation used makes it challenging to maintain consistency in a comprehensive text on the subject. We provided this section, along with Table 1.1, in an attempt to keep expressions as straightforward as possible. We recommend bookmarking this section on your first reading so that you may return to it quickly if the notation becomes confusing.

Conventional telemetry data consist of a finite set of spatially referenced geographic locations ($\mathbf{S} \equiv \{\mathbf{s}_1, \ldots, \mathbf{s}_i, \ldots, \mathbf{s}_n\}$) representing the individual’s observed location at a set of times spanning some temporal extent of interest (e.g., a season or year). We use the notation, $\{\boldsymbol{\mu}_1, \ldots, \boldsymbol{\mu}_n\}$ to represent the corresponding true positions of the animal. Sometimes, the observed telemetry data are assumed to be the true positions (i.e., no observation error); however, in most situations, they will be different. The times at which locations are observed can be thought of as fixed and part of the “design,” or as observed random variables. In either case, a statistical notation with proper time indexing becomes somewhat tricky. To remain consistent with the broader literature on point processes (and with Chapter 2), we assume that there are n telemetry observations collected at times $\mathbf{t} \equiv (t_1, \ldots, t_i, \ldots, t_n)'$ such that $t_i \in \mathcal{T}$ and $\mathbf{t} \subset \mathcal{T}$. The seemingly redundant time indexing accounts for the possibility of irregularly spaced data in time. If the differences ($\Delta_i = t_i - t_{i-1}$) between two time points at which we have telemetry observations are all equal, we could just as easily use the direct time indexing where the data are $\mathbf{s}_t$ for $t = 1, \ldots, T$. In that case, we have $T = n$. From a model-building perspective, it is sometimes less cumbersome to index telemetry observations in time (i.e., $\mathbf{s}_t$) and deal with temporal irregularity during the implementation. However, there are some situations, for example, when the points are serially dependent, where we need the Δ_i notation. A further perspective on notation arises when considering that the true animal location process is a continuous process in time. To formally recognize this, we often index the observed location vectors as $\mathbf{s}(t_i)$ (or $\boldsymbol{\mu}(t_i)$, in the case of the true positions). The parenthetical notation at least admits that we are often modeling animal locations as a continuous function. Thus, prepare yourself to see all types of indexing, both in this text and in the vast animal movement literature.

TABLE 1.1
Statistical Notation

Notation	Definition
i	Observation index for $i = 1, \ldots, n$ total observations.
t	Time point at which the data or process occurs (in the units of interest).
$\mathcal{T}$	The set of times at which the process exists; typically compact interval in continuous time such that $t \in \mathcal{T}$.
t_i	Time associated with observation i.
T	Either largest time in observations or process, or upper temporal endpoint in study, depending on context.
$\mathbf{s}_i$	Observed telemetry observation for $i = 1, \ldots, n$. $\mathbf{s}_i$ is a 2×1 vector unless otherwise stated. Also written as: $\mathbf{s}(t_i)$ in continuous-time context.
$\mathcal{S}$	The spatial support for the observed telemetry observations (i.e., $\mathbf{s} \in \mathcal{S}$).
$\boldsymbol{\mu}_i$	True individual location (i.e., position) for $i = 1, \ldots, n$. $\boldsymbol{\mu}_i$ is a 2×1 vector unless otherwise stated. Also written as: $\boldsymbol{\mu}(t_i)$ in continuous-time context.
$\mathcal{M}$	The spatial support for the true individual locations (i.e., $\boldsymbol{\mu}(t) \in \mathcal{M}$). Typically, the support for the true locations $\mathcal{M}$ is a subset of the support for the observed locations $\mathcal{S}$ (i.e., $\mathcal{M} \subset \mathcal{S}$).
$\mathbf{X}$	A "design" matrix of covariates, which will often be decomposed into rows $\mathbf{x}_i$ for row i, depending on the context in which it is used.
$\boldsymbol{\beta}$	Vector of regression coefficients (i.e., $\boldsymbol{\beta} \equiv (\beta_1, \beta_2, \ldots, \beta_p)'$), where p is the number of columns in $\mathbf{X}$.
$\boldsymbol{\beta}'$	The "prime" symbol ($'$) denotes a vector or matrix transpose (e.g., converts a row vector to a column).
σ^2	Variance component associated with the observed telemetry data, true position process, or a model parameter.
$\boldsymbol{\Sigma}$	Covariance matrix for either a parameter vector such as $\boldsymbol{\beta}$ (if subscripted) or the data or process models.
$f(\cdot)$, $[\cdot]$	Probability density or mass function. $p()$, $P()$, and $\pi()$ are used in other literature. The $[\cdot]$ has become a Bayesian convention for probability distributions.
$E(y)$	Expectation of random variable y; an integral if y is continuous and sum if y is discrete.
$\propto$	Proportional symbol. Often used to say that one probability distribution is proportional to another (i.e., only differs by a scalar multiplier).

1.4 STATISTICAL CONCEPTS

We focus mostly on parametric statistical models[*] in this book; thus, we rely on both Bayesian and non-Bayesian models using maximum likelihood. Occasionally, for example, in Chapters 2 through 4, we present statistical methods that are nonparametric or involve implementation methods that do not involve Bayesian or maximum likelihood approaches. A generic data model statement will appear as $y_i \sim [y_i|\boldsymbol{\theta}]$,

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[*] Parametric statistical models involve the specification of known probability distributions with parameters that are unknown but estimated in the model fitting procedure.

where y_i are the observations (we use $\mathbf{s}_i$ for telemetry observations instead of y_i) for $i = 1, \ldots, n$, $\boldsymbol{\theta}$ are the data model parameters, and the bracket notation "[·]" represents a probability distribution. The data model is often referred to as the "likelihood" by Bayesians, but the likelihood used in maximum likelihood estimation (MLE) is proportional to the joint distribution of the data conditioned on the parameters. When the observations are conditionally independent, the likelihood is often written as $[\mathbf{y}|\boldsymbol{\theta}] = \prod_{i=1}^{n}[y_i|\boldsymbol{\theta}]$, where individual data distributions can be multiplied to obtain the joint distribution because of independence. To fit the model using MLE, the likelihood is usually maximized numerically to find the optimal parameter values $\hat{\boldsymbol{\theta}}$.

The Bayesian approach involves the specification of a probability model for the parameters, $\boldsymbol{\theta} \sim [\boldsymbol{\theta}]$, that depend on fixed hyperparameters assumed to be known. The prior probability distribution should contain information about the parameters that is known before the data are collected, except for cases where regularization-based model selection is desired (Hooten and Hobbs 2015), in which case, the prior can be tuned based on a cross-validation procedure. Rather than maximizing the likelihood, the Bayesian approach seeks to find the conditional distribution of the parameters given the data (i.e., the posterior distribution)

$$[\boldsymbol{\theta}|\mathbf{y}] = \frac{[\mathbf{y}|\boldsymbol{\theta}][\boldsymbol{\theta}]}{\int [\mathbf{y}|\boldsymbol{\theta}][\boldsymbol{\theta}]\, d\boldsymbol{\theta}}, \tag{1.1}$$

where $\mathbf{y}$ is a vector notation for all the observations and the denominator in Equation 1.1 equates to a scalar constant after the data have been observed. For complicated models, the multidimensional integral in the denominator of Equation 1.1 cannot be obtained analytically (i.e., exactly by pencil and paper) and must be either numerically calculated or avoided using a stochastic simulation procedure. Markov chain Monte Carlo (MCMC; Gelfand and Smith 1990) allows us to obtain samples from the posterior distribution while avoiding the calculation of the normalizing constant in the denominator of Equation 1.1. MCMC algorithms have many advantages (e.g., easy to develop), but also limitations (e.g., can be time consuming to run).

Hierarchical models are composed of a sequence of nested probability distributions for the data, the process, and the parameters (Berliner 1996). For example, a basic Bayesian hierarchical model is

$$y_{i,j} \sim [y_{i,j}|z_i, \boldsymbol{\theta}], \tag{1.2}$$

$$z_i \sim [z_i|\boldsymbol{\beta}], \tag{1.3}$$

$$\boldsymbol{\theta} \sim [\boldsymbol{\theta}], \tag{1.4}$$

$$\boldsymbol{\beta} \sim [\boldsymbol{\beta}], \tag{1.5}$$

where z_i is an underlying process for individual i and $y_{i,j}$ are repeated measurements for each individual ($j = 1, \ldots, J$). Notice that the process model parameters $\boldsymbol{\beta}$ also require a prior distribution if the model is Bayesian. The posterior for this model is a generalized version of Equation 1.1 such that

$$[\mathbf{z}, \boldsymbol{\theta}, \boldsymbol{\beta} | \mathbf{y}] = \frac{[\mathbf{y}|\mathbf{z}, \boldsymbol{\theta}][\mathbf{z}|\boldsymbol{\beta}][\boldsymbol{\theta}][\boldsymbol{\beta}]}{\iiint [\mathbf{y}|\mathbf{z}, \boldsymbol{\theta}][\mathbf{z}|\boldsymbol{\beta}][\boldsymbol{\theta}][\boldsymbol{\beta}]\, d\mathbf{z}\, d\boldsymbol{\theta}\, d\boldsymbol{\beta}}. \tag{1.6}$$

Throughout the remainder of this book, we use both Bayesian and non-Bayesian models for statistical inference in the settings where they are appropriate. Many complicated hierarchical models are easier to implement from a Bayesian perspective, but may not always be necessary. Hobbs and Hooten (2015) provide an accessible description of both Bayesian and non-Bayesian methods and model-building strategies as well as an overview of basic probability and fundamental approaches for fitting models. Hereafter, we remind the reader of changes in notation and modeling strategies as necessary without dwelling on the details of a full implementation because those can be found in the referenced literature.

1.5 ADDITIONAL READING

The timeless reference describing the mathematics of animal movement processes is Turchin (1998), and while newer references exist, Turchin (1998) is still the default for many scientists. For a newer synthesis, the special issue in the *Philosophical Transactions of the Royal Society of London B* provided a cross section of contemporary ideas for modeling animal movement and analyzing telemetry data (see Cagnacci et al. 2010 for an overview). Schick et al. (2008) proposed a general hierarchical modeling structure to modeling telemetry data that many contemporary efforts now follow.

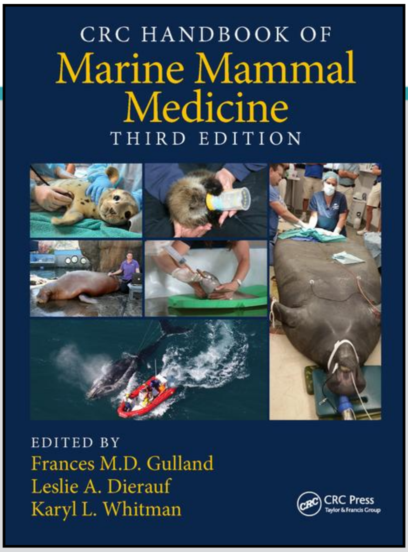
Historical, but still very relevant, references describing approaches for collecting and analyzing telemetry data include White and Garrott (1990), Kenward (2000), Millspaugh and Marzluff (2001), and Manly et al. (2007), although they focused more on vital rates (e.g., survival), resource selection, and home range estimation from radio telemetry data because that technology preceded current satellite telemetry devices.

Connecting telemetry data with population demographic data is still nascent. However, the field of SCR models is advancing rapidly and a few developments of SCR models have formally incorporated telemetry data to better characterize space use and resource selection. Also, individual-based movement models, in general, provide us with a better understanding about how animals are interacting with each other and their environment and the learning that is gained from fitting them can be used to develop smart demographic models that best account for features of population and community dynamics that depend on movement.

CHAPTER

2

SEAL AND SEAL LION MEDICINE



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SEAL AND SEA LION MEDICINE

CARA L. FIELD, FRANCES M. D. GULLAND, SHAWN P. JOHNSON, CLAIRE A. SIMEONE, AND SOPHIE T. WHORISKEY

Contents

Introduction

Seals and sea lions are commonly managed in display facilities and rehabilitated after stranding, with much of the medicine presented here learned from care of the California sea lion (*Zalophus californianus*), northern fur seal (*Callorhinus ursinus*), South American sea lion (*Otaria flavescens*), harbor seal (*Phoca vitulina*), gray seal (*Halichoerus grypus*), and northern elephant seal (*Mirounga angustirostris*). While disease prevalences vary widely across species and environment, much of the knowledge gained from care of these more common species may be applied to lesser known species.

Husbandry

Pools, Haul-Out Areas, and Enclosures

All pinnipeds require both water and haul-out space. Although seals and sea lions can survive without access to water for weeks at a time, they appear more content when given free access to water. Most pinnipeds will eat more readily when offered food in water, particularly in a rehabilitation situation. Fur seals will defecate and groom when given access to a pool; if left in a dry haul-out area, they may appear clinically depressed and fur quality may be compromised by contact with urine and feces. Pool design should aim at accommodating the behavioral and physical needs of the animals housed, as well as maintaining water quality (see **Chapter 31**). For otariids, the pool may be sunken below ground or raised, with access by ramps. As phocids do not have the climbing abilities of otariids, a sunken pool with the water level close to the edge to allow easy exit from the pool is preferred. Debilitated pinnipeds may have difficulty exiting pools, regardless of design, though gently sloping sides or ledges just below the surface of the water both facilitate the egress of any species and allow seals to rest in shallow water.

Pinnipeds should be housed in salt water; however, they are often housed in freshwater systems due to economic or logistical constraints. Ophthalmic problems are more common in freshwater than in salt water, and in pools without shade (Dunn et al. 1996; Colitz 2010b; see section below entitled Eyes; see **Chapter 23**). Fur seals in particular should be housed in salt water, as they may not groom properly in freshwater, resulting in loss of fur integrity and poor thermoregulation. While freshwater is generally not available to wild pinnipeds, provision of freshwater (low-lying bucket or pan) to pinnipeds in salt water systems may help them maintain hydration, particularly during rehabilitation and when housed in particularly warm environments. When housed in freshwater, oral salt supplementation should be provided to prevent hyponatremia (Geraci 1972a; Lair et al. 2002).

Lighting should mimic the natural photoperiod for the species as closely as possible. Harbor seals maintained in continuous light conditions have had disrupted molt cycles that reverted to normal when a natural photoperiod was reinstated (Mo, Gili, and Ferrando 2000). Extremes of both heat and cold should be prevented, although in general most species are better able to tolerate cold than heat. Geraci (1986) states that healthy, robust harbor, gray, harp (*Pagophilus groenlandicus*), and ringed seals (*Phoca hispida*) can tolerate water at freezing temperatures, and air temperature below −20°C (−4°F), although a northern elephant seal died after being exposed suddenly to an outdoor temperature of −15°C (5°F) for 30 minutes. Hyperthermia can be avoided by providing access to shade, pools, or sprinklers, when ambient temperatures rise above 26°C (79°F). Hypothermia is rare, but can be a significant problem in thin, malnourished animals in rehabilitation. Provision of waterproof heating pads, plastic pads, platforms off concrete floors, or kennel areas with heat lamps, as well as permanent structures that provide protection from wind and rain, can help prevent hypothermia.

Feeding

Although wild pinnipeds feed on a variety of prey, managed animals are usually maintained on a diet of herring (*Clupeidae* spp.), smelt (*Osmeridae* spp.), mackerel (*Scombridae* spp.), capelin (*Mallotus villosus*), and squid (*Loligo* spp.). Care should be taken if feeding mackerel and other scombroid fish to ensure it has been appropriately stored to avoid scombroid toxicity. As herring is a relatively fatty fish, it is commonly fed to produce rapid weight gain. Details of the nutritional content of different diets and the methods to calculate calorific requirements of marine mammals are provided (see **Chapter 29**), while hand-rearing techniques are given in **Chapter 30**. As a rough guideline, young growing pinnipeds are fed 8–15% of their body weight of food per day, and older animals 4–8% per day. Thiamine at 25 to 35 mg/kg fish and vitamin E at 100 IU/kg fish are recommended to prevent nutritional disorders associated with a frozen fish diet. When supplementing an animal's diet, it is advisable to feed a fish containing the supplements prior to the main feed to ensure the animal receives all of its medications.

Restraint

The methods commonly used to restrain pinnipeds may be classified into behavioral, physical, mechanical, and chemical, with choice depending upon the objective. For example, if the desired objective is to perform an abdominal ultrasound, a mechanical squeeze may be safest for handlers and the animal, but may be suboptimal for effective ultrasound positioning. Different types of restraint are often used in combination. For example, a chemical sedative such as a benzodiazepine may be given to an animal to augment physical restraint. Many of these techniques are depicted well in Geraci and Lounsbury (1993).

Behavioral Restraint Behavioral restraint is an extremely effective technique for most captive pinniped species and can be either free- or protected-contact. The participation of an animal in its own health evaluations can be far less stressful and time-consuming than other restraint techniques, though the lack of a barrier in a free-contact situation may also be dangerous to people or animals (see **Chapter 39**).

Physical Restraint Physical restraint is limited by size and species, the animal's level of aggression and alertness, and the experience and physical ability of the restrainers. It is usually very safe for the animal, but human safety is a concern with larger animals. Physical restraint requires a thorough knowledge of the behavior and anatomy of the species being restrained. For example, larger otariids have tremendously strong forelimbs in comparison with phocids. The fore flippers may have to be secured by additional personnel to prevent the animal from gaining leverage and rising up (Gentry and Holt 1982). Creative use of towels, blankets, bags, and nets will aid physical restraint and increase the safety of personnel. A common method of restraint of a smaller pinniped (phocids under approximately 60 kg and otariids under approximately 30–40 kg) is to place a hoop net or wrap large towel over the animal's head to restrict vision and mobility prior to restraining. The primary restrainer can then control the head by holding the base of the skull with both hands and pushing the head toward the ground. The primary restrainer should straddle the animal by resting their knees on the ground and controlling the side-to-side and upward motion. It is critically important that the restrainer rest their body weight on their own knees and not on the animal, as the pressure can severely restrict the animal's respirations. Care must also be taken to ensure that the animal's nares and mouth are clear of netting or towels to allow full respirations.

Mechanical Restraint Mechanical restraint is limited by the availability of adequate equipment, the cost of which varies considerably. Many types of mechanical restraint devices have been used with pinnipeds, including chutes, herding boards, restraint boards, stretchers with straps, restraint boxes, squeeze cages, and slings (Cornell 1986; Gentry and Casanas 1997). As some mechanical restraint equipment can be very large and heavy, it may be difficult to use in field situations. In general, mechanical restraint devices are designed to maximize safety to human operators, but may pose some risk to the animal. Some restraint boards require a padded, hinged guillotine to secure the neck, and could obstruct the airway. Mechanical squeeze cages should be used with caution, and only by experienced personnel, since it is possible to use excessive pressure and cause trauma or interfere with adequate ventilation. Be aware that some of the mechanical restraint devices limit full access to the animal.

Chemical Restraint The ability to use chemical restraint relies on the expertise of the operators, and often requires the presence of a specially trained veterinarian (see **Chapter 26**). Some commonly used agents for sedation of phocids include diazepam, or midazolam +/− butorphanol intravenously (IV) or intramuscularly (IM; though diazepam has relatively poor IM absorption), and for anesthesia are IV propofol, alfaxalone, or tiletamine/zolazepam. Induction agents are likely to induce apnea; thus, the clinician should be prepared to intubate. Masking with isoflurane or sevoflurane is possible, but may prove difficult due to breath-holding; however, both are commonly used for anesthetic maintenance. Some common agents used in otariids include midazolam with medetomidine and butorphanol IM, which can be reversed with flumazenil, atipamezole, and naltrexone, respectively. Alternatively, midazolam with either alfaxalone or ketamine IM can be used effectively, although the ketamine dose is generally lower than that used in terrestrial mammals. Isoflurane and sevoflurane are also commonly used safely in conjunction with injectable agents, and smaller otariids can be readily masked to an anesthetic plane (with either inhalant) while manually restrained. Additional information on sedative and anesthetic drugs and dosages is given in **Chapters 26 and 27**.

Diseases

Details of viral, bacterial, fungal, protozoal, parasitic, and noninfectious diseases of pinnipeds are provided in **Chapters 14 and 17 through 21**, respectively. To avoid repetition, this chapter focuses on the clinical signs of these diseases, describes these by affected organ system for ease of differential diagnosis, and then discusses treatment. Drug dosages for recommended therapeutic agents are given in **Chapter 27**.

Integumentary System

Multiple viruses cause dermal lesions in pinnipeds, with sealpox and calicivirus among the most common. Documented sealpox viral infections are generally of the Parapoxvirus family (Becher et al. 2002; Nollens et al. 2006), though an Orthopoxvirus has been identified in two wild Steller sea lion pups in Alaska (Burek et al. 2005). Poxvirus infections typically occur in animals that have been recently weaned or are in a rehabilitation setting; then these infections spread rapidly among a susceptible population (Hastings et al. 1989; Müller et al. 2003; Nollens et al. 2005). These viruses cause pathognomonic lesions, which consist of round, raised, firm skin nodules 0.5 to 1 cm (0.4 in) in diameter that gradually increase in size over the first week, and may ulcerate or suppurate (see **Chapter 17**). Lesions commonly occur over the head and neck, but may also arise over the thorax and abdomen, perineal regions, or in the oral cavity (Müller et al. 2003; Nollens et al. 2005). Satellite lesions appear in the second week and may spread rapidly. Lesions are usually self-limiting and regress after 4–6 weeks, although some have persisted for months. Animals usually remain active when affected, although lesions around the lips and eyes may cause sufficient discomfort to reduce appetite. Marked neutrophilia and hyperglobulinemia may occur in association with nodule development. Diagnosis can be made through skin biopsy (see **Chapter 17**). Treatment is usually unnecessary, although broad-spectrum antibiotics may be needed to control secondary bacterial infections, and nonsteroidal anti-inflammatory drugs (NSAIDs) can be used to reduce discomfort associated with the lesions. In vitro studies suggest that cidofovir could be an effective antiviral in treating sealpox (Nollens et al. 2008). Sealpox is zoonotic and proper personal protective equipment (PPE) should be worn when handling affected individuals (see **Chapter 4**).

San Miguel sea lion virus is a calicivirus that in California sea lions causes vesicles on both dorsal and ventral surfaces of the flippers, occasionally around the lips, on the dorsum of the tongue, and on the hard palate (Gage et al. 1990; Smith and Boyt 1990; Van Bonn et al. 2000; see **Chapter 17**). The vesicles usually erode, leaving rapidly healing ulcers, but may become secondarily infected by bacteria, especially in malnourished and debilitated animals. Calicivirus has also been shown to cause gastroenteritis on the onset of infection, with signs of vomiting, abdominal pain, and diarrhea. Sea lions will respond to supportive care of fluid therapy and antibiotic coverage. Hematologic changes can include neutropenia, lymphopenia, and thrombocytopenia. The disease can progress to vesicles following the enteritis phase (Schmitt 2009). Diagnosis is confirmed with PCR or isolation of the virus from aspirated vesicular fluid or feces, but is often presumptive based on clinical appearance. Treatment is supportive, aimed at preventing secondary infection and enhancing nutritional status of the animal. Occasionally, stranded sea lions are observed with severe gangrenous necrosis of the phalanges. Although development of these lesions has not been observed, it is suspected that they may result from vesicles that became secondarily infected with bacteria. These lesions are treated with debridement, topical wound care, and systemic antibiotic therapy based on culture and antibiotic sensitivity results. NSAIDs can also be used to reduce discomfort. A novel papillomavirus was identified in two California sea lions with proliferative and focally extensive skin lesions. PCR was used to characterize the virus and the lesions regressed, without treatment, after several months (Rivera et al. 2012).

Herpesviruses have been isolated from harbor and gray seals with small erosive skin lesions, and observed in epithelial plaques in harbor seals and California sea lions. Although infrequent, herpesviruses should be considered in the differential diagnosis of skin lesions, and skin biopsies should be examined for inclusions.

Morbillivirus dermatitis has been diagnosed in both a hooded seal (*Cystophora cristata*) and a harp seal. Skin lesions consisted of epithelial hyperplasia, hyperkeratosis, degeneration, and necrosis, and the systemic infection was fatal in both cases. Diagnosis of morbillivirus is described in **Chapter 17**.

Bacterial infections are common in pinnipeds, especially in dermal abscesses in stranded animals, though are rarely reported in the literature as the primary cause of dermal disease (see **Chapter 18**). Multifocal circular ulcers 1–2 cm (0.4–0.8 cm) in diameter have been observed in California sea lions and northern elephant seals. Histologically, these appear to be the consequence of vasculitis and thrombosis. Microabscesses are also common on the ventral abdomen of sea lions following septicemia. Diagnosis is based on the histological appearance of biopsies, and treatment with systemic antibiotics is recommended. Secondary bacterial infections are common with traumatic injuries and bite wounds. Antibiotic therapy should be selected based on culture and sensitivity when possible. Bite wound infections can lead to severe systemic disease, as in the case of one California sea lion, which developed a focal bacterial meningitis and paraparesis from a chronic dermal ulcer. *Escherichia coli* serovar *haemolytica* and *Clostridium perfringens* were identified as the primary underlying agents (Braun et al. 2015). Subcutaneous abscesses due to infection with *Mycobacterium chelonii* in a captive gray seal (Stoskopf et al. 1987) and *M. smegmatis* in a captive California sea lion (Gutter, Wells, and Spraker 1987) were diagnosed after culturing the organisms from aspirated fluid. The gray seal was treated successfully with minocycline, while the sea lion died with concurrent pulmonary abscesses. Methicillin-resistant *Staphyloccocus aureus* (MRSA) has been documented in a stranded harbor seal. Treatment was successful and based on culture and sensitivity (Fravel et al. 2011).

A number of fungal diseases of the skin have been described. Fungal acanthosis and alopecia associated with *Candida albicans* and *Fusarium* spp. infections typically occur at mucocutaneous junctions, around nail beds, and in the axillae. Lesions are most often observed in managed animals maintained in freshwater. Diagnosis is based on skin scrapings and fungal culture, PCR, and/or histological examination of biopsies. Topical treatment is difficult without limiting access to water, but systemic treatment of an elephant seal with fluconazole at 0.5 mg/kg was effective in clearing clinical signs (Gulland, unpubl. data)

Trychophyton rubrum infection caused multifocal to coalescing, ulcerative, and nonpruritic lesions over the lumbar region in a Patagonian sea lion. Oral terbinafine at approximately 2.3 mg/kg per os (PO) SID and a topical dilution of enilconazole over a period of 75 days were successful in clearing the infection (Quintard, Lohmann, and Lefaux 2015). Similar treatment was employed for two California sea lions with *Microsporum gypseum* dermatomycosis with complete resolution of lesions after 65 days of therapy. Lesions were well demarcated, depigmented, were covered in crusts, and were most extensive over the flippers (Sós et al. 2013). *Trichophyton mentagrophytes*, *Malassezia* spp., and *Yarrowia* (*Candida*) *lipolytica* were isolated in a group of captive harbor seals and gray seals that presented with erythematous, thickened, alopecic skin lesions. Lesions were primarily found over the face and flippers, particularly around the nail bed. Various treatments were initiated including topical treatment with miconazole and chlorhexidine, and systemic treatment with oral itraconazole at 5 mg/kg PO BID with variable responses. Environmental factors, including overchlorination of water and warm water temperatures, contributed to occurrence of disease (Pollock, Rohrbach, and Ramsay 2000). Cystofilobasidiales infection caused systemic mycoses in a California sea lion. This animal presented with ring lesions over the flippers, which progressed to dermal nodules over the flippers, abdomen, and muzzle. Itraconazole (2.5 mg/kg PO BID), and later voriconazole (4 mg/kg PO BID), failed to resolve the infection. Acute liver failure was noted, likely due to voriconazole toxicity, and thus caution is recommended in using voriconazole to treat fungal infections (Field et al. 2012).

Alopecia, broken hair shafts, and pruritus are common in debilitated seals and sea lions associated with lice infestation. Most infections are species specific; the California sea lion louse is *Antarctophthirius microchi*, and the harbor seal louse is *Echinophthirius horridis*. Lice may be observed with the naked eye and are readily treated with ivermectin, dichlorvos, or disophenol systemically, or with topical rotenone louse powder. Demodicosis, also characterized by alopecia and pruritus, has been observed in California sea lions, northern fur seals (Spraker, pers. comm.), and harbor seals (Kim, Lee, and Kwak 2015). Diagnosis based on histological detection in biopsies and treatment with Amitraz (0.01% once weekly) and ampicillin (10 mg/kg PO SID) has been effective in clearing clinical symptoms of demodectic mange (Sweeney 1986b; Kim, Lee, and Kwak 2015). *Peladora strongyloides* parasites have caused mild superficial dermatitis and perifolliculitis in Pacific harbor seals. Diagnosis was made by biopsy and histology (McHuron et al. 2013).

Traumatic skin wounds are common in stranded animals. Net entanglements, fishhooks, and gunshot injuries are especially common in California sea lions (Goldstein et al. 1999). Diagnosis of gunshot injuries is dependent upon radiographic detection of lead fragments or pellets, or recovery of the projectile, although many wounds suggestive of exit wounds are observed in pinnipeds from which no evidence of gunshot can be detected. Differential diagnoses include bite wounds (usually paired holes of similar size) and bird damage. The characteristics of shark bite wounds vary with species of shark. Management of traumatic skin wounds is based on removal of foreign bodies and debris, debridement of devitalized tissue, control of infection, and promotion of healing, as in domestic animals. Many topical therapies have been employed including Betadine ointment, chlorhexidine scrubs, silver alginate dressings, platelet-rich plasma, Granulex sprays, honey, laser therapy, and many more. Choice of topical agents should be made on a case-by-case basis. Placing an animal in salt water rather than freshwater may enhance wound cleansing. Tetracycline and penicillin have been used to treat shark wounds, as *Vibrio* spp. and *Clostridium* spp. are frequently isolated from these wounds (Pavia et al. 1989; Klontz et al. 1993). Severe tissue avulsion from traumatic injury is managed best with debridement of necrotic tissue and topical treatment to encourage granulation and healing by secondary intention rather than surgical closure.

Rare neoplastic diseases of the skin have been diagnosed in pinnipeds. A cervical dermal melanoma was described in a 7-month-old stranded harbor seal. Diagnosis was made by fine needle aspirate and subsequent biopsy and histopathology, though the animal died during surgery to remove the mass. The melanoma was described as low grade, and no evidence of metastasis was found on histopathology (Morick et al. 2010). Pleomorphic liposarcoma was described in a captive South African fur seal that presented with a large, progressive, ulcerated mass over the right shoulder. The animal died, and pulmonary, hepatic, splenic, and lymph node metastases were noted on necropsy (Pervin et al. 2016). A cutaneous mast cell tumor was identified in an adult captive California sea lion. Biopsy was needed for diagnosis, and surgical excision was successful in removing the tumor (Staggs, Henderson, and Labelle 2016). An invasive cutaneous squamous cell carcinoma was documented in a Hawaiian monk seal, and surgical excision was elected (Doescher et al. 2010). Benign mammary hyperplasia resulting in a mammary mass development was identified in a managed subadult female sea lion and surgically excised with no recurrence (Schmitt, unpubl. data).

Alopecia and acanthosis have occurred in captive harbor seals that failed to molt when maintained in constant photoperiod (Mo, Gili, and Ferrando 2000). Diagnosis was based upon clinical history, and restoration of a natural photoperiod resulted in new hair growth. Cutaneous lupus erythematosus was diagnosed in a captive gray seal that for 9 years had continuous ulcerative nasal dermatitis and intermittent ulcerative dermatitis of the nail beds and dorsum of the body (Burns 1993). Treatments with systemic prednisone, antibiotics, and antifungals, and with topical steroids, and protection from ultraviolet radiation, were unsuccessful, and the seal died during the second week of treatment. A pruritic allergic dermatitis, with loss of guard hairs over the dorsum, was described in a captive sub-Antarctic fur seal (*Arctocephalus tropicalis*; Bodley, Monaghan, and Mueller 1999). Diagnosis was based on positive reactions to allergens prepared from weed, grass, tree pollens, and some insects. Symptomatic treatment with oral antihistamines was only partially successful, but specific allergen immunotherapy using 10 allergens was effective, despite side effects.

Alopecia of an unknown cause is well documented in juvenile Australian fur seals. Affected individuals are generally in poorer body condition than healthy conspecifics and have higher circulating T4 levels, possibly due to increased thermoregulatory demands. Higher levels of PCBs in association with thyroid disruption have been documented in this population, though thyroid disturbance does not appear to be the cause of the alopecia (Lynch, Keeley, and Kirkwood 2014). Guard hair alopecia of unknown cause has also been observed in stranded northern fur seals and Guadalupe fur seals (Field, unpubl. data).

A skin condition characterized by hyperkeratosis, alopecia, and ulceration has been well described in northern elephant seals, but its etiology remains obscure (Beckmen et al. 1997). This disease has been associated with decreased levels of circulating thyroxine (T4) and triiodothyronine (T3); however, thyroid function testing was normal in affected individuals (Yochem et al. 2008). Another ulcerative skin disease of obscure etiology has been described by Anderson et al. (1974) in gray seals. In 2011, a new ulcerative dermatitis disease syndrome was described in a number of Arctic pinniped species, including Pacific walruses (*Odobenus rosmarus divergens*), bearded seals (*Erignathus barbatus*), ringed seals (*Phoca hispida*), ribbon seals (*Phoca fasciata*), and spotted seals (*Phoca largha*). This unusual mortality event (UME) was characterized by generalized ulcers/erosions in Pacific walruses, and similar lesions with alopecia over the eyes, muzzle, hind flippers, tail, and trunk of ice seals. Affected individuals were more approachable and lethargic, with a tendency to haul out more frequently. Some mortality has been associated with the syndrome, and histopathology indicates significant involvement of the liver, lung, immune system, and the skin's vascular bed. To date, no associated bacterial, viral, or fungal agent has been identified, and no toxin or pollutant has been implicated in causing this disease (Burgess et al. 2013; Stimmelmayr et al. 2013).

Musculoskeletal System

Diseases involving the pinniped musculoskeletal system include infectious causes, trauma, and congenital abnormalities. Numerous bacteria can cause deep abscesses, myositis, osteomyelitis, and arthritis (Thornton, Nolan, and Gulland 1998). Most of these bacteria are opportunistic, occurring following trauma, introduction through contaminated hypodermic needles or surgical instruments, or hematogenous spread, as a result of generalized sepsis (see **Chapter 18**). *Clostridium perfringens* has been isolated from cases of severe myositis following poor injection technique (Greenwood and Taylor 1978), and *Otariodibacter oris* was isolated from seals and sea lions with abscesses or osteomyelitis, as well as a variety other bacteria (Hansen et al. 2013).

Sarcocystis infection causes myositis, as well as neurologic and generalized disease in pinnipeds (see **Chapter 20**). Antemortem diagnosis may be based on clinical presentation, as well as antibody levels, with confirmation by histology and PCR of muscle biopsies. Treatment with oral ponazuril at 10 mg/kg for at least 4 weeks, along with supportive care (fluids and anti-inflammatory medication to reduce inflammation secondary to parasite die-off), has been clinically effective in some cases (Carlson-Bremer et al. 2012; Alexander et al. 2015), although optimal treatment duration is still unclear, and up to 3 months of treatment may be required to clear an infection (Mylniczenko, Kearns, and Melli 2008). Parasites, including the filariid *Acanthocheilonema odenhali* and inactive *Uncinaria* spp. larvae, may be found in muscles and fascia, but do not usually cause clinical signs of disease.

Trauma is especially common in free-ranging, stranded pinnipeds. Osteomyelitis affecting the extremities, in particular, is a common occurrence secondary to trauma (Thurman, Downes, and Barrow 1982), or superficial infections such as calicivirus (see Integumentary System above). Antimicrobial treatment is generally utilized in these cases. Fractures may require surgical repair or amputation, particularly with open, chronic, fractures and osteomyelitis (Bennett, Dunker, and Gage 1994; Lucas, Barnett, and Reiley 1999; Lewer et al. 2007; Malabia et al. 2011; Hespel et al. 2013; Garcia et al. 2015; see Surgery below). Rhabdomyolysis secondary to general anesthesia and surgery are described (Bailey et al. 2012), and patient positioning and support, as well as close perioperative and postoperative monitoring, is recommended for longer surgical procedures, particularly involving larger animals. Monofilament line entanglement or fishhooks in the skin often require general anesthesia to cut material free and clean wounds. Intervertebral disc protrusion, collapsed thoracic disc spaces, or spondylitis has been observed in wild animals, secondary to blunt force trauma, or managed animals performing repetitive behaviors, such as standing vertical against a wall (Schmitt, pers. comm.). The spinal cord in pinnipeds terminates between the 8th and 12th thoracic vertebrae, so any trauma to the cranial spine or collapsed thoracic disc space can result in paresis or paralysis of hind flippers.

Some neoplastic diseases can manifest clinical signs in the musculoskeletal system. Carcinomas may erode the lumbar spine, affecting neurological function, as well as potentially resulting in pathological fractures. Animals may exhibit hind-end paresis or paralysis (Gulland et al. 1996a). Lymphosarcoma has affected the bone marrow in a harbor seal (Stroud and Stevens 1980), and a rhabdomyosarcoma was noted in a free-ranging Steller sea lion (Zabka et al. 2004). High levels of polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethane (DDT) have been associated with pathological bone lesions and reproductive failure in seals in the Baltic Sea, likely due to alterations in bone and thyroid homeostasis; however, the effects of these compounds remain to be fully characterized (Routti et al. 2008). A variety of congenital bone malformations and abnormalities have been reported in pinnipeds, including occipital bone dysplasia, atlantoaxial subluxation, and cribriform plate aplasia (Dennison et al. 2009; Maclean et al. 2008).

Physical examination, fine-needle aspiration with cytology and culture of the aspirate, muscle biopsy, radiographs, computerized tomography, and ultrasound (see **Chapters 24 and 25**) will all facilitate diagnosis of musculoskeletal problems. Treatment is dictated by the diagnosis, though certain techniques commonly used in other species may be difficult in pinnipeds, such as splinting. Initial wound care is similar to other species, and fracture repair of extremities has been performed using both internal and external fixator systems (see Surgery below). Bandaging is particularly difficult in these species due to their fusiform body shape, flipper shape, and aquatic environment. Wounds are often left open for second intention healing while allowing animals access to water where they appear to be more comfortable.

Digestive System

Otariids will show behavioral signs of discomfort with abdominal pain, such as fore flippers extended down over the ventral abdomen, or logging at the surface or clutching to the edge of a pool edge on their side with fore and hind flippers with a hunched abdomen. Dental disease in pinnipeds can be ascertained by animals showing complete inappetence, dropping fish, dysphagia (playing with food), or prehending food on one side and not the other.

Oral lesions are often viral or traumatic in origin. Herpesvirus, morbillivirus, and poxviruses can cause ulcerative oral lesions in pinniped species. Treatment is largely supportive, and targeted at controlling secondary bacterial infections and reducing discomfort. Trauma secondary to foreign bodies such as fishhooks or entanglements is also relatively common. Partial glossectomy was effective in removing necrotic lingual tissue secondary to fishhook entanglement in a Hawaiian monk seal (Barbieri et al. 2013). Megaesophagus and concurrent intestinal volvulus have been described in harbor seals in two separate cases. Clinical symptoms included aerophagia, regurgitation, vomiting, diarrhea, bloat, abdominal pain, and occasional inappetence. Megaesophagus was diagnosed using contrast radiography. Both were medically managed using gastric support medications, but eventually died from complications (Tuomi et al. 2011). Ingested foreign bodies are not uncommon in dehydrated and malnourished seals and sea lions. On the East coast, rescued "ice seals," such as harp and hooded seals, have been diagnosed with gastric impaction secondary to ingestion of rocks. Gastrotomy has been performed to remove rocks, with successful recovery and return to the wild (Schmitt, pers. comm.). Wild sea lions are diagnosed with monofilament line and fishhook ingestion commonly, and successful treatment is based on the degree of tissue damage, and if the hook can be removed with endoscopy or gastrotomy (Schmitt, pers. comm.)

Gastritis and gastric ulcers are common in pinnipeds. Stress and high burdens of gastric nematodes can cause gastric ulceration and chronic emesis. Gastric nematodes have also caused duodenal perforations leading to peritonitis and death in stranded California sea lions (Fletcher et al. 1998). Gastroprotectants and anthelmintics can be used to manage animals with suspected ulcers (see end of this section for details). Several novel *Helicobacter* spp. have been associated with gastritis in an Australian sea lion and in harp seals (Harper et al. 2003; Oxley, Powell, and McKay 2004). In the sea lion, recurrent episodes of anorexia and abdominal discomfort prompted endoscopy and subsequent biopsy of gastric and intestinal mucosa. *Helicobacter* spp. and *Wolinella* spp. were identified by PCR. Treatment included amoxicillin at 10 mg/kg PO BID and metronidazole at 10 mg/kg PO BID. Initially the animal's condition improved with therapy, but repeated flare-ups occurred over several years.

Primary neoplasias of the oral and gastrointestinal tracts have been documented in pinnipeds. Lingual squamous cell carcinoma has been described in a California sea lion (Sato et al. 2002), and esophageal squamous cell carcinoma has occurred in several aged captive harbor seals (Flower et al. 2014). Clinical symptoms included intermittent dysphagia, inappetence, regurgitation, and abnormal posturing. The tumors were often ulcerated and occurred near the gastroesophageal junction. Bloodwork abnormalities in these cases included azotemia, hyperproteinemia, hyperglobulinemia, and leukocytosis. Gastric carcinoma developed in a captive, aged South American sea lion. Vomiting, anorexia, and weight loss occurred, with hematemesis and melena in end stage disease (Yamazaki, Koutaka, and Une 2016).

Enteritis in pinnipeds can be caused by a variety of infectious agents. Viral causes of enteritis include morbillivirus, which has caused chronic ulcerative stomatitis and acute hemorrhagic enteritis in wild harbor seals in Europe (Jauniaux et al. 2001). In an outbreak of herpesvirus in juvenile harbor seals, early clinical symptoms included vomiting, diarrhea, and fever. Severe hepatic necrosis was found postmortem (Borst et al. 1986). Enteritis has been linked to bacteria, including *Clostridium* spp. and *Salmonella* spp. in different pinniped species. The interpretation of culture of these organisms from fecal samples is difficult, as they have been cultured from both clinically normal animals and those with severe hemorrhagic enteritis. Disseminated blastomycosis was identified in two California sea lions in different captive facilities. *Blastomyces dermatitidis* was the suspected primary pathogen, and postmortem findings included enteritis with subsequent rupture and peritonitis, infiltration of the spleen and liver, severe pyogranulomatous pneumonia, and ulcerative skin lesions (Zwick et al. 2000).

Most gastrointestinal parasites are part of the normal flora of free-ranging pinnipeds and do not significantly affect the host; however, they can be responsible for clinical disease. Nematodes may potentiate malnutrition in already compromised animals, especially young animals, and high parasite burdens have the potential to obstruct the intestinal lumen (Banish and Gilmartin 1992). Juvenile Hawaiian monk seals with cestode infections, primarily *Diphyllobothrium* spp., tend to be in poorer body condition than those without infections (Reif et al. 2006; Gobush, Baker, and Gulland 2011). Treatment with praziquantel at 5 mg/kg IM for 2 days in Hawaiian monk seals has shown some seasonal promise in improving body mass and survivorship (Gobush, Baker, and Gulland 2011), although higher doses have been used to clear cestode infection in rehabilitated monk seals. Acanthocephalans have caused gastrointestinal perforation and peritonitis in gray and harbor seals. Hookworm infections causing enteritis and bacteremia have been associated with increased wild California sea lion pup mortalities on San Miguel Island (Spraker et al. 2007). California sea lions appear to be the definitive host for enteric coccidian parasites, with only mild associated enteritis. This parasite, however, was implicated in causing protozoal lymphadenitis, hepatitis, myocarditis, and encephalitis in a neonatal harbor seal (Colegrove et al. 2011), suggesting varying interspecies pathogenicity (see **Chapter 20**).

Hepatitis has been associated with adenovirus infection in otariid species (Dierauf, Lowenstine, and Jerome 1981; Goldstein et al. 2011; Inoshima et al. 2013). Clinical signs of affected animals included diarrhea, anorexia, abdominal pain, posterior paresis, polydipsia, and photophobia. Bloodwork abnormalities include markedly elevated AST and ALT. Adenoviral infection can be fulminant and fatal (Inoshima et al. 2013). Hepatic necrosis and intranuclear inclusions are typical postmortem findings. To date, at least one novel adenovirus has been described in association with hepatitis, Otarine Adenovirus 1 (OtAdV-1; Goldstein et al. 2011). Several types of bacteria associated with hepatitis have been isolated from the livers of pinnipeds (Thornton, Nolan, and Gulland 1998). Mycotic agents including *Coccidioides immitis* have also affected the liver of California sea lions (Fauquier et al. 1996), and neoplastic diseases may manifest themselves in the liver of pinnipeds (see **Chapter 14**, **Table 14.1**)

Hemochromatosis has been observed in managed California sea lions and northern fur seals, but the etiology is obscure (Garcia et al. 2000; Clauss and Paglia 2012).

Primary pancreatic disease has been rarely reported, though may be underreported due to nonspecific clinical signs and lack of species-specific tests. Chronic pancreatitis has been reported in an adult captive California sea lion, with no identifiable underlying cause. The animal developed secondary diabetes mellitus and was managed with glargine insulin injections, gastric protectants, and a high-protein, low-fat diet (Meegan et al. 2008). Pancreatic adenocarcinoma has been described in an adult captive Steller sea lion. Postmortem secondary lesions included pancreatitis, bile duct obstruction, hepatitis, and hepatic encephalopathy (Goertz et al. 2011).

Small amounts of rectal bleeding, irregular in frequency and of varying duration, in harbor seals and California sea lions have been associated with a postmortem finding of ileocecocolic intussusception (Lair and Lamberski, pers. comm). A case of antemortem diagnosis of ileocecocolic intussusception occurred in a captive harbor seal that initially presented for anorexia and a leukopenia with degenerative left shift. Malodorous diarrhea developed, with concurrent tenesmus and regurgitation. Abdominal radiographs revealed gas dilated loops of intestine, and an exploratory laparotomy revealed significant ischemic compromise leading to euthanasia (Heym et al. 2011). Congenital abnormalities, including cleft palate (Suzuki et al. 1992) and hiatal herniation, have been seen in stranded pinnipeds (Beekman 2008; Biancani et al. 2012). Laparoscopic gastropexy was successfully used to repair a hiatal hernia in a stranded weanling elephant seal (Greene et al. 2015).

Iatrogenic causes of gastrointestinal disease include feeding inappropriate formulas or spoiled fish, using poorly designed feeding tubes, or feeding at an inappropriate rate or volume. Young animals, especially when debilitated, often go through a period of regurgitation and malabsorption if formula is introduced too quickly. Adequate rehydration and a gradual reintroduction to complex diets may aid in decreasing the frequency of emesis and diarrhea (see **Chapter 30**). Impactions caused by solidifying formula in neonates have been seen and may also be prevented by feeding appropriate formulas, monitoring hydration, and a gradual introduction to complex diets.

Clinical symptoms associated with diseases of the digestive tract in pinnipeds include inappetence, emesis, regurgitation, icterus, melena, hematochezia, diarrhea, straining, and/or steatorrhea. Abdominal pain or discomfort is often manifested as inappetence, lethargy, or depression. Otariids with abdominal discomfort will often tuck their flippers to their abdomen. In the water, they may float with tucked flippers and a hunched back.

Diagnosis of gastrointestinal disease often requires a series of diagnostic techniques beginning with physical examination. Physical examination helps detect broken, missing, or worn teeth, oral ulcers, oral foreign bodies such as fish spines and fishhooks, abdominal distension, abdominal masses, a palpable fluid wave, perineal swelling, or prolapsed rectum. A complete blood count may help identify an infectious cause. Clinical chemistry findings may indicate specific organ involvement, hypoproteinemia, gastrointestinal hemorrhaging, and electrolyte imbalances associated with chronic emesis or diarrhea (see **Appendix 1**, **Tables A1.2** [Phocids] and A1.3 [Otariids], Clinical Laboratory Values). Ultrasound may be used to identify a variety of abnormalities within the abdomen, including ascites, ileus, foreign bodies, and organ abnormalities. Abdominocentesis of a distended abdomen can differentiate peritonitis and hemoperitoneum. Culture and cytology of aspirated fluid may help further define disease. As many pinnipeds have large intra-abdominal vessels and large spleens, aspiration of frank blood does not necessarily indicate hemoperitoneum, and ultrasound-guided aspiration will help guide sample collection. Further diagnostics may include radiographs to detect gastric foreign bodies, gastric impaction, or constipation. Although it is often difficult to achieve good contrast in pinniped abdominal radiographs due to the relative lack of visceral fat, in young and thin animals, it is possible to achieve some indication of organ size, displacement, and intra-abdominal masses. Endoscopy can be used to diagnose gastric ulcers, gastritis, colitis, and gastric foreign bodies, as well as obtain gastric and colonic biopsies. Laparoscopic examination can enable direct visualization of the gastrointestinal serosa, as well as liver, pancreas, and associated structures. Biopsies of the liver and other tissues may be obtained either laparoscopically or by ultrasound-guided biopsy (see **Chapter 24**).

Supportive therapy for gastrointestinal disease is critical, as fluid, electrolyte, and protein abnormalities can quickly result in mortality if they are not resolved. Since many animals with gastrointestinal disease vomit or regurgitate, parenteral administration of fluids, medications, and potentially even nutrition should be provided (see above). GI protectants such as sucralfate, famotidine, ranitidine and omeprazole, antiemetics including maropitant citrate and ondansetron, and prokinetics, such as metoclopramide, can all be used in treating gastrointestinal disease. Attempts to induce emesis with apomorphine, xylazine, or hydrogen peroxide have been unsuccessful. Simethicone has been used to reduce bloating. Mirtazapine, orally and rectally, has been used to promote appetite with variable effects. Probiotics have been used in animals on chronic antibiotics or with chronic gastrointestinal disease, but little is known about their efficacy in pinniped species (see **Chapter 27**). Parenteral nutrition (PN) was administered to six severely malnourished (third-stage starvation) northern elephant seal pups or weanlings, using AminosynTM amino acid solution and Intralipid® lipid emulsion. A 19-gauge spring-reinforced intravenous catheter was placed into the epidural sinus, and PN was administered with either a portable syringe pump housed in a water-resistant case secured to the patient by a harness, or by “bolusing” the solutions over a 1- to 2-hour time period three times daily while the seal was confined in a smaller area (approx. 1.5 × 1.5 m [5 × 5 ft.] area; Frankfurter et al. 2014). CBC, serum chemistry, and electrolyte values were monitored regularly, and antibiotics and fluids were administered concurrently. Serum glucose, insulin, and glucagon levels indicated likely appropriate metabolic responses. Reintroduction of tube-fed oral electrolytes was initiated within 3–5 days, followed by a semielemental diet (Emeraid Piscivore®) for several days and gradual incorporation of ground fish slurries. Although only one out of the six seals ultimately survived to be released, PN appeared to be safe and well tolerated by these gravely ill animals, and may be of great benefit to severely nutritionally compromised animals.

Respiratory System

Respiratory disease is common in pinnipeds, and these species are capable of masking severe disease. Canine distemper virus (CDV) has caused epizootics of pneumonia and death in Baikal seals (*Phoca sibirica*) and Caspian seals (*Phoca caspica*), and phocine distemper virus (PDV) has most frequently been associated with epizootics in harbor seals with occasional smaller mortality events in gray, harp, and hooded seals (Duignan et al. 2014). Ocular and nasal discharges, cough, cyanosis of mucous membranes, dyspnea, diarrhea, fever, and central nervous signs, such as depression or seizures, are observed in affected seals. Subcutaneous emphysema of the neck and thorax may occur as a sequel to pulmonary damage, and seals may have difficulty swimming and diving (Siebert et al. 2010). Antemortem diagnosis may be detected by rising serum antibody titers, though animals may succumb to disease prior to developing a strong serologic response. Virus isolation is difficult, yet necessary to confirm identification of the virus. Treatment consists of supportive care, and controlling secondary bacterial infections that commonly cause death in infected seals (Baker and Ross 1992). Antibiotics effective against *Bordatella bronchiseptica*, *Corynebacterium* spp., and *Streptococcus* spp. are recommended. Although clinical recovery is documented, CDV has been isolated from asymptomatic carriers (Lyons et al. 1993). No commercially available vaccine for PDV currently exists, but commercially available attenuated CDV vaccine has been used to immunize stranded gray and harbor seals (Carter et al. 1992). Experimental inoculation of harbor seals with inactivated and subunit CDV vaccines have provided some protection from clinical disease (Visser et al. 1989, 1992; Van Bressem et al. 1991; Quinley et al. 2013). Most recently, vaccination of the wild population of Hawaiian monk seals (*Neomonachus schauinslandii*) was undertaken, because of the animals' low abundance, the fact that the population is naive to PDV, and that they have potential for exposure to a devastating PDV or CDV epizootic (Aguirre et al. 2007).

Influenza virus has also caused epizootics in harbor seals, with clinical signs similar to those in seals with PDV and CDV (Geraci et al. 1982; Anthony et al. 2012). These included dyspnea, lethargy, blood-stained nasal discharge, and subcutaneous emphysema, with pneumonia as the predominant postmortem lesion. There is evidence for interspecies transmission between birds, seals, and humans, suggesting that seals can both become infected and transmit influenza viruses to other species (Webster 1981; Goldstein et al. 2013). Phocine herpesvirus-1 (PhHV-1) has caused pneumonia in neonatal harbor seals in rehabilitation (Borst et al. 1986), while another herpesvirus was isolated from a California sea lion with acute hemorrhagic pneumonia (Kennedy-Stoskopf et al. 1986). Diagnosis of both infections is based on viral isolation, and treatment is supportive. Harbor seals with pneumonia associated with influenza virus were also infected with a mycoplasma, so therapy with antibiotics such as tetracyclines may be beneficial (Geraci et al. 1984).

Bacterial pneumonias are common in seals and sea lions, both as primary infections and secondary to viral and lungworm infections. A variety of organisms may be involved, although Gram-negative organisms are most common (Keyes, Crews, and Ross 1968; Sweeney 1986a; Spraker et al. 1995; Thornton, Nolan, and Gulland 1998; Haulena et al. 2006; Jang et al. 2010). Clinical signs include tachypnea, dyspnea, lethargy, and cough. Diagnosis is based upon auscultation of the chest, radiography of the lung fields, and bronchoscopy. Treatment with the appropriate systemic antibiotic may be based upon prediction of the likely organism, or culture and sensitivity of organisms from tracheal or bronchial washes (Johnson, Nolan, and Gulland 1998). Mucolytics such as acetylcysteine, and bronchodilators such as albuterol and aminophylline, have been used regularly on stranded harbor seals and California sea lions in rehabilitation.

Pneumonia in otariids may occur with heavy infestation of *Parafilaroides decorus*, although asymptomatic infection is common in young animals. *Parafilaroides gymnurus* infects alveoli of phocids, and *Otostrongylus circumlitus* may cause obstructive bronchitis and bronchiolitis in harbor, harp, and ringed seals, and yearling northern elephant seals (see **Chapter 21**). The degree of inflammatory response to *Parafilaroides* infections varies from none to marked suppurative and granulomatous pneumonia. Reaction may be more severe to dead and degenerate worms. Diagnosis depends upon detection of larvae in feces or sputum. Treatment with fenbendazole or ivermectin removes infection, but in severe cases, simultaneous treatment with antibiotics and either corticosteroids or nonsteroidal anti-inflammatories is strongly recommended to control secondary bacterial infections and reduce the inflammatory response to dying parasites. Interestingly, a *Brucella* spp. isolate was obtained from the lung of a harbor seal with *Parafilaroides* spp. infestation (Garner et al. 1997). Histological examination revealed most of the inflammation and *Brucella* spp. to be around the dead parasites. A more recent study confirmed these findings in stranded harbor seals (Lambourn et al. 2013); however, the role of *Parafilaroides* spp. in the epidemiology of *Brucella* infections remains unclear.

Pulmonary granulomas due to infection with *Mycobacterium pinnipedii* have been reported in captive and wild pinnipeds (Forshaw and Phelps 1991; Bastida et al. 1999; Cousins et al. 2003; Jurczynski et al. 2011). An enzyme-linked immunosorbent assay (ELISA) test (Cousins 1987) and intradermal tuberculin tests have been used for diagnosis of infection in live pinnipeds, although interpretation of results is difficult (Needham and Phelps 1990; Jurczynski et al. 2012), and successful treatment of clinical cases has not been documented. Similar lesions may also result from fungal infections. *Coccidioides immitis* and *C. posadasii* infections are not uncommon in pinnipeds throughout California (Fauquier et al. 1996, Huckabone et al. 2015), and *Cryptococcus* spp. (Mcleland et al. 2012) and *Blastomyces dermatitidis* (Zwick et al. 2000) infections have also been diagnosed. Diagnosis is usually made postmortem based on histological detection of organisms and culture as disease is generally advanced. Treatment has rarely been described, but a walrus with coccidioidomycosis was treated successfully with voriconazole for years (Schmitt and Procter 2014).

Cardiovascular System

Anemia is common in young otariids as a consequence of hookworm (*Uncinaria* spp.) infestation, or secondary to malnutrition, and has also been reported in Mediterranean monk seals (A. Komnenou, pers. comm.). Affected animals are weak, are occasionally dyspneic, and have pale mucous membranes. Diagnosis of hookworm infestation is based on detection of ova in feces (see **Chapter 21**), although animals may remain anemic for weeks after patent infection ceases. Treatment with anthelmintics and supplementation with iron and vitamin B12 is usually effective. Nonregenerative anemia is seen in California sea lions as a consequence of chronic renal damage, usually as a result of leptospirosis (see below). Disseminated intravascular coagulation (DIC), characterized by bleeding from the nares, hematoma formation, thrombocytopenia, hypofibrinogenemia, and extended clotting times, is relatively common in stranded northern elephant seals (Gulland et al. 1996b). It may occur with septicemia or vasculitis associated with migrating *Otostrongylus* larvae (Gulland et al. 1997a). Diagnosis of *Otostrongylus* infestation in live seals during the prepatent period is not currently possible, although clinical signs and season of occurrence are highly suggestive of infection. Clinicopathologic changes include elevated white blood count greater than 40,000 with a left shift, reduced platelet count, and increased aminotransaminases (ALT and GGT). Serum amyloid A, an acute phase protein, has the potential to serve as a diagnostic tool in prepatent *Otostrongylus* infections in elephant seals prior to the development of clinical signs (Sheldon et al. 2015). *Otostrongylus* worms have also been found in the right ventricle and pulmonary arteries in California sea lions causing similar clinical signs as seen in elephant seals (Kelly et al. 2005). Elephant seals with signs of DIC are treated with antibiotics, corticosteroids, and supportive care, but therapy is rarely successful. A lysine analogue antifibrinolytic drug, ε-aminocaproic acid (EACA), shows promise in treating the bleeding associated with prepatent *Otostrongylus* arteritis in northern elephant seals (Kaye et al. 2016). Other cases of anemia have included hyperestrogenism-induced medullar aplasia in a gray seal (Lacave, pers. comm.) and hemolytic anemia of unknown origin in a northern fur seal (Chelysheva and Romanov 2008).

Cardiac insufficiency in pinnipeds can be caused by cardiomyopathy related to toxin or capture stress, bacterial endocarditis, and heartworm infestation. In California sea lions, domoic acid (DA) toxicosis can cause a degenerative cardiomyopathy associated with decreased cardiac contractility and cardiac output (Zabka et al. 2009; Barbosa et al. 2015). Serum troponin-I and EKG tracings are not predictive of the severity of DA-associated cardiomyopathy. Electrocardiograms described in otariids and phocids are consistent with other animals, and the ventricular activation (QRS complex orientation) falls into category B with swine, horses, and cetaceans (Hamlin, Ridgway, and Gilmartin 1972; Dassis et al. 2016). Both ventricles depolarize simultaneously in bursts of canceling activity, leading to potential limitations of using ECGs in pinnipeds for diagnosing cardiac pathology. Echocardiography is currently the only tool for diagnosis of cardiac insufficiency in sea lions affected by domoic acid. In South American fur seal pups, capture stress has also induced cardiomyopathy, characterized by myocardial contraction band necrosis and endothelial disruption (Seguel et al. 2013). Q1 Bacterial endocarditis caused by *Staphylococcus aureus* and *Escherichia coli* has been documented as a cause of mortality in seals and sea lions and should be ruled out for cardiac insufficiency in pinnipeds (Kim et al. 2002, Chinnadurai et al. 2009).

A variety of microfilarid species have been documented in pinnipeds (see **Chapter 21**). Infection by either the canine heartworm *Dirofilaria immitis* or the phocid parasite *Acanthocheilonema spirocauda* may cause dilatation of the pulmonary artery and right ventricle, and can be detected radiographically. Microfilaria observed in blood smears must be distinguished from those of the noncardiopathogenic fascial worm, *A. odenhali*. The vast majority of microfilaria noted in wild California sea lions are *A. odenhali*. Commercially available canine heartworm antigen tests cross-react with *A. odendhali* in California sea lions, and results from these tests should be interpreted with caution when diagnosing heartworm in sea lions (Krucik, Van Bonn, and Johnson 2016). Successful treatment of documented heartworm cases has not been described. Preventive treatment of captive animals in *D. immitis* endemic regions with ivermectin at 0.6 mg/kg every month during the mosquito season is recommended, as well as removal of lice from stranded animals, as the seal louse *Echinophthirius horridus* has been shown to transmit *A. spirocauda* (Geraci et al. 1981).

In phocids, patency of the foramen ovale (f.o.) and ductus arteriosus (d.a.) occurs longer after birth than is described in terrestrial mammals. The f.o. may be patent up to 7 weeks of age, and the d.a. may be patent up to 6 weeks of age without evidence of clinical consequence (Dennison et al. 2011). Q2 Patency should only be considered abnormal if there is evidence of cardiac enlargement or hemodynamic derangement, and care should be taken not to fluid-overload the pups during initial days of treatment.

Urogenital System

Leptospirosis, caused by pathogenic spirochetes within the genus *Leptospira*, is well recognized in free-ranging California sea lions stranded in northern California. Although rarer, infection has also been reported in Steller sea lions, northern fur seals, Pacific harbor seals, and northern elephant seals (Smith et al. 1977; Stamper, Gulland, and Spraker 1998; Stevens, Lipscomb, and Gulland 1999; Colegrove, Lowenstine, and Gulland 2005; Cameron et al. 2008). Antibodies, providing evidence of prior exposure, have been detected in Hawaiian monk seals, New Zealand fur seals, and a bearded seal (MacKereth et al. 2005; Aguirre et al. 2007; Calle et al. 2008). Clinical signs are best documented in California sea lions, and include depression, anorexia, polydipsia, dehydration, vomiting, diarrhea, melena, oral ulcers, abdominal pain, and muscular tremors. Hematological changes include elevations in blood urea nitrogen, phosphorus, sodium, creatinine, and neutrophil count. However, asymptomatic chronic infection and leptospire shedding also occur (Prager et al. 2013, 2015).

Diagnosis is based on clinical signs and serum chemistry abnormalities consistent with leptospirosis, in addition to the absence of clinical signs suggestive of the other causes of azotemia, (i.e., amyloidosis, urogenital carcinoma, pyelonephritis, or severe dehydration). Infection can be confirmed through PCR detection of *Leptospira* DNA, or culture and isolation from urine or kidney tissue (Ahmed et al. 2012). To date, the only serovar isolated from free-ranging California sea lions and northern fur seals is *L. interrogans* serovar *pomona*, while both *L. interrogans* serovar *pomona* and *L. kirschneri* have been isolated from northern elephant seals (Smith et al. 1977; Cameron et al. 2008; Zuerner and Alt 2009; Delaney et al. 2014). Several other *L. interrogans* serovars have caused renal disease in both managed and free-ranging pinnipeds (Calle et al. 2003; Kik et al. 2006; Patchett et al. 2009). Sea lions with single microscopic agglutination test (MAT) titers over 1:100 are considered exposed, but clinically active cases of *L. interrogans* serovar *pomona* in sea lions usually have titers greater than 1:3200 (Colagross-Schouten et al. 2002). Cross-reaction with other *Leptospira* serovars with the MAT is common, and therefore a positive MAT titer against a particular serovar does not confirm infection with that serovar.

Treatment consists primarily of supportive care directed toward the clinical manifestations of the individual animal, such as fluids, gastric protectants, and analgesics. In vitro, *Leptospira* are susceptible to many antibiotics, including those in the penicillin and tetracycline families, and a 10- to 14-day course is recommended. In California sea lions, there is currently no evidence that penicillin-based antibiotics alone are effective in clearing an infection in vivo (Prager et al. 2015); however, a longer duration treatment course with tetracycline antibiotics may be effective in elimination of leptospiruria. Clinical signs and blood values can resolve with treatment, but, due to the severity of renal disease, roughly two-thirds of California sea lions presenting with clinical leptospirosis die despite treatment (Gulland et al. 1996).

Renal disease may also occur as a consequence of renal calculi, congenital renal aplasia, and amyloidosis (see **Chapter 14**). California sea lions diagnosed with amyloidosis exhibited signs of renal disease, with elevated BUN, creatinine, and phosphorus, plus hypoalbuminemia (Chinnadurai et al. 2008; Colegrove et al. 2009). Premortem diagnosis of amyloidosis requires a renal biopsy, and diagnoses of congenital renal aplasia and renal calculi require radiography and ultrasound. Treatment of these rare conditions has not been reported.

Urogenital tumors are common in free-ranging California sea lions (see **Chapter 14**). Clinical signs in these animals usually result from pressure on ureters and invasion of local organs. Initial presentation is often nonspecific with signs of malnutrition, and signs suggestive of metastatic cancer include posterior paresis, perineal and scrotal edema, ascites, and vaginal or rectal prolapse. Ultrasound often reveals hydroureter and hydronephrosis caused by ureter obstruction. Additional diagnostic tools include abdominocentesis and cytology, radiology, and laparoscopic biopsy techniques. Treatment has not been attempted. Other tumors of urogenital origin include renal cell carcinoma in a Steller sea lion (Romanov et al. 2015), choriocarcinoma in a California sea lion (Fravel et al. 2013), and an ovarian interstitial cell tumor in a South American sea lion (Biancani et al. 2010).

Abortions and stillborn pups are frequently observed on pinniped rookeries. Leptospires (Gilmartin et al. 1976), herpesviruses (Dietz, Heide-Jorgensen, and Harkonen 1989), caliciviruses (Smith and Boyt 1990), *Coxiella burnetii* (Lapointe et al. 1999), high levels of DDTs (Gilmartin et al. 1976), and domoic acid (Goldstein et al. 2009) have all been reported in aborting pinnipeds. Unlike cetaceans, *Brucella* spp. have not been found to be the causative agent of abortion in pinnipeds despite some investigation. An aborted California sea lion fetus had positive immunostaining for *Brucella* spp. in the respiratory and reproductive tissue, and the placenta was culture positive; however, the dam suffered from concurrent DA toxicity, and thus the primary cause of the abortion remains unknown (Sidor et al. 2008). Vaginal prolapse has been observed in California sea lions and Australian sea lions (*Neophoca cinerea*; Read et al. 1982). Treatment of the latter by ovariohysterectomy was successful. Uterine torsions and ruptures have been observed in California sea lions with DA intoxication, and were believed to be consequences of severe convulsions (Gulland et al. 2000). In pregnant California sea lions intoxicated with DA, fetal and amniotic fluid may act as a reservoir of DA initially ingested by pregnant females. Clinical improvement is often observed in the adults after abortion of the pup. To induce abortion, dexamethasone given at 0.25 mg/kg IM SID for 3–5 days is usually successful. If there is no response to dexamethasone, prostaglandin F2 alpha (i.e., dinoprost tromethamine; Lutalyse®) at 250 µg/kg IM SID for 3 days can be attempted, though a lower dose may also be successful.

Endocrine System

Few primary endocrine disorders have been documented in pinnipeds. Both hyper- and hyponatremia are common in stranded animals (see **Chapters 8 and 29**), and may be consequences of inappropriate stress responses. Adrenal necrosis resulting from infection by a herpesvirus, PhHV-1, has been associated with severe electrolyte and glucose abnormalities in stranded neonatal harbor seals undergoing rehabilitation (Gulland et al. 1997b).

Hypothyroidism has been suspected as attributing to obesity in captive California sea lions, and seems to be responsive to treatment with exogenous thyroid hormone. One adult, captive, California sea lion developed diabetes mellitus secondary to chronic pancreatitis. The animal was managed with glargine insulin injections, gastric protectants, and a high-protein, low-fat diet (Meegan et al. 2008). Environmental exposure of ringed seals to persistent organic pollutants in the Baltic Sea appears to affect endocrine homeostasis in these animals, though long-term health effects have yet to be described (Routti et al. 2010).

Severely malnourished animals are frequently hypoglycemic, and intravascular access in hypovolemic, minimally responsive, otariids can be challenging in an emergency situation. Fravel et al. (2016) showed that intraperitoneal (IP) administration of a dextrose bolus (500 mg/kg) will increase blood glucose levels to the same degree as an IV bolus, and thus can be administered during a hypoglycemic crisis. In the authors' experience, this technique has resulted in the successful revival of numerous hypoglycemic California sea lion and northern fur seal pups.

Eyes

Pinniped eyes are characterized by a large globe, prominent tapetum lucidum, rounded lens, and a narrow, tear-shaped pupil (Miller, Colitz, and Dubielzig 2010). The visual system of pinnipeds is adapted to both aquatic and terrestrial habitats, and most pinnipeds have good vision below the surface of the water in low light and above the surface in bright light (Wartzok and Ketten 1999). Pinnipeds have very active lacrimal glands producing constant tears that protect the cornea. Lack of tearing is often used as an indication of dehydration.

Eye lesions are common in both free-ranging and captive pinnipeds (see **Chapter 23**; Stoskopf et al. 1985; Schoon and Schoon 1992; Haulena, McKnight, and Gulland 2003; Colitz et al. 2010a,b). There may be an increased frequency of eye lesions in animals that are maintained in freshwater environments (Sweeney 1986b; Dunn et al. 1996), but water quality, oxidation by-products, UV light exposure, viral infections, underlying uveitis, and trauma all contribute to the multifactorial etiology of eye lesions in captive pinnipeds. Corneal lesions are most frequently encountered, followed by cataracts, traumatic injuries, infectious processes, and neoplasia (Miller et al. 2013). Captive otariids are frequently affected by a form of progressive keratitis, characterized by corneal opacities, edema, recurrent ulceration, and blepharospasm (Colitz et al. 2010a). Chronic exposure to sunlight appears to be an important risk factor (see **Chapter 31**), and progression of the disease is associated with secondary bacterial and fungal infections. Oral nonsteroidal anti-inflammatory drugs help to control pain and uveitis, and topical cyclosporine or tacrolimus appears to diminish recurrence of active disease. Treatment of active infection is imperative, and topical (triple antibiotic suspensions, serum, or platelet-rich plasma) and oral medications typically include doxycycline to stabilize the corneal stroma and speed re-epithelialization, and for its ability to be secreted in the tear film (Solomon et al. 2000; Freeman et al. 2013). Various bacteria have been cultured from traumatic lesions, conjunctivitis, and keratitis in pinnipeds (Thornton, Nolan, and Gulland 1998), and targeted therapy following culture and sensitivity is advised.

Visually impaired pinnipeds will thrust their vibrissae forward if investigating noises or new surroundings. Although normal pinnipeds will also do this, visually impaired animals tend to exaggerate the action and extend their vibrissae for prolonged periods of time. The menace response may be difficult to evaluate, since the vibrissae are very sensitive to air movement. Visually impaired animals, if placed into new surroundings, may not avoid obstacles well, but can accommodate very quickly using tactile and acoustic cues, making diagnosis of blindness difficult. Ophthalmic examination is difficult in pinnipeds because of a prominent nictitating membrane, strong eyelids, and the ability to retract the globe into the ocular cavity. Very narrow pupils limit visualization of internal eye structures such as the lens and retina, and pinnipeds do not tend to dilate their pupils very well when topical mydriatic agents are applied to the cornea. Retrobulbar block has been utilized to revert the ventral rotation that frequently follows anesthesia, and this produces excellent mydriasis to examine the interior of the globe (Gutierrez et al. 2016).

Cataracts are common in otariids, and frequently lead to synechiae formation, anterior prolapse, and rupture of the globe (see **Chapter 23**). The lenses of young animals may be removed by phacoemulsification (Colitz et al. 2011; Esson et al. 2015), but lenses in older animals are harder than in many terrestrial species, and lensectomy is required in the majority of cases (Colitz et al. 2011). Lensectomy has also been performed following globe perforation in phocids (Colitz et al. 2013).

Treatment of ocular lesions of pinnipeds is similar to that of domestic animals (see **Chapter 23**). However, the use of saline washes, most readily given as saltwater baths, appears to help decrease corneal edema. Both oral and topical anti-inflammatories and analgesics are helpful to treat pain associated with uveitis and corneal ulcers.

Nervous System

Numerous infectious agents have been identified as the cause of neurologic disease in pinnipeds. Viral encephalitis secondary to morbillivirus, herpesvirus, and influenza are commonly reported, with small to very large-scale outbreaks Q4 in wild populations (Geraci 1982; Phillippa et al. 2009; Philip Earle et al. 2011; Duignan et al. 2014; also see Respiratory section above and **Chapter 17**). Several cases of West Nile Virus (WNV) and Eastern Equine encephalitis (EEE) virus have also been described in captive phocids (Stremme 2003; Dalton, Dickerson, and Wigdahl 2004; Gentz and Richard 2004; McBride et al. 2008). A single case of rabies has been described in a ringed seal (Odegaard and Krogsrud 1981), and a novel parvovirus was detected in the brain of a harbor seal with meningoencephalitis (Bodewes et al. 2013). Clinical signs of these diseases are similar and may include depression, lethargy, ataxia, coma, recumbency, tremors, seizures, and coma. Other body systems, particularly the respiratory system, may also be affected. Some viral infections may be diagnosed on the basis of rising antibody titers, although confirmation is often made postmortem on histological examination of brain tissue, using immunoperoxidase and immunofluorescent techniques. Treatment is supportive and may include fluids, anticonvulsants, anti-inflammatory medication, and antibiotics for secondary infection. L-lysine supplementation did not alter the course of herpesvirus infection of harbor seal pups in a rehabilitation facility (Guarasci et al. 2010), and the efficacy of antiviral medications in these species is unknown. Vaccination is recommended against WNV using a recombinant canarypox vaccine, because it induced presumptively protective antibody levels in Steller sea lions (Tuomi et al. 2014). Harbor seals (Schmitt, pers. comm.) and several phocid species, including endangered Hawaiian monk seals, have been safely vaccinated with a recombinant DNA vaccine against canine distemper virus (see Respiratory section above).

Protozoal, bacterial, and fungal infections can cause similar neurologic signs. Any number of bacteria may infiltrate the nervous system through hematogenous spread. Various fungi including zygomycetes (Sosa et al. 2013; Barnett et al. 2014), *Coccidioides* spp. (Huckabone et al. 2015), *Cryptococcus* spp. (Rosenberg et al. 2016), and *Scedosporium apiospermum* (Haulena et al. 2002) have been detected in nervous and other tissues (see **Chapter 19**). *Toxoplasma gondii* and *Sarcocystis* spp. infections have been found in numerous wild pinniped species and some captive individuals (see **Chapter 20**).

Biotoxin exposure can also cause severe central nervous disease in pinnipeds. Neuronal necrosis in the hippocampus of California sea lions is caused by domoic acid (DA) exposure (Scholin et al. 2000; see **Chapter 16**). Common neurological signs include seizures, tremors, and ataxia. Repeated exposure to DA results in permanent hippocampal damage with memory loss and often a chronic epileptic state (Goldstein et al. 2008; Buckmaster et al. 2014; Cook et al. 2016). Treatment for biotoxin exposure is supportive and includes anticonvulsants, fluid therapy, and anti-inflammatory medication. Control of seizures with lorazepam (longer antiseizure effect than other benzodiazepines), midazolam, diazepam, or other benzodiazepines, and phenobarbital is beneficial. Current treatment for DA toxicosis at The Marine Mammal Center includes phenobarbital (4 mg/kg IM twice daily for 2 days, then 2 mg/kg IM or PO twice daily for 5 days) and lorazepam (0.2 mg/kg IM twice daily for the first 1–2 days, or longer as needed to control seizures). Subcutaneous (SC) fluids and dexamethasone (in the absence of ocular ulcer) are also generally administered for the first few days. An additional 0.2 mg/kg lorazepam is given IM if seizures do not stop 10–15 minutes after the first dose, and a third dose may also be given. If seizure activity does not stop after three doses of at least 0.2 mg/kg lorazepam (over approximately 45 minutes), euthanasia is recommended due to poor prognosis. Alpha-lipoic acid (ALA), a powerful antioxidant that crosses the blood–brain barrier, is also currently being administered to sea lions that strand at TMMC with DA toxicosis (10 mg/kg SC once daily), in an effort to reduce oxidative damage secondary to neuronal damage and necrosis. Successful control of idiopathic seizures in a captive adult California sea lion has been achieved with 1 mg/kg SID oral phenobarbital (Gage, pers. comm.), and a young California sea lion with intracranial structural anomalies using oral phenobarbital 4 mg/kg once daily (Dold et al. 2005).

Various anomalous and developmental brain lesions have been identified in pinnipeds. Pneumocerebellum, attributed to gas bubble formation, was noted in two stranded California sea lions (Van Bonn et al. 2011, 2013). Intracranial space-occupying lesions, usually tumors, have caused seizures in captive sea lions. Although hydrocephalus occurs in young stranded elephant seals (Trupkiewicz, Gulland, and Lowenstine 1997), sudden death, rather than neurological signs, usually occurs. Other reported congenital and anomalous neurologic abnormalities in various pinnipeds include hemicerebral anomalies (McKnight et al. 2005), bilateral caudate nucleus inflammation (Dennison et al. 2011b), cerebral infarction (Stevens et al. 2010), and discospondylitis (Tuomi et al. 2004); and multicentric neurofibromatosis was diagnosed in a geriatric California sea lion (Rush, Ogburn, and Garner 2012).

Thiamine deficiency is common in pinnipeds fed with frozen fish, particularly fish with high thiaminase content, and can result in polioencephalomalacia with acute neurological signs. Antemortem diagnosis is based on clinical signs and lack of supplementation, coupled with diet evaluation and response to supplementation, as clinicopathologic findings are generally nonspecific (Croft et al. 2013). Thiamine-dependent enzyme activity (transketolase) in blood and tissue samples can also be measured. Hyponatremia presents with similar clinical signs, and is also diagnosed by a combination of history of lack of supplementation (particularly in freshwater), plasma biochemistry, and response to treatment with sodium chloride (Geraci 1972b). Electrolyte imbalances associated with renal disease and/or nutritional deficiencies may also cause neurological signs (see **Chapters 8 and 29**). Selenium toxicosis was reported for several captive California sea lions that were fed with a diet later found to be high in selenium (Edwards et al. 1989).

Surgery

Surgical procedures for pinnipeds are generally comparable to those of canids with some species-specific adjustments. Commonly performed procedures are described below, and many are summarized in Higgins and Hendrickson (2013). Ocular surgery is discussed in **Chapter 23**.

Surgical procedures of the integument generally include mass removal, biopsy collection, and wound debridement and care. Standard sterile and surgical technique should be followed, including clipping hair from the affected site, sterile preparation of the incision site, and sterile procedure. Care should be taken with fur seals to minimize clipping, due to these species' reliance on fur for thermoregulation. An alternative to clipping in fur seals is to part the hair down the incision line using a tight comb, such as a flea comb, and apply betadine gel to prepare the skin, a technique used in sea otter surgical procedures (gel prepared by combining 12 ml betadine solution with 4.5-ounce sterile, water-based, lubricant; Murray, pers. comm.).

As pinnipeds generally recline on, and often ambulate on their ventral surface, surgical approach should be dorsolateral when possible to avoid contact of the incision site (postoperatively) with the ground. The thick hypodermis (blubber layer) often necessitates good retraction for proper exposure. Closure of skin and deeper layers should include tension relieving suture patterns in most areas, due to high tension and pressure on tissues. The hypodermis has poor holding capacity, and in healthy individuals is at least several centimeters thick, and even thicker in more robust animals. Tension-relieving suture patterns in this location are particularly important, as this layer must be closed to reduce dead space. Incisions that are full thickness (into the abdomen), or deep tissues, should be closed with four or five layers to help prevent dehiscence. Staples and sutures are both effective in closing the skin. Pain control with opioids and/or NSAIDS is strongly recommended perioperatively and postoperatively for most invasive procedures (see **Chapter 27** for drugs and dosages).

The duration of time to return an animal to water postoperatively varies greatly, though is only occasionally reported. Return to water may depend largely on the procedure, species, status (free-ranging vs. captive), and incision location. Free-ranging California and Steller sea lions with satellite tag transmitters implanted into the abdomen were returned to enclosures with access to water within hours postsurgery (Horning et al. 2008). None of the animals experienced dehiscence or infection of the surgical site. In the authors' experience, contamination of surgical sites with urine and feces, especially over the abdomen and extremities, can lead to infection and dehiscence; thus, most animals are allowed full-time access to water within a matter of days to a week. Alternatively, animals may be given access to water daily for restricted periods of time for hygiene, feeding, and comfort. Contamination of a surgical site by waterborne pathogens is also possible; thus, regular monitoring of incision sites is required. If not allowed access to water, animals should be kept in a clean, dry area with a smooth surface, particularly if surgery was performed on the ventrum or extremities.

Surgery of the musculoskeletal system frequently involves long bone or phalanx repair or amputation, and skull trauma including dental surgery. Fracture repair of long bones is rarely reported in the literature. One report describes the placement of a string-of-pearls locking plate, impregnated with antibiotics, to repair a closed, complete transverse diaphyseal fracture of the tibia of a 2-week-old gray seal (Hespel et al. 2013). A yearling California sea lion that presented with osteomyelitis of the left carpus was successfully released following fusion of the joint, using external fixation (Field, unpubl. data; **Figure 41.1**).

Initial systemic antibiotic treatment of the infection with multiple different antibiotics was unsuccessful; thus, polymethylmethacrylate (PMMA) beads impregnated with amikacin were placed around the joint, two rows of pins were placed in the radius and metacarpals, and PMMA bars made of thermoplastic polymeric material were placed to stabilize the joint (**Figure 41.2a and b**).

The fixator was removed 6 weeks later, following successful joint fusion.

Amputation of phalanges, digits, or limbs is not uncommon when bone is exposed or infection cannot be controlled with antimicrobial drugs. A nerve block using a local anesthetic, such as lidocaine or bupivacaine, is strongly recommended for both pain control and to help reduce minimal alveolar concentration (MAC) for general anesthesia. Phalanx amputation is common and similar to other species. It is of particular importance to preserve as much of the surrounding tissue as possible by undermining around the affected bone(s) to allow adequate subcutaneous tissue and skin

Figure 41.1 External fixation device on the dorsal surface a California sea lion yearling front flipper.

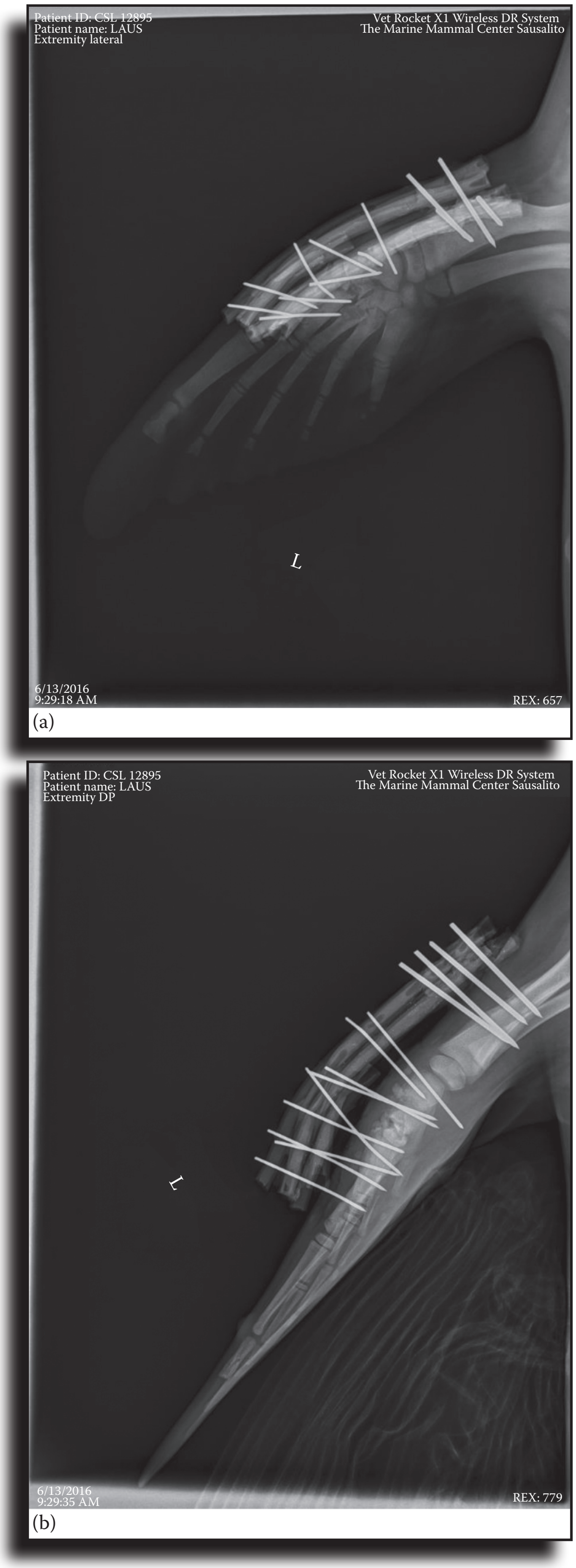

Figure 41.2 (a, b) Dorsoventral and lateral radiographs of the external fixation device of California sea lion yearling with osteomyelitis incorporating the left carpus. Polymethylmethacrylate antibiotic impregnated beads are visible in the joint.

closure. A dorsal approach is recommended, since these distal sites are in regular contact with the ground, and the dorsal surface is easily visualized for recheck examination. If insufficient tissue is present to entirely close the end of a joint or limb, mid-diaphyseal amputation of the next proximal bone is recommended to prevent high tension and dehiscence of the incision site.

Partial or complete front or hind flipper amputations have also been performed with return to normal, or near normal, locomotion. The impact of amputation surgery on the ability of free-ranging animals to successfully forage for live prey and have adequate mobility on land should be strongly considered prior to the procedure, and must be assessed prior to releasing the animal. **Figure 41.3** depicts the successful amputation of the right hind flipper of a yearling California sea lion at the level of the coxofemoral joint subsequent to severe limb damage (**Figure 41.4**).

The joint was approached from the lateral aspect and care was taken to isolate and ligate the blood vessels around the joint (Da Costa Gomez, pers. comm.). Soft tissue over the tarsus/tibiotarsus is particularly limited and difficult to close; thus, mid-diaphyseal amputation of the tibia and fibula with

Figure 41.3 California sea lion yearling post-amputation of right hind flipper at the coxofemoral joint using a lateral surgical approach.

Figure 41.4 Dorsoventral radiograph of hind limbs of a California sea lion yearling prior to leg amputation. Findings include right femoral distal diaphyseal fracture with metaphyseal and epiphyseal lysis, displaced and lytic patella, and proximal tibial fracture with epiphyseal and diaphyseal lysis.

closure using surrounding muscle and skin is recommended. This technique is described by Garcia et al. (2015) for harbor seal weanlings suffering from necrotizing infections of the tarsus or tibiotarsal joint. Bandage maintenance is challenging in these species, even when maintained out of water, given their fusiform body shape and their aquatic environment.

Surgeries involving the pinniped skull are generally confined to dental surgery and mandibular repair secondary to trauma. Fractured and loose teeth should be extracted (see **Chapter 22**). Lewer et al. (2007) described a case of closed left mandibular fracture in a geriatric harbor seal, which healed successfully after 12 months with the use of an oral dental acrylic splint and cerclage wire. A bilateral mandibular fracture in a 12-year-old South African fur seal was reduced and plated using two 3.5 mm positioning and compression device (PCD) plates and autotype screws (Flanagan et al. 2009). Both fractures resolved within 2 months. A harbor seal pup that stranded with a closed, complete fracture of the right caudal mandible developed a bony sequestrum at the fracture site. A ventral approach was used to debride the lesion and place an intraosseous wire. Canine trabecular bone powder and equine lamellar cortical bone matrix were used, along with platelet-rich plasma as a graft. The seal did well postoperatively (Rosenberg et al. 2015).

Surgery of the respiratory tract of pinnipeds has not been reported in the literature, despite common occurrence of severe respiratory disease. Tracheal perforation secondary to entanglement in monofilament fishing line occurs occasionally in free-ranging pinnipeds. Successful repair of tracheal perforation in California sea lions has been accomplished by initial debridement to freshen wound edges, and release incisions of existing scar tissue, to decrease tension. Mucosal margins of the trachea are closed with simple interrupted sutures, if possible. Overlying muscle layers are closed with interrupted horizontal mattress and cruciate sutures followed by standard closure of subcutaneous and skin layers with tension-relieving sutures (Da Costa Gomez, pers. comm.)

Abdominal surgery is performed most commonly for gastrotomy, or for procedures involving the reproductive tract. Esophageal surgery for fishhook removal has been performed in Hawaiian monk seals, as well as partial glossectomy of necrotic lingual tissue for the same reason (Barbieri et al. 2013; Levine, pers. comm.). Gastric foreign bodies are not uncommon in pinnipeds and are often found incidentally on necropsy of free-ranging pinnipeds with no evidence of associated pathology. Many animals will regurgitate or vomit foreign objects, or objects may be retrieved using gastroscopy. Surgery is indicated for gastric impaction, gastric perforation, fishhooks embedded in tissue, or other severe disease. The pinniped stomach is strongly u-shaped, but is otherwise similar to the canine. Gastrotomy for fishhook removal has been performed in numerous Hawaiian monk seals (Levine and Barbieri, pers. comm.). Gastric impaction by rocks, sand, or other abnormal ingesta is frequently noted in juvenile harp and hooded seals that strand on the east coast of the United States (Helmick, Dunn, and St. Aubin 1995) and western European coast (Alonso-Farre et al. 2011). The reason for foreign material ingestion is unknown, and seals are often critically dehydrated with severe gastric disease on presentation. Rehydration and administration of mineral oil and small amounts of water through an orogastric tube may allow sand and smaller rocks to pass, or in some cases rocks can be removed through endoscopy or laparoscopically. Gastrotomy was successful in treating rock impaction in a stranded juvenile harp seal with concurrent severe pneumonia (**Figure 41.5**).

This harp seal was maintained on IV fluids and antibiotics, IM famotidine, and oral fluids and mineral oil for nearly 3 weeks until the pneumonia had resolved sufficiently to allow surgery (Field, Schuh, and Tuttle 2009).

Intestinal surgery has also not been reported in the literature, though a variety of intestinal diseases, including gastric torsion, gastric or mesenteric volvulus, intussusception, obstruction, and other surgical conditions have been found on necropsy. Laparotomy on a severely debilitated free-ranging Hawaiian monk seal with a jejunal intussusception was initially successful; however, the animal died several days later secondary to mesenteric torsion (Levine and Barbieri, pers. comm.). Though these severe intestinal diseases

Figure 41.5 Radiograph of a juvenile harp seal with gastric impaction from rock ingestion.

appear relatively uncommon, a successful outcome generally requires rapid diagnosis and surgical intervention.

Surgery of the reproductive tract has been reported for both male and female pinnipeds. Ovariohysterectomy was performed in a South Australian fur seal with a vaginal prolapse; the procedure was performed similar to that of a dog, with a ventral midline incision, exteriorization of the uterus, ligation of the ovarian, broad ligament and uterine vessels, and ligation of the uterine body at the cervix, using overlapping horizontal mattress sutures followed by oversewing of the uterine stump (Read et al. 1982). Caesarian section has been performed in California sea lions (Schmitt, pers. comm.) and in an 8-year-old harbor seal with uterine torsion. In this case, the dam became acutely lethargic and anorexic, and the fetal heart rate and movement were reduced. The uterine torsion prevented cervical dilation and pup expulsion, and the pup was successfully resuscitated following surgical intervention. The uterus was closed in two layers, the abdomen in four layers, and the skin effectively sealed with Dermabond (Gili, pers. comm.). Most other reported abdominal procedures, including gastropexy for a hiatal hernia, ovariectomy, and tissue biopsies, have been performed laparoscopically (see **Chapter 25**).

In male pinnipeds, orchiectomy has been performed in a number of otariids (scrotal testes); however, this procedure is rarely performed in phocids because their testes are para-abdominal. Otariid testes can retract strongly, so castration of mature males during breeding season when the testes have descended may be advantageous. If out of season or if animals are immature, testes can be pushed into the scrotum with rectal manipulation. A prescrotal incision is generally recommended, and the procedure can be done closed or open. Open is recommended for mature animals to ensure adequate ligation of larger vessels. Two cases of partial penis amputation subsequent to persistent paraphimosis were reported in South African fur seals (Lacave, Guglielmi, and Mantratz 2008). One animal required partial os penis amputation and urethral reconstruction; the other required amputation of the tip of the penis; both recovered well.

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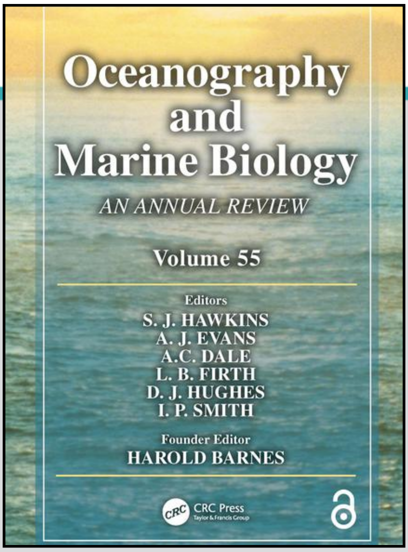
CHAPTER

3

A REVIEW OF HERBIVORE EFFECTS ON SEAWEED INVASIONS



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A REVIEW OF HERBIVORE EFFECTS ON SEAWEED INVASIONS

SWANTJE ENGE[1,2], JOSEFIN SAGERMAN[3], SOFIA A. WIKSTRÖM[3] & HENRIK PAVIA[4]

[1]Department of Plant and Environmental Sciences,
University of Copenhagen, 1871 Frederiksberg, Denmark
[2]Institute for Chemistry and Biology of the Marine Environment,
University of Oldenburg, 26382 Wilhelmshaven, Germany
[3]Baltic Sea Centre, Stockholm University, 106 91 Stockholm, Sweden
[4]Department of Marine Sciences-Tjärnö, University of Gothenburg, 452 96 Strömstad, Sweden
**Corresponding author: Henrik Pavia*
e-mail: henrik.pavia@marine.gu.se

Almost 300 non-native seaweeds are identified worldwide and an increasing number of these are classified as invasive with potential negative effects on the diversity and functioning of native ecosystems. Marine herbivores affect seaweed biomass and community structure in marine habitats across the globe. Consequently, herbivore-seaweed interactions are expected to be important for the establishment and invasion success of non-native seaweeds. To synthesize current knowledge of consumer effects on non-native seaweeds, we performed a meta-analysis on feeding preferences of native herbivores for non-native versus native seaweeds. Data were included from 35 studies, published from 1992–2015 and comprising 18 non-native seaweeds. Results showed that overall, native herbivores tended to prefer to feed on native rather than non-native seaweeds. Preferences were, however, variable across studies with significant differences between taxonomic and functional groups of seaweeds. In particular, filamentous red non-native seaweeds were of low palatability to native herbivores. No general feeding preferences were apparent between natives and non-natives for brown and green seaweeds, or for leathery and corticated seaweeds. In addition, we reviewed the existing studies on the effects of consumers on the performance of native and non-native seaweeds in invaded communities. This indicated that non-native seaweeds performed better than their native competitors in the presence of grazers, but in many cases had superior competitive abilities also in the absence of herbivory. To achieve a comprehensive evaluation of consumers' role in seaweed invasion success, future research should have a larger focus on manipulative community experiments, ideally on time scales that include seasonal changes and complete life cycles of the seaweeds.

Introduction

At any time, several thousand marine species are shuffled between biogeographical regions of the world's oceans (Johnson & Chapman 2007). Some of these species establish in their new communities and become widespread and abundant, being deemed invasive, with significant impacts on community composition and ecosystem properties (Williamson & Fitter 1996). The global number of non-indigenous seaweeds has reached more than 270 species (Williams & Smith 2007), many of them reported to negatively affect native seaweed communities in terms of cover, density and biodiversity (Schaffelke & Hewitt 2007, Engelen et al. 2015, Maggi et al. 2015). Identification of the factors that control establishment and invasion success of non-native species is a key challenge in invasion ecology and important for risk assessment and management of non-indigenous seaweeds.

Herbivores have large influence on the abundance and community structure of both terrestrial and marine primary producers across ecosystems (e.g. Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Hawkins et al. 1992, Hay & Steinberg 1992, Burkepile & Hay 2008, Poore et al. 2012). Consequently, herbivore-plant interactions have long been suggested to be crucial also for the outcome of plant invasions. On the one hand, herbivores are recognized to contribute to biotic resistance against the establishment and proliferation of non-native plants (Elton 1958, Maron & Vila 2001). On the other hand, herbivore foraging has been suggested to drive invasions, when native herbivores preferably consume native over the non-native plant species. The latter argument forms the basis for the enemy release hypothesis (ERH), which states that non-native species become invasive since they escape the regulation of their co-evolved enemies in their native range and are less affected by enemies compared to the native competitors in their new range (Darwin 1859, Elton 1958, Keane & Crawley 2002). The reduced negative impact of herbivores is expected to give the non-native species a competitive advantage over the native plants in the community, leading to dominance and a biological invasion (Keane & Crawley 2002).

The concepts of biotic resistance and enemy release originate from terrestrial plant systems; the findings from these systems have been summarized in several reviews and meta-analyses (Colautti et al. 2004, Levine et al. 2004, Liu & Stiling 2006, Parker et al. 2006, Chun et al. 2010). Recently, Kimbro et al. (2013) published a meta-analysis on biotic resistance in marine environments, indicating negative effects of consumers on non-native marine primary producers. Seaweeds were only represented by seven studies in their analysis and seaweed data were analyzed together with data on a non-native salt marsh grass. Thus, a comprehensive quantitative synthesis of research on herbivore effects on non-native seaweeds is still lacking.

Seaweed communities are strongly dominated by generalist herbivores (Hawkins & Hartnoll 1983, Hawkins et al. 1992, Hay & Fenical 1992), which are more likely than specialists to include newly encountered species into their diet. Accordingly, generalist consumers have been suggested to counteract invasions by providing biotic resistance instead of facilitating invasions through enemy release (Parker & Hay 2005, Parker et al. 2006). There are, however, mechanisms by which non-native plants can escape generalist herbivores in their new range, especially by means of chemical defences (Wikström et al. 2006, Verhoeven et al. 2009, Forslund et al. 2010, Schaffner et al. 2011, Enge et al. 2012, Nylund et al. 2012). Seaweeds are known to be rich in secondary metabolites (Hay & Fenical 1992) and there is an increasing number of examples where potent chemical defences against native herbivores have been demonstrated in non-native seaweeds (Lemee et al. 1996, Lyons et al. 2007, Nylund et al. 2011, Enge et al. 2012). It is not known, however, if low palatability to generalist herbivores is a common trait of non-native seaweeds or if this trait is important for invasion success in seaweed communities.

The aim of this study was to review and synthesize current findings of consumer effects on non-native seaweeds. As part of the predictions of the ERH, we specifically explored via a meta-analysis whether non-native seaweeds are less palatable than native species, and thus generally experience a reduced impact by herbivores compared to native competitors. We further examined if there are differences among 1) seaweed taxonomic groups, 2) seaweed functional groups, 3) herbivore groups or 4) regions. Furthermore, we reviewed and summarized the literature that assessed the effects of herbivory on the competitive outcome between non-native and native seaweeds in a community.

Material and methods

Literature search and data extraction

Relevant studies for the meta-analysis were identified in the online database ISI Web of Science in August 2015, with no restrictions on publication year, using the following combination of search terms: ((introduced OR invasive OR non-native OR exotic OR alien OR non-indigenous) AND (seaweed* OR alga* OR macroalga*) AND (herbivor* OR consum* OR *graz* OR enem* OR prefer*)). In order to retrieve studies that tested non-native seaweeds but without specifying the species as non-native in the title or abstract, we performed an additional search for all non-native seaweeds listed in Williamson & Smith (2007) using the search terms: ((‘algal species name’) AND (enem* OR herbivor* OR consum* OR graz*)). To determine if the seaweeds in these studies were non-native, we compared the study region with the reported natural distribution of the species. We further included three as yet non-peer-reviewed datasets (S.A. Wikström unpublished, K. Hill unpublished, S. Jakobsson unpublished). All titles and abstracts of the search results were screened for studies assessing feeding preferences or herbivore damage on non-native compared to native seaweeds, as well as for studies examining seaweed performances and competitive relationships between the non-native and native seaweeds in the presence and absence of herbivory. To be included in the final dataset, the studies had to meet the following criteria: 1) the investigated seaweed was non-native to the study region while the seaweeds used for comparison and the herbivores were native to the study region; 2) the study assessed herbivore preference, damage or their effects on both non-native and native seaweed performance under laboratory or field conditions in two- or multiple-species experiments using living algal material; 3) the experimental design included proper controls and presented all necessary measures for calculating the effect size. We excluded data of epifaunal abundances on non-native compared to native seaweeds because abundance may reflect habitat choice rather than food preference (e.g. work on refuges from predation: Duffy & Hay 1991, Enge et al. 2013). We also excluded data from no-choice feeding experiments since consumption in a no-choice situation can be confounded by compensatory feeding (Cruz-Rivera & Hay 2000). Furthermore, studies using gut content analysis of herbivores collected in the field were excluded because it was not possible to relate gut content to the availability of seaweeds in the field. Finally, studies where herbivores were preconditioned on one of the experimental seaweeds by either being specifically collected from or fed with only that seaweed prior to the experiments were also excluded.

For the retained studies the following data were compiled (see Table 1): seaweed species name, taxonomic and functional group, the study region and its corresponding climate region, the origin of the non-native seaweeds, herbivore species identity and phylum, as well as the experiment type (i.e. two- or multiple-choice). Mean values and measures of dispersion were extracted from figures using the WebPlotDigitizer software (Rohatgi 2015) or directly from text, tables or original datasets. All retrieved studies on herbivore feeding preference reported consumption or relative growth of the seaweeds as the response variable, which were either presented already corrected for autogenic changes of the seaweeds or together with the means of controls for autogenic changes. In the latter case, the consumption or relative growth data were corrected for the autogenic changes before values were entered into the database. To obtain a reference value for the native seaweeds in multiple-choice experiments, we calculated the average consumption of all native seaweeds and used their pooled variance as a measure of variability, which assumes the means of the populations to differ but their variances to be the same.

Meta-analysis

Hedges’ d standardized mean difference (Hedges & Olkin 1985) was used as the effect size measure and was calculated as the difference between non-native and native seaweeds: $d = [(\overline{X}_{NN} - \overline{X}_{N})/s]$, where $\overline{X}_{NN}$ corresponds to the mean consumption of the non-native seaweed and $\overline{X}_{N}$ to the mean consumption of the native species, s designates their pooled standard deviations and J is the small-sample-size bias correction factor. Positive Hedges’ d values thereby reflect herbivore preference for the non-native seaweeds, while negative values reflect herbivore preference for the native seaweeds.

Many publications reported data of several independently performed two- or multiple-choice experiments using different native seaweed species and/or different herbivores, which resulted in up to 16 data entries from one study and for one non-native seaweed. To balance the influence of studies in the analyses and to decrease possible non-independence of these multiple entries, we

Table 1 Summary of the data on herbivore preference used in the meta-analysis

Species	Functional group	Studies (number of data entries per study)	Studied regions	Climate region	Origin	Herbivore phylum	Herbivore species	Experiment type
Chlorophyta								
Caulerpa filiformis	Corticated	Davis et al. 2005 (1); Cummings & Williamson 2008 (1)	SW Pacific	Subtropical	Indo-Pacific	Mollusca	*Turbo undulatus*[4]; natural herbivore assemblage	Multiple-choice
Caulerpa racemosa var *cylindracea*[1]	Corticated	Tomas et al. 2011a (1); Tomas et al. 2011b (1)	Mediterranean Sea	Subtropical	SW Pacific	Chordata; Echinodermata;	*Paracentrotus lividus*; *Sarpa salpa*	Two-choice
Codium fragile ssp. *atlanticum*	Corticated	Trowbridge & Todd 1999 (1)	NE Atlantic	Temperate	NW Pacific	Mollusca	*Littorina littorea*	Two-choice
Codium fragile ssp. *tomentosoides*[2]	Corticated	Prince & Leblanc 1992 (1); Trowbridge 1995 (3); Cruz-Rivera & Hay 2001 (1); Scheibling & Anthony 2001 (1); Chavanich & Harris 2002 (1); Levin et al. 2002 (2); Sumi & Scheibling 2005 (1); Hill (unpublished data) (2); Lyons & Scheibling 2007 (1); Jakobsson (unpublished data) (1)	NW Atlantic; NE Atlantic; SW Pacific	Temperate; Subtropical	NW Pacific	Arthropoda; Echinodermata; Mollusca	*Ampithoe longimana*; *Cookia sulcata; Evechinus chloroticus*; *Idotea granulosa*; *Lacuna vincta*; *Strongylocentrotus droebachiensis; Turbo smaragdus*[5]	Two-choice; Multiple-choice

Continued

Table 1 (Continued) Summary of the data on herbivore preference used in the meta-analysis

Species	Functional group	Studies (number of data entries per study)	Studied regions	Climate region	Origin	Herbivore phylum	Herbivore species	Experiment type
Phaeophyceae								
Fucus evanescens	Leathery	Schaffelke et al. 1995 (1); Wikström et al. 2006 (2)	NE Atlantic	Temperate	N Circumpol	Arthropoda; Mollusca	*Idotea granulosa*; *Littorina obtusata*	Two-choice; Multiple-choice
Fucus serratus	Leathery	Wikström et al. 2006 (1); Steinarsdóttir et al. 2009 (3); Wikström unpublished data (2)	NE Atlantic	Subpolar	N Circumpol	Arthropoda; Mollusca	*Gammarus obtusatus*[6]; *Idotea granulosa*; *Littorina littorea*; *Littorina obtusata*	Two-choice
Sargassum muticum	Leathery	Britton-Simmons 2004 (1); Pedersen et al. 2005 (1); Hill (unpublished data) (2); Monteiro et al. 2009 (6); Strong et al. 2009 (1); Cacabelos et al. 2010 (4); Britton-Simmons et al. 2011 (1); Engelen et al. 2011 (3)	NE Atlantic; NE Pacific	Temperate; Subtropical	NW Pacific	Arthropoda; Echinodermata; Mollusca	*Aplysia punctata*; *Dexamine spinosa; Gammarus insensibilis*; *Gibbula* spp.; *Hydrobia ulvae*[7]; *Idotea granulosa; Lacuna vincta*; *Littorina littorea; Littorina obtusata*; *Paracentrotus lividus*; *Psammechinus miliaris*; *Stenosoma nadejda*; *Strongylocentrotus droebachiensis*	Two-choice; Multiple-choice

Continued

Table 1 (Continued) Summary of the data on herbivore preference used in the meta-analysis

Species	Functional group	Studies (number of data entries per study)	Studied regions	Climate region	Origin	Herbivore phylum	Herbivore species	Experiment type
Undaria pinnatifida	Leathery	Thornber et al. 2004 (1)	NE Pacific	Subtropical	NW Pacific	Arthropoda	*Pugettia producta*	Two-choice
Rhodophyta								
Acrothamnion preissii	Filamentous	Tomas et al. 2011a (1)	Mediterranean Sea	Subtropical	Indo-Pacific	Echinodermata	*Paracentrotus lividus*	Two-choice
Bonnemaisonia hamifera	Filamentous	Hill (unpublished data) (2); Enge et al. 2012 (4)	NE Atlantic	Temperate	NW Pacific	Arthropoda; Mollusca	*Aplysia punctata*; *Gammarellus angulosus*; *Gammarus locusta*; *Idotea neglecta*; *Littorina littorea*	Two-choice
Gracilaria salicornia	Corticated	Smith et al. 2004 (4)	N Pacific	Tropical	Indo-Pacific	Chordata	*Acanthurus blochii*; *Acanthurus triostegus*; juvenile scarids; *Zebrasoma flavescens*	Two-choice
Gracilaria vermiculophylla	Corticated	Weinberger et al. 2008 (2); Nejrup et al. 2012 (3)	Baltic Sea; NE Atlantic	Temperate	NW Pacific	Arthropoda; Mollusca	*Gammarus locusta*; *Idotea balthica; Littorina littorea*; *Littorina* sp.	Two-choice

Continued

Table 1 (Continued) Summary of the data on herbivore preference used in the meta-analysis

Species	Functional group	Studies (number of data entries per study)	Studied regions	Climate region	Origin	Herbivore phylum	Herbivore species	Experiment type
Heterosiphonia japonica[3]	Filamentous	Low et al. 2015 (2); Sagerman et al. 2015 (2)	NE Atlantic; NW Atlantic	Temperate	NW Pacific	Arthropoda; Mollusca	*Gammarellus angulosus*; *Gammarus locusta*; *Idotea balthica*; *Idotea granulosa*; *Lacuna vincta*	Two-choice; Multiple-choice
Lophocladia lallemandii	Filamentous	Tomas et al. 2011a (1)	Mediterranean Sea	Subtropical	Indo-Pacific	Echinodermata	*Paracentrotus lividus*	Two-choice
Mastocarpus stellatus	Corticated	Yun & Molis 2012 (2)	NE Atlantic	Temperate	NE Atlantic	Arthropoda; Mollusca	*Idotea balthica*; *Littorina littorea*	Two-choice
Womersleyella setacea	Filamentous	Tomas et al. 2011a (1)	Mediterranean Sea	Subtropical	Circum-equatorial	Echinodermata	*Paracentrotus lividus*	Two-choice
Gracilaria salicornia + *Acanthophora spicifera* + *Kappaphycus* sp.	Mixed	Stimson et al. 2007 (1)	N Pacific	Tropical	Indo-Pacific; NW Atlantic	Echinodermata	*Tripneustes gratilla*	Multiple-choice

Note: The functional group division follows Littler & Littler (1984): filamentous = delicately branched, uniseriate to slightly corticated; corticated = coarsely branched, corticated; leathery = thick branched, heavily corticated or thick walled.

[1] *Caulerpa racemosa* var. *cylindracea* currently known as *Caulerpa cylindracea*; [2] *Codium fragile* ssp. *tomentosoides* currently known as *Codium fragile* ssp. *fragile*; [3] *Heterosiphonia japonica* currently known as *Dasysiphonia japonica;* [4] *Turbo undulatus* currently known as *Lunella undulata*; [5] *Turbo smaragdus* currently known as *Lunella smaragda*; [6] *Gammarus obtusatus* currently known as *Echinogammarus obtusatus*; [7] *Hydrobia ulvae* currently known as *Peringia ulvae*.

calculated a study-specific mean effect size for each herbivore species and non-native species across all experiments testing different combinations with native seaweeds in a study. In this way, we kept the resolution between the non-native seaweed and herbivore species, but reduced the problem of overweighing and consequent false precision estimates (Rothstein et al. 2013). We also calculated a study-specific mean effect size when experiments were repeatedly performed at different times during the year. In both cases, the study-specific mean effects were estimated using a fixed-effects model, which assumes the results of the different experiments in one study to vary only because of random sampling error. This procedure reduced the number of entries in the dataset with a factor of up to five for some publications and in total from 145 to 74 entries.

The meta-analysis on consumer preference for non-native versus native seaweeds was conducted using the metafor-package in R (Viechtbauer 2010) and the OpenMee software (Dietz et al. 2016). The weighted overall mean effect of herbivore preference for non-native or native seaweeds was calculated by a random-effects model using the restricted maximum-likelihood estimator for residual heterogeneity. Bootstrapped 95% confidence intervals were calculated for the overall mean effect size generated from 4999 iterations. To check the robustness of the meta-analysis outcome, we calculated the fail-safe number with the weighted method of Rosenberg (2005), which represents the number of additional studies with no effect needed to change the result of the meta-analysis from significant to non-significant. Publication bias was further examined with a funnel-plot and the rank correlation test for funnel plot asymmetry (Begg & Mazumdar 1994). The influence of outliers on the overall mean effects size was tested by evaluating the change of the overall effect when one study at a time was left out of the analysis. Since hypothesis-driven research tends to favour large effect sizes in support of the hypothesis in earlier publications, we examined temporal trends in the data with a cumulative meta-analysis sorted by publication year (Jennions & Møller 2002).

We used meta-regression with mixed-effects models and with a restricted maximum-likelihood estimator for residual heterogeneity to assess if the predefined covariables explained any of the observed heterogeneity and to explore their influence on consumer preference as well as differences between subgroups. Specifically, we tested how much of the observed heterogeneity the non-native seaweed itself accounted for, if there were differences in consumer preferences among phyla or functional groups of the non-native species, and if the climate region of the study site, herbivore phylum and experiment type influenced the study outcome. Origin and study region as covariables were omitted from these analyses since subgroups were often only represented by one or two species and few data entries in some of the subgroups, which were considered insufficient for a valid interpretation.

Only five studies that tested for consumer effects on the performance of non-native and native seaweeds on a community scale were identified, too few to perform a formal meta-analysis. However, findings of the few existing studies were summarized and discussed.

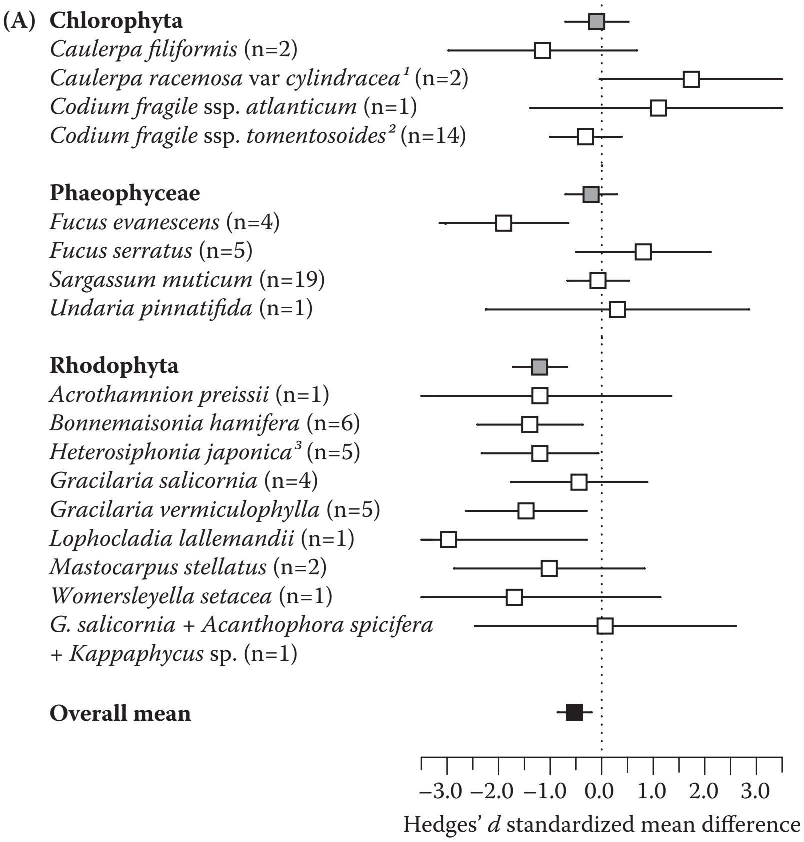
Results

The literature search identified 35 studies published from 1992–2015 that examined feeding preferences of native herbivores for non-native compared to native seaweeds. These studies addressed in total 18 non-native seaweed taxa: four green algae (Chlorophyta), four brown algae (Phaeophyceae) and ten red algae (Rhodophyta) (Table 1). This is comparable with the taxonomic composition of all registered non-native seaweeds reported by Williams & Smith (2007): of 276 taxa, 45 were green algae, 66 brown algae and 165 red algae. Accordingly, between 6–9% of all non-native seaweeds in each of the taxonomic groups were covered by our meta-analysis. All comparisons were made between non-native seaweeds and native seaweeds with the exception of one study with five data entries where the palatability of non-native seaweeds was compared to a seagrass species. By far the most intensively studied seaweeds in the context of feeding preference of herbivores were *Codium fragile* ssp. *tomentosoides* (currently accepted name *Codium fragile* ssp. *fragile*) and *Sargassum muticum*, which also resulted in the highest number of entries for these species in the meta-analysis

(Table 1). More than two thirds of the non-native seaweeds included in the meta-analysis have their original distribution in the north-west Pacific and Indo-Pacific, whereas the most intensively studied region of introduction was the north-east Atlantic (Table 1). Isopods and amphipods (Arthropoda), gastropods (Mollusca), sea urchins (Echinodermata) and herbivorous fish (Chordata) constituted the majority of the tested herbivores in the studies (Table 1).

Meta-analysis of consumer preference

The weighted overall mean effect was estimated to be –0.528 with a bootstrapped 95% CI = (–0.872, –0.187). This effect was significantly different from zero (p = 0.002, Figure 1) and showed



(B)

Co-variable	Q_M	Q_E	I^2	R^2
Species	31.27*	466***	92.33	17.53
Phylum	9.34**	725***	92.95	11.72

Figure 1 (A) Forest plot of the estimated effect sizes (Hedges' *d* standardized mean difference) grouped by each non-native species (open squares) and by the phylum of the non-native species (grey squares). The black square indicates the overall mean effect size of feeding preferences. Error bars represent 95% confidence intervals. The numbers in brackets describe the number of dataset entries for each species. (B) The results of the meta-regression with the non-native seaweed or phylum of the non-native species as an explanatory variable in a random-effects model; * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$. [1]Currently accepted name *Caulerpa cylindracea*; [2]Currently accepted name *Codium fragile* ssp. *fragile*; [3]Currently accepted name *Dasysiphonia japonica*.

that non-native seaweeds were on average less preferred by native herbivores compared to native seaweeds. The results of the different studies were, however, highly heterogeneous (residual heterogeneity among studies: $Q_{1,74} = 909.67$, $p < 0.001$, $I^2 = 93.8\%$). Including the predefined covariables in the model showed that the identity of the non-native seaweed, taxonomic and functional groups as well as the experiment type explained significant amounts of the observed heterogeneity (Figures 1 and 2). Residual heterogeneity was always high indicating that there may be other moderators not embraced by our analysis that influenced the outcome.

Grouping the non-native species by their taxonomic group revealed that only non-native red seaweeds were of low palatability to native herbivores, while the non-native green and brown seaweeds did not differ significantly in palatability compared to native seaweeds (Figure 1). Grouping according to functional groups suggested that only non-native filamentous seaweeds were less preferred, whereas the palatability of corticated or leathery non-native seaweeds did not differ from native counterparts (Figure 2). Due to the dataset structure, functional and taxonomic group were highly confounded: all green algae were corticated, all brown algae were leathery macrophytes and all filamentous algae were red seaweeds (Table 1). However, when functional groups were separately

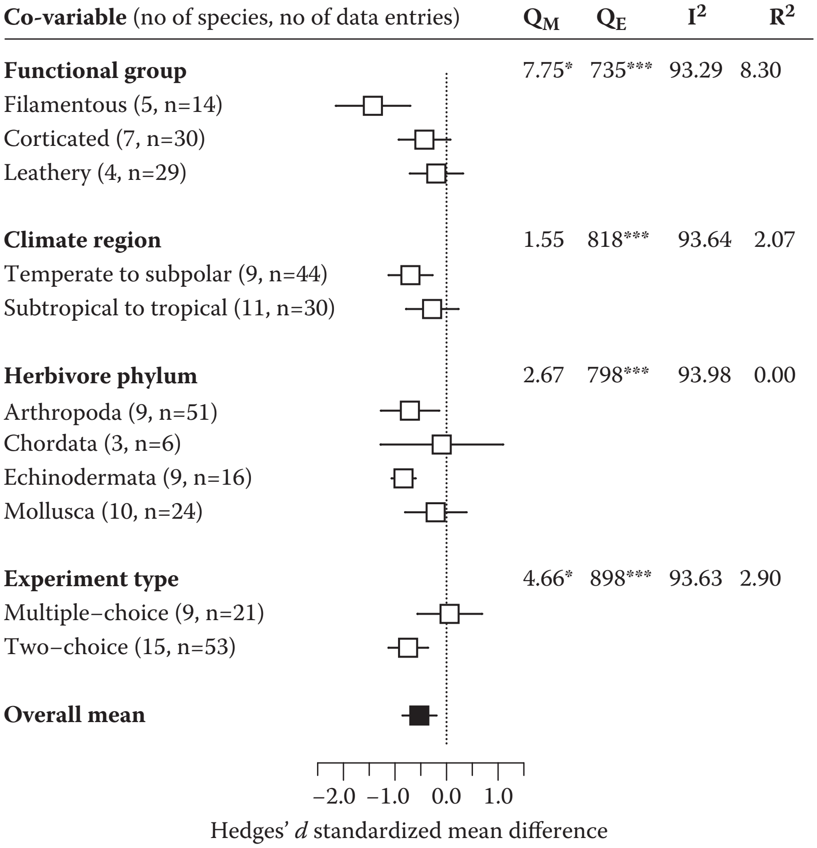


Figure 2 Forest plot of the estimated effect sizes (Hedges' *d* standardized mean difference) grouped by explanatory variables (open squares). The black square indicates the overall mean effect size of the dataset. Error bars represent 95% confidence intervals. The numbers in brackets describe the number of non-native species and the number of dataset entries represented by each subgroup. The statistics of the meta-regression of a random-effects model using functional group of the non-native seaweed, climate region and experiment type as an explanatory variable are displayed to the right; * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$.

tested for non-native red seaweeds, only filamentous seaweeds were again significantly less preferred ($Z_{\text{filamentous}} = -4.28$, $p < 0.001$; $Z_{\text{corticated}} = -1.80$, $p = 0.07$).

Analysis of the herbivore grouping revealed that arthropods and echinoderms found non-native seaweeds less palatable than native seaweeds, whereas molluscs and fish did not show any preference (Figure 2). Furthermore, herbivores from temperate to subpolar regions significantly preferred native seaweeds to non-native seaweeds, but herbivores from tropical or subtropical regions did not show a preference (Figure 2).

The experiment type had a significant influence on the effect size. In contrast to the two-choice experiments, the multiple-choice experiments, in which consumption of the non-native seaweed was compared to the averaged consumption of all native seaweeds, did not detect an overall significant feeding preference for native or non-native seaweeds (Figure 2).

Sensitivity analysis, publication bias and temporal trends

There was no indication that the results obtained from the meta-analysis lacked robustness. Exclusion of any data entry in the meta-analysis always resulted in similar overall mean effect size and confidence intervals (results not shown), which indicated that there were no serious outliers present. The cumulative meta-analysis by publication year showed that from the eighth data entry (2001), the overall mean effect size was constantly negative, oscillating between –0.628 and –0.302, though the 95% confidence interval included zero over some periods (Figure 3). Furthermore, Rosenberg's fail-safe number was sufficiently large (4219) to conclude that the observed outcome was a reliable estimate of the overall effect size. Additionally, the funnel plot and rank correlation test for funnel plot asymmetry gave no indication that publication bias affected the observed outcome (rank correlation test, Kendall's $T = 0.098$, $p = 0.2196$, Figure 4).

Review of community studies

Our literature search identified nine studies that examined adult performance of non-native seaweeds in the presence and absence of consumers. Only five reported effects on cover or biomass for both the non-native species and native seaweeds. These studies included one green, two brown and two red algal taxa and are summarized in Table 2. All taxa were also covered by the meta-analysis of feeding preference.

In the presence of herbivores, the filamentous red alga *Bonnemaisonia hamifera* reached higher cover and its biomass increased in short-term community experiments under laboratory conditions. In the absence of herbivores, *B. hamifera* was an inferior competitor compared to the native red seaweeds in the community and decreased in abundance (Enge et al. 2013, Sagerman et al. 2014). In contrast, the filamentous red alga *Heterosiphonia japonica* (currently accepted name *Dasysiphonia japonica*) dominated the community independent of herbivore presence due to its extreme growth rate (Sagerman et al. 2014). Compared to six native species, the leathery brown alga *Sargassum muticum* was the only seaweed that could maintain clear positive growth in the presence of herbivores in a short-term laboratory community experiment, but was also a superior competitor in the absence of herbivores (Engelen et al. 2011). Grazing had no effect on the cover of the corticated green alga *Codium fragile* ssp. *tomentosoides* (currently accepted name *Codium fragile* ssp. *fragile*) in a 13-week field experiment, while the native competitor *Laminaria longicruris* (currently accepted name *Saccharina longicruris*) could not persist and cover of turf algae strongly decreased under natural sea urchin densities. But again, *Codium fragile* ssp. *tomentosoides* had superior competitive abilities compared to *Laminaria longicruris* even in the absence of herbivores (Sumi & Scheibling 2005). On sea urchin barrens, grazing could not prevent canopy development of the leathery brown *Undaria pinnatifida* over a 30-month period, while the native canopy species did not exceed more than 0.7% cover (Valentine & Johnson 2005). In addition, the native canopy species showed inferior

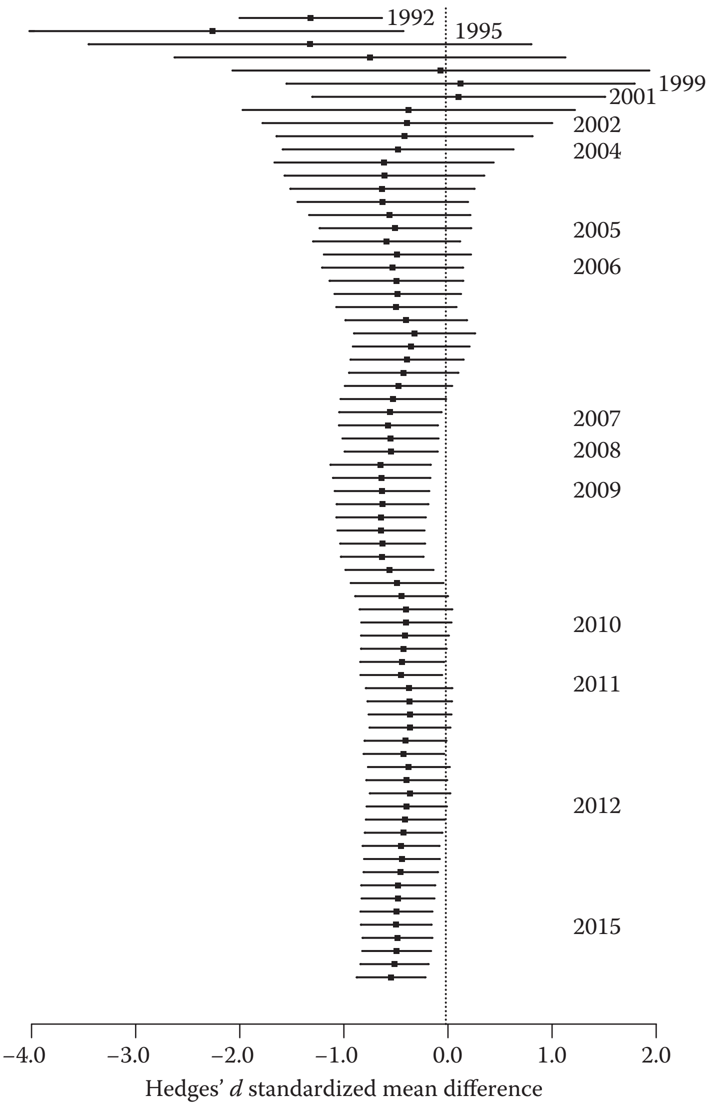


Figure 3 Forest plot of the cumulative meta-analysis of herbivore feeding preference between native and non-native seaweeds, ordered by publication year. Each data point represents the change of the estimated overall mean effect size (Hedges' *d* standardized mean difference) by adding the next newest entry into the meta-analysis. The dotted line indicates the absence of a significant effect. Error bars represent 95% confidence intervals.

competitive abilities compared to *U. pinnatifida* in the absence of herbivores (Valentine & Johnson 2005).

Discussion

Our meta-analysis showed that overall, non-native seaweeds tend to be less palatable than native seaweeds to herbivores in the new community. However, the meta-analysis also revealed considerable variability among the results of different studies. This variability could largely be explained by the identity of the seaweed taxon, indicating that the relative palatability of native compared

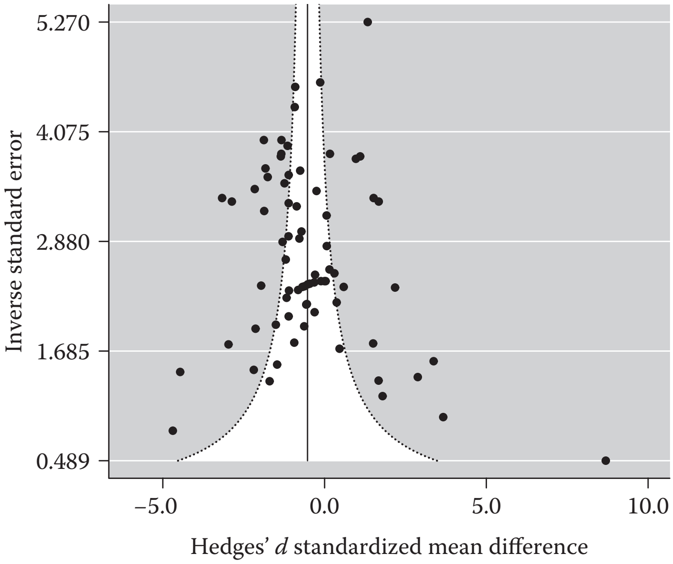


Figure 4 Funnel plot for the meta-analysis of feeding preferences using a random-effects model. Each data entry is represented by a circle showing the relation of the effect size (Hedges' *d* standardized mean difference) to its inversed standard error. The black line indicates the estimated overall mean effect and the white region represents the region in which 95% of the studies are expected to lie in the absence of biases and heterogeneity.

Table 2 Summary of community studies on herbivore effects on non-indigenous seaweeds

Species	Taxonomic group	Functional group	Studies	Method
Codium fragile ssp. *tomentosoides*[1]	Chlorophyta	Corticated	Sumi & Scheibling 2005	Field experiment
Sargassum muticum	Phaeophyceae	Leathery	Engelen et al. 2011	Laboratory experiment
Undaria pinnatifida	Phaeophyceae	Leathery	Valentine & Johnson 2005	Field experiment
Bonnemaisonia hamifera	Rhodophyta	Filamentous	Enge et al. 2013, Sagerman et al. 2014	Laboratory experiment
Heterosiphonia japonica[2]	Rhodophyta	Filamentous	Sagerman et al. 2014	Laboratory experiment

Note: The Functional group classification follows Littler & Littler (1984): filamentous = delicately branched, uniseriate to slightly corticated; corticated = coarsely branched, corticated; leathery = thick branched, heavily corticated or thick walled.

[1] currently accepted name *Codium fragile* ssp. *fragile*

[2] currently accepted name *Dasysiphonia japonica*

to non-native seaweeds differs between the groups of red, brown and green seaweeds. It was only for reds, but not for the brown and green seaweeds, that the meta-analysis demonstrated an overall difference in herbivore preference between native and non-native species. Furthermore, the meta-analysis revealed that filamentous non-native species, which were all red seaweeds in our analysis, tended to be of low palatability to native herbivores.

Feeding preference of herbivores is positively correlated to the nutritional quality and the shelter provided by the seaweed, and seaweeds can in turn deter herbivores by structural and chemical defences (Lubchenco & Gaines 1981, Hay & Fenical 1992). The low herbivore preference for non-native filamentous algae is an unexpected result because filamentous algae are commonly regarded to be palatable and highly susceptible to most consumers (Littler & Littler 1980, Steneck & Watling

1982, Littler et al. 1983). Consequently, this group could be expected to face a higher degree of consumptive biotic resistance in new regions, compared to non-native seaweeds from other functional groups. Our result matches recent findings suggesting that leathery and foliose algae are more susceptible to herbivores than filamentous or corticated algae (Poore et al. 2012), which indicates that structural traits, such as tissue toughness, is far from always a determining factor for food choice of herbivores and that feeding preferences are driven by other seaweed traits.

The presence of chemical defences can explain low palatability of certain seaweeds to marine herbivores (Hay & Fenical 1992, Pavia et al. 2012). Accordingly, it has been postulated that chemical defences can protect non-native seaweeds, as well as vascular plants, from being attacked by native herbivores in a new region, either by comparatively high defence concentrations or by molecular structures that are evolutionarily novel to the native herbivores (Cappuccino & Arnason 2006, Wikström et al. 2006, Verhoeven et al. 2009, Enge et al. 2012). Red seaweeds in particular produce an immense diversity and high quantities of often halogenated secondary metabolites, which have been frequently demonstrated to possess effective antimicrobial (Persson et al. 2011, Nylund et al. 2013), antifouling (Dworjanyn et al. 2006), allelopathic (Svensson et al. 2013) and antiherbivore activities (Kladi et al. 2005, Cabrita et al. 2010, Enge et al. 2012). The diversity of chemical defence compounds in red algae may explain why non-native red seaweeds showed especially low palatability in our meta-analysis.

The establishment of a specific chemical basis for a low preference of potential native consumers for an introduced organism is, however, a demanding task and marine examples are still rare. Evidence for chemical defences against native herbivores has so far only been provided for a few non-native seaweed species. The green algae, *Caulerpa taxifolia* and *C. racemosa*, produce caulerpenyne with effects on sea urchins (Amade & Lemée 1998, Dumay et al. 2002). *Codium fragile* ssp. *fragile* (=*Codium fragile* ssp. *tomentosoides*) possesses wound-activated defences involving dimethylsulfoniopropionate (DMSP), which deters native sea urchins (Lyons et al. 2007). The arctic brown alga, *Fucus evanescens*[*], contains significantly higher concentrations of phlorotannins (polyphenolic defence compounds) than native fucoids in its new range, deterring native isopods and molluscs (Wikström et al. 2006, Forslund et al. 2010). The highly invasive red alga, *Gracilaria vermiculophylla*, produces prostaglandins, hydroxylated fatty acids and arachidonic acid-derived lactones on wounding, which provides resistance against native isopods and molluscs (Nylund et al. 2011, Hammann et al. 2016). Another red seaweed, the filamentous *Bonnemaisonia hamifera,* produces volatile brominated compounds that provide defence against native isopods, gammarids and ophistobranch consumers (Enge et al. 2012). These examples show that chemical defence can explain the low palatability of some non-native seaweeds, but further studies are needed before it can be concluded that chemical defence is a common trait of low-preferred non-native seaweeds (especially of the filamentous red algae).

Notably, two of the species for which chemical defences have been characterized (*Caulerpa racemosa* and *Codium fragile* ssp. *tomentosoides*) were not consistently of low preference to native herbivores in our meta-analysis. In both cases, the chemical defence compound was only documented to be active against one herbivore species, while multiple herbivores were tested in the feeding preference experiments. A specific chemical defence is usually not effective against all herbivore species, since herbivores can adapt to and/or circumvent the effects of secondary metabolites (Sotka, 2005). Furthermore, concentrations and the effectiveness of the chemical defence compounds can vary between seaweed and herbivore populations (Pavia et al. 2003, Sotka 2005), which makes it

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[*] *Fucus evanescens* may have expanded its range naturally, but available evidence suggests that the spread of this species to southern Scandinavia and the British Isles was aided by human transport. It exhibits a disjunct distribution with new occurrences that were discovered in harbours in the beginning of the 20th century, making introduction from shipping plausible. Thus, we chose to include *Fucus evanescens* in the definition of a non-native species that we used in the literature search, i.e. a species that has been translocated to a new range by humans.

important that the palatability of non-native species introduced into several regions are tested with a set of the native herbivores that are relevant in the new regions.

Herbivore preference can be a first indicator for plant performance and competitive ability, but cannot be directly translated into community composition and population dynamics under natural conditions. We found that studies using long-term community experiments assessing the effects of consumers on non-native seaweeds in interaction with native seaweeds are essentially lacking. The few existing studies included in our review showed that performance of non-native seaweeds can be increased, equal or reduced in the presence of herbivores. To date, the most rigorous example of a successful seaweed invasion based on chemical defence concerns the filamentous red alga *Bonnemaisonia hamifera* (Figure 5). The documented chemical defence (1,1,3,3-tetrabromo-2-heptanone) provides this relatively poor competitor (in the absence of native herbivores), with a strong competitive advantage in its new range in the presence of native herbivores (Enge et al. 2013, Sagerman et al. 2014). In addition, the same brominated compound inhibits the recruitment of native algal competitors (Svensson et al. 2013) and reduces bacterial load (Nylund et al. 2008). Thus, the multiple ecological benefits of this compound outweigh the cost of its production for the invader in the new range (Nylund et al. 2013). In some of the other studies the non-native seaweeds often performed better than their native competitors in the presence of herbivores, but the non-native species were superior competitors also in the absence of herbivores. Thus, the extent to which low herbivore preference contributes to invasion success of non-native seaweeds remains elusive. There is a need for more studies on the effects of herbivores on non-native seaweed populations, ideally experiments that include seasonal changes and complete life cycles of the seaweed and grazers. This is a challenging task in marine environments with species with complex life cycles.

In conclusion, the results of our meta-analysis show that low palatability does not seem to be a universal trait among non-native seaweeds and only certain seaweeds escape native herbivores in

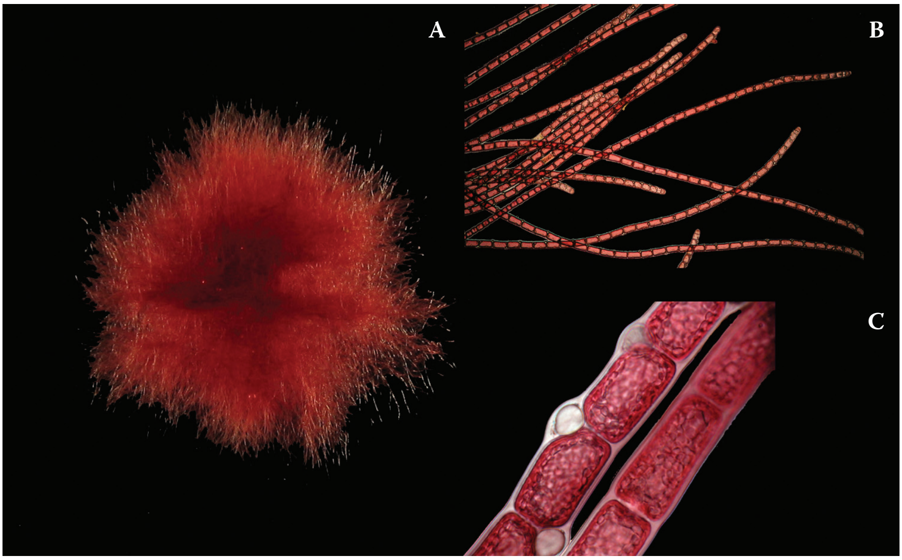

Figure 5 The invasive filamentous red seaweed *Bonnemaisonia hamifera*, which produces a potent chemical defence (1,1,3,3-tetrabromo-2-heptanone) that makes it unpalatable to native herbivores in the north Atlantic, thereby providing it with a strong competitive advantage over native seaweeds in its new range. (A) Tetrasporophytic phase, growing as small turfs, which consist of numerous sparsely branched filaments (B). Filaments are one cell-layer thick and have numerous gland cells, containing chemical defences, located between the vegetative cells (C). (From Nylund et al. 2008.)

their new range. Accordingly, the prediction of the enemy release hypothesis that introduced species are less attacked by herbivores than their native counterparts in the new range (Keane & Crawley 2002), does not hold for all non-native seaweeds. Interestingly, we found that non-native filamentous red seaweeds tend to be especially less palatable to herbivores. This is an important finding considering the majority of seaweed introductions are filamentous or corticated red algae (Williams & Smith 2007). Due to their morphology, these species can often be cryptic or less apparent compared to larger brown and green seaweeds. Probably, therefore, they are less frequently studied and often overlooked in their community impacts, even though effects on biodiversity and ecosystem processes have been proven (Schaffelke & Hewitt 2007, Sagerman et al. 2014). The low preference for many non-native filamentous red algae indicates that low impact of herbivores may contribute to invasion success in this group. However, to assess if consumers play a crucial role in seaweed invasions, future research should focus on examining consumer impacts on competitive interactions between non-native and native seaweeds.

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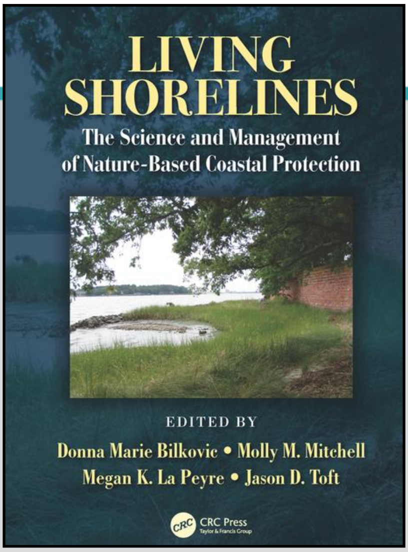
CHAPTER

4

A PRIMER TO LIVING SHORELINES



This chapter is excerpted from

Living Shorelines: The Science and Management of Nature-Based Coastal Protection

by Donna Marie Bilkovic, Molly M. Mitchell, Megan K. La Peyre, Jason D. Toft.

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CHAPTER 1

A Primer to Living Shorelines

Donna Marie Bilkovic, Molly M. Mitchell, Jason D. Toft, and Megan K. La Peyre

CONTENTS

1.1 THE CHALLENGE: A HISTORY OF SHORELINE ARMORING

For centuries, estuarine and coastal shorelines have been dramatically modified by humans for far-ranging and, at times, conflicting purposes, such as water access, commerce, aquaculture, and property protection. Legal principles governing these uses often tend to favor the interests of coastal property owners or societal rights to access and exploit natural resources. For example, in most coastal communities, shoreline armoring is allowed and accepted if property is deemed to be at risk. As a result, shorelines have been extensively armored globally and ecosystem function has diminished. The amount of shoreline armoring along a given coast varies depending on surrounding land use, with major coastal cities often having more than 50% of their shores hardened (e.g., Chapman and Bulleri 2003). However, shoreline armoring is not restricted to dense urban areas, as coastal areas in the process of change (e.g., agriculture to suburban) may experience the fastest rates of shoreline hardening (Isdell 2014). In sum, the United States has roughly 14% (22,000 km) of its extensive coastline armored (Gittman et al. 2015). In Europe, more than half of the >15,000 km of coastline that is eroding is artificially stabilized (EC 2004). Likewise, more than half of Mediterranean coastlines are armored and developed (EEA 1999). In Japan, approximately half of its coastline is reportedly eroding (15,900 km of the 34,500 km of total coast) and approximately 27% of that coastline has been hardened (Koike 1993). In Australia, the densely populated coastal cities typically have more than 50% of their coastlines armored (Chapman 2003). Pressures to abate erosion and secure shorelines in place will only continue, and likely increase, as the proportion of the global population living within 100 km of the coasts grows from one-third to an expected one-half by 2030 (Small and Nicholls 2003) and sea level continues to rise. This may be particularly problematic in areas where heavily urbanized landscapes intersect with higher-than-average rates of sea level rise; for example, the North American Gulf and mid-Atlantic coasts have the highest rates of rise in the United States (Boon and Mitchell 2015) and respectively have the third and fifth fastest-growing coastal populations in the continental United States (Crossett et al. 2004).

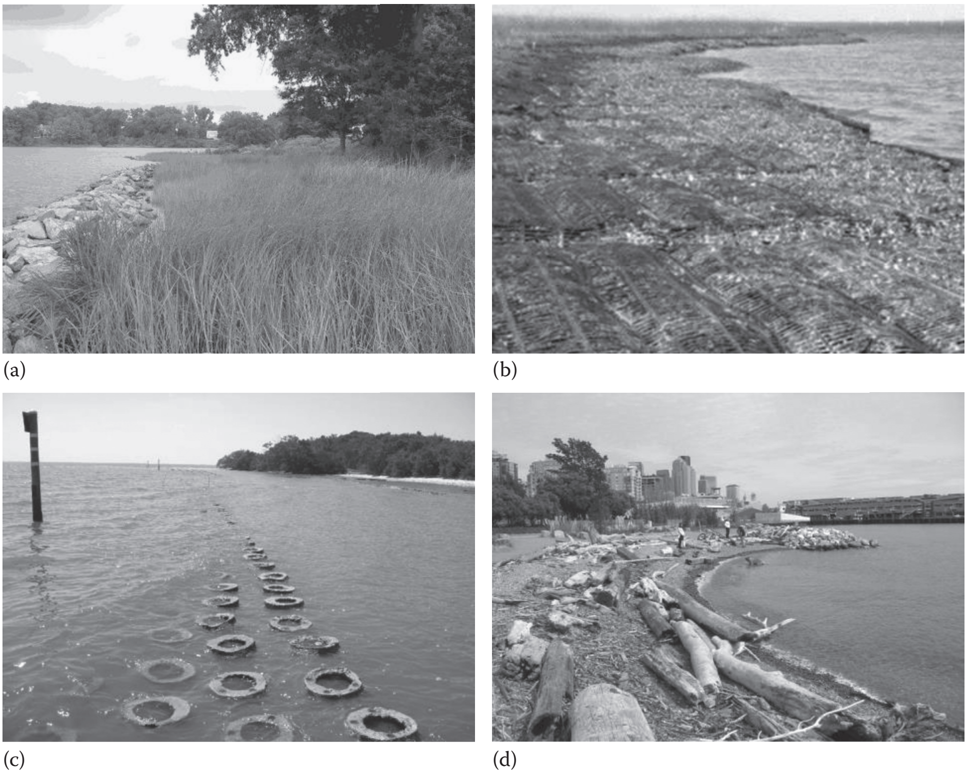
Closely associated with shoreline modification is the loss or alteration of intertidal and shallow subtidal habitats (e.g., wetlands, seagrasses) and ecosystem function (e.g., Bilkovic and Roggero 2008; Chapman and Bulleri 2003; Dethier et al. 2016; Dugan et al. 2011; Peterson and Lowe 2009 and references within). This has implications for ecosystem service provision to coastal communities including shore protection, fisheries production, and water quality benefits (e.g., Arkema et al. 2013; Bilkovic et al. 2016; Gedan et al. 2011; Scyphers et al. 2015). Growing concern about the cumulative effects of piecemeal alterations to the coastlines has reinforced the need for alternative shoreline management strategies.

While wetlands have been long recognized as providing some level of protection to coastal communities from wave-induced erosion, the intentional use of natural habitat elements to reduce shoreline erosion was first reported in the early 1970s (Garbisch and Garbisch 1994). Since that time, the understanding and practical application of nature-based techniques have grown tremendously. In recent years, nature-based approaches are being extensively promoted and practiced globally primarily because of (1) growing acknowledgment of the value of ecosystem services provided by coastal habitats (Barbier et al. 2011; Costanza et al. 1997) and the adverse effects of traditional armoring to coastal systems, (2) the extensive ongoing loss of many threatened coastal habitats (marsh, seagrasses) (Duarte 2009; Halpern et al. 2008; Waycott et al. 2009), and (3) the realization that dynamic erosion protection approaches that incorporate natural ecosystem elements (e.g., marsh, beach) may be more responsive and resilient in some settings to storm events than traditional armoring (Gedan et al. 2011; Gittman et al. 2014). However, the field of shoreline restoration in human systems is in its nascent stages. In particular, challenges remain to reconcile conflicting uses and establish a path-forward to effectively manage shorelines for both ecological and human protections, leading to our topic of living shorelines.

1.2 WHAT'S IN A NAME?

With any new discipline, there tends to be a growing period when terminology has not been formally defined and accepted by all participants, which can lead to a certain amount of confusion, setbacks, and misinformation. This is especially true for shoreline management when goals can be at cross-purposes and depend on the viewpoint. The countless terms that exist to describe shoreline protection approaches that integrate nature elements illustrate the difficulties that remain for the field. These terms include living shorelines, nature-based shoreline protection, green shorelines, geomorphic engineering, soft stabilization, building with nature, and variances thereof. For simplicity, we will refer to these shoreline approaches as *Living Shorelines* henceforth. A near consensus among practitioners is that these approaches are intended to not only protect shorelines and infrastructure but also conserve, create, or restore natural shoreline functions in estuarine, marine, and aquatic systems. In practice, living shorelines should predominantly consist of organic techniques and materials that are characteristic of the local system, such as wetland, riparian, and dune plantings; beach nourishment; shellfish reefs; and emplaced large woody debris. The connection between aquatic and terrestrial habitats should be maintained, and dynamic movement of habitat features should be allowed in response to storm events and to promote sediment capture. Last, in higher-energy sites that require hybrid approaches with engineered structures to provide the requisite wave attenuation to sustain planted vegetation and habitats, engineered structures should be minimized to not overwhelm the living habitat features they are supporting (Figure 1.1).

Public policy actions to promote the use of living shorelines have been implemented by regional and national governmental entities in the United States and Europe. In the United States, many coastal states have opted for either legislative requirements or the more popular option of



(a) (b) (c) (d)

Figure 1.1 Living shorelines: (a) planted marsh with supporting stone sill (from Bilkovic and Mitchell, Chapter 15, this book); (b) bio-engineered oyster reef (gabion mats) with marsh (From La Peyre et al., Chapter 18, this book); (c) oyster reef bases designed to encourage oyster recruitment (From Hall et al., Chapter 13, this book); (d) created pocket beach habitat for juvenile salmon excavated from a stretch of riprap-armored shoreline (From Cordell et al., Chapter 21, this book).

employing incentives (expedited permit process, fee waivers) or fiscal aid (e.g., low interest loans) for the implementation of living shorelines as a preferred shoreline management approach (Bilkovic and Mitchell, Chapter 15, this book). Likewise, federal agencies including the National Oceanic and Atmospheric Administration (NOAA), United States Environmental Protection Agency, and United States Army Corps of Engineers (USACE) have developed funding and planning initiatives to support living shoreline implementation. Moreover, the USACE and NOAA helped initiate a Community of Practice to enhance collaboration among academic institutes, nongovernmental organizations, and state and federal agencies called Systems Approach to Geomorphic Engineering (SAGE) to use living shorelines as a tool to achieve larger-scale community resilience (Bilkovic et al. 2016). In Europe (e.g., United Kingdom, Belgium, the Netherlands, and France), “building with nature” initiatives that involve the implementation of nature-based solutions as flood risk reduction measures are often driven by national and European legislation and are a growing trend (Borsje et al., Chapter 8, this book; Esteves et al., Chapter 9, this book).

These efforts are not without criticism. Many of the criticisms voiced are related to the (often unintentional) misidentification of a practice that does not meet standard criteria as a living shoreline (e.g., Pilkney et al. 2012). There are many practices, particularly in urban settings, designed to enhance or mitigate adverse effects of engineered shorelines (e.g., seawalls) in high-energy or high-risk settings where living shorelines are not suitable. For instance, a common practice in Europe is the inland realignment of a coastal protection line (seawall). Elsewhere, armored shorelines are being reengineered to increase their habitat value, such as adding complexity to the surface of a seawall to encourage invertebrate recruitment (Browne and Chapman, Chapter 22, this book) or incorporating beach and cobble areas along coastlines where seawalls maintain coastal integrity of highly urbanized areas (Cordell et al., Chapter 21, this book) (Figure 1.2). However, care should be taken to ensure that these efforts are termed living shorelines only if they fully meet the definition requirements in that the connection between aquatic and terrestrial habitats is maintained and engineered structures do not dominate. When engineered structures dominate the landscape, and shoreline protection is dependent solely on the maintenance of these engineered structures, the litmus test for a living shoreline has failed. For example, in some oyster reef restoration projects, a failure to recruit oysters that survive, grow, and build a reef over time may result in some level of shoreline protection, but this fails to be a living shoreline. In a final summary chapter of this book, we draw from the contributed works of the edited volume to more fully discuss the terminology of shoreline restoration and engineering and place living shorelines into a better context. Our hope is that this book will serve to better define living shorelines in a manner that can help refine the use of the term living shorelines as well as identify common concerns and the means to remedy or lessen some of these concerns.

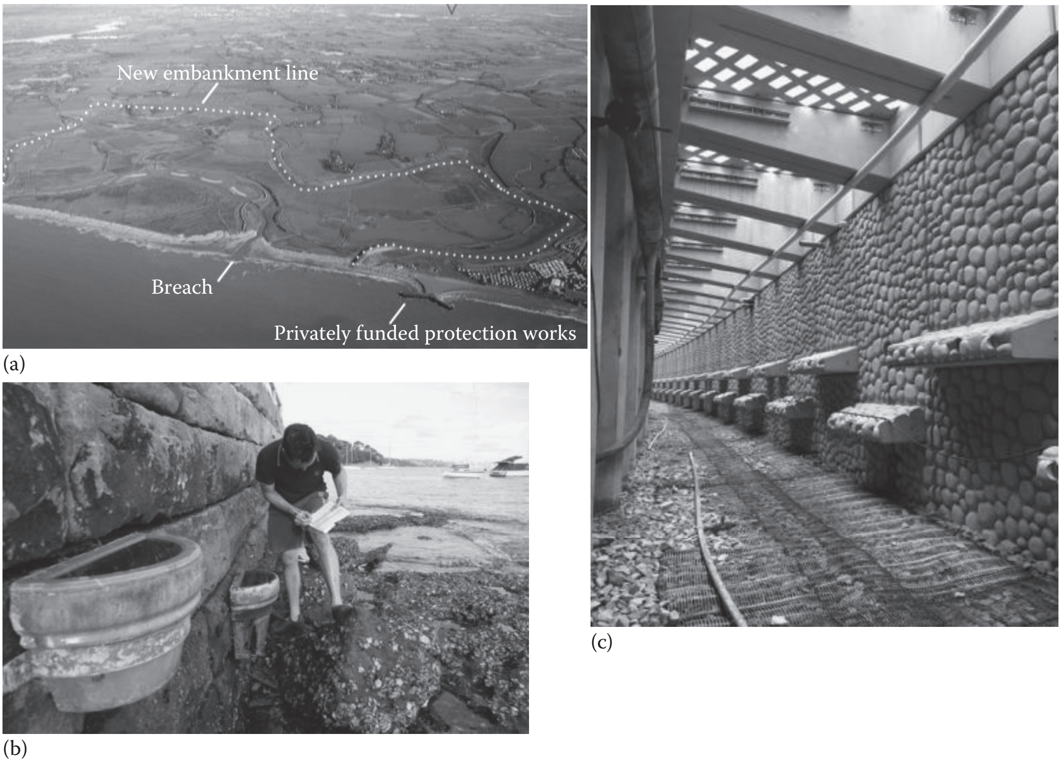


Figure 1.2 Urban shoreline enhancement practices: (a) Managed realignment strategies practiced in Europe such as managed retreat and breaching of seawalls to support intertidal habitat creation most clearly fall within the definition of a living shoreline. Other practices developed for higher energy or at-risk urban settings such as inland realignment of the coastal protection line may not fulfill the definition of a living shoreline. (From Esteves, L.S. and Williams, J.J., Chapter 9, this book.) (b) Reengineered seawall practices to increase complexity and enhance habitat use and diversity. (From Browne, M.A. and Chapman, M.G., Chapter 22, this book.) (c) Habitat enhancements in the new construction of Seattle's seawall including light penetrating surfaces in the sidewalk, intertidal benches, and seawall relief and texturing. (From Cordell et al. Chapter 21, this book.)

1.3 ROLE FOR LIVING SHORELINES IN CONSERVATION AND CLIMATE ADAPTATION STRATEGIES

While living shorelines are grounded in well-established restoration science and practices, these projects are designed in different ways to accommodate both human use and ecological goals. Because of this, there is often a risk that ecological goals may be sacrificed for perceived shoreline or infrastructure protection. Therefore, living shorelines deviate from the traditional perspective of restoration or conservation, but these efforts can be complementary. The advantage that living shorelines confer is new feasible opportunities, particularly in urban or ex-urban settings, to offset previous or inevitable coastal habitat losses. The added benefit of protecting a shoreline can help overcome a "restoration" hurdle by providing an economically attractive rationale for the individual or community shouldering the cost. Further, the use of a living shoreline in place of armoring will act to curb additional loss to globally threatened habitats.

These shoreline management approaches represent a paradigm shift as they work with rather than against natural nearshore processes. Such "process-based" planning and design is a worthy goal that can be difficult to achieve, but not impossible. The potential added value of a dynamic living shoreline serving as a climate adaptation strategy to conserve coastal resilience makes that goal particularly meaningful. While in many settings where landward migration is restricted there may be a foreseeable end date for a living shoreline, the benefits of maximizing ecosystem service provision in the near term may still be substantial. Moreover, there are techniques and certain natural elements that may be incorporated to allow living shorelines to keep pace with sea level rise and extend their lifespan. For example, in the right location, an oyster reef used for shoreline protection can respond to changing conditions including subsidence and sea level rise (Casas et al. 2015; La Peyre et al., Chapter 18, this book; Mann and Powell 2007; Walles et al. 2015) and structural support can be designed to encourage the capture of sediment so that accretion rates are sufficient for the persistence of created marshes in place (Currin et al., Chapter 11, this book).

1.4 PURPOSE AND BOOK ORGANIZATION

To help guide future shoreline management and restoration, this edited volume assembles, synthesizes, and interprets the current state of the knowledge on the science and practice of living shorelines, as well as some outside the realm of living shorelines that still attempt to incorporate nature-based approaches, in order to provide context. Researchers, managers, and practitioners have gained valuable knowledge to inform the science of living shorelines, but that information has not been summarized in a single source, nor is it readily accessible to the broad spectrum of users in different disciplines (e.g., engineering, ecology, geology, and social sciences) that shoreline management and restoration require.

To cover the spectrum of topics, the book is divided into five major sections: (1) Background: History and Evolution; (2) Management, Policy, and Design; (3, 4) Synthesis of Living Shoreline Science: Physical and Biological Aspects; and (5) Summary and Future Guidance. After this introductory chapter, Arkema and others adeptly detail how ecosystem service concepts can inform living shoreline science and implementation. The second section of the book provides insights on significant management, policy, and other social factors that influence the success of living shoreline projects, as well as effective living shoreline designs. The third and fourth section of the book synthesizes the literature that is available with data from new studies on the physical aspects of living shorelines including information on trajectories of living shoreline ecosystem development. The fifth section of the book summarizes information presented throughout the book to help guide future research and management strategies. The first summary chapter details the gaps in our understanding of living shorelines. In the second summary chapter, the editors synthesize author perspectives on three focal areas to examine commonalities and differences among the contributed works. The three focal areas are as follows:

1. Lessons learned from the practice of shoreline restoration/conservation
2. Longevity and stability of projects in the near and long term with considerations for climate change and human development
3. What is the path forward? Research needs, strategies for working across different disciplines, training options, and future opportunities

This book will serve as a valuable reference to guide scientists, students, managers, planners, regulators, environmental and engineering consultants, and others engaged in the design and implementation of living shorelines. Our intent is to provide a background and history of living shorelines; understandings on management, policy, and project designs; technical synthesis of the science related to living shorelines including insights from new studies; and the identification of research needs, lessons learned, and perspectives on future guidance. To capture international efforts, the book includes perspectives from leading researchers and managers in Europe; the East, West, and Gulf coasts of the United States; and Australia who are working on natural approaches to shoreline management. The broad geographic scope and interdisciplinary nature of contributing authors will help facilitate dialogue and transfer of knowledge among different disciplines and across different regions. It is our hope that this book will provide coastal communities with the scientific foundation and practical guidance necessary to implement effective shoreline management that enhances ecosystem services and coastal resilience now and into the future.

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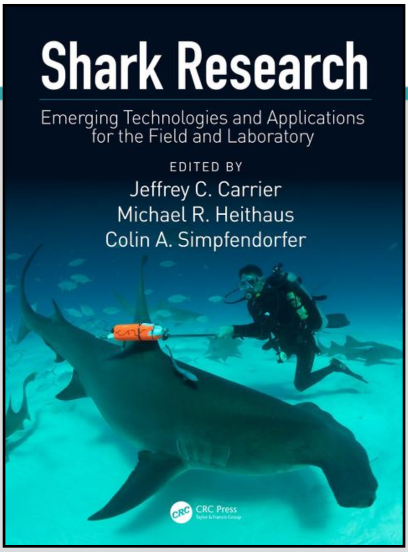
CHAPTER 5

USE OF AUTONOMOUS VEHICLES FOR TRACKING AND SURVEYING OF ACOUSTICALLY TAGGED ELASMOBRANCHS



This chapter is excerpted from

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by Jeffery C Carrier, Michael R. Heithaus, Colin A. Simpfendorfer .

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CHAPTER 6

Use of Autonomous Vehicles for Tracking and Surveying of Acoustically Tagged Elasmobranchs

Christopher G. Lowe
Shark Lab, California State University, Long Beach, California

Connor F. White
Shark Lab, California State University, Long Beach, California

Christopher M. Clark
Lab for Autonomous and Intelligent Robotics, Harvey Mudd College, Claremont, California

CONTENTS

6.1 INTRODUCTION

Although great strides have been made in understanding shark behavior and ecology due to advances in technology, many technical challenges still exist in quantifying how elasmobranchs behave in response to their environment, conspecifics, prey, and predators. Telemetry (acoustic and satellite), sensor, video, and data logger technology have all provided new insights into how sharks move, select habitat, and interact with other species; however, data collection can be arduous, expensive, time consuming, and spatially and temporally limiting. Satellite telemetry can provide valuable data on the water temperature and depths that wide-ranging elasmobranchs move through, but this technology does not provide much in the way of fine-scale geospatial positions or behavioral state. Alternatively, acoustic telemetry (see Chapter 8 in this volume) can provide either short-term, high-resolution position information and corresponding environmental data (e.g., water temperature, depth, activity rate) via active tracking or longer term, lower resolution position information for many animals simultaneously, but over a much more limited spatial scale via passive tracking. Active tracking, in particular, is typically labor intensive and allows for tracking of one individual at a time, whereas passive tracking is much less labor intensive but spatially limited by the size of a stationary array.

Advances in underwater robotics, inertial measurement unit (IMU), global positioning system (GPS), and autonomous control systems have greatly enhanced our ability to measure a wide array of oceanographic parameters via autonomous mobile underwater or surface vehicles and simultaneously provide high positional accuracy. Commercially available autonomous underwater vehicles (AUVs) and autonomous surface vehicles (ASVs) have been developed and used primarily for oceanographic purposes; however, recent attempts have been made to incorporate acoustic telemetry hydrophones and receivers into these robots for fully autonomous active tracking of elasmobranchs tagged with acoustic transmitters. The primary benefits of these coupled technologies are they allow for accurate, fine-scale positioning of tagged elasmobranchs but can also simultaneously record environmental conditions, map the benthos, and record biota surrounding focal individuals. The information discussed in this chapter covers the types of autonomous vehicles, previous uses for surveying and tracking of elasmobranchs, and the future of this technology.

6.2 USE OF AUTONOMOUS UNDERWATER VEHICLES IN OCEANOGRAPHY AND MARINE SCIENCE

In 1957, the first autonomous underwater vehicle (AUV) was developed at the University of Washington's Applied Physics Laboratory. The vehicle, named SPURV (Special Purpose Underwater Research Vehicle), had the ability to dive down to 3000 m and measure water temperature and conductivity. Figure 6.1A shows the SPURV being deployed. Its form, consistent with early torpedo designs, was long and thin with a motor-driven propeller located at the rear of the vehicle for propulsion. Four control surfaces at the rear enabled steering for direction control (yaw, pitch, and roll). This general design is still predominant in the AUV industry.

6.2.1 Types of AUVs and Capabilities

Since SPURV was introduced to the research community, a large number of other underwater vehicles with different form factors have been designed, constructed, and deployed (Figure 6.1B,C). Unlike AUVs, which are typically untethered, fully autonomous, and designed to cover longer distances, remotely operated vehicles (ROVs) are tethered to a pilot's control console located above the surface. Figure 6.1B shows an example of a micro-class ROV obtaining samples with a manipulator arm. Different again are autonomous surface vehicles (ASVs), which are restricted to motion on the surface (Figure 6.1C). These vehicles are generally compared based on their depth rating, speed, level of autonomy (e.g., how much pilot interaction is required during a mission), endurance, sensor payload capacity, maneuverability, and data availability (e.g., whether or not data can be transmitted to the pilot in real time).

6.2.1.1 Remotely Operated Vehicles

Remotely operated vehicles (ROVs) are differentiated from other vehicles by the fact that there is a tether that connects the vehicle to a control station typically located on a dock or boat. Pilots manually control the ROV via a joystick, allowing the pilot to send control signals to the vehicle's actuators (e.g., motors) through a wire bundle inside the tether. Similarly, vehicle sensor data are relayed from the vehicle back to the control station through the tether. These data can take on the form of video, depth, sonar, temperature, etc. and are typically necessary for pilot navigation. Power is also provided through the tether, removing the need for an onboard power supply. The presence of this tether offers several advantages when conducting fish or shark surveys. It provides real-time feedback to a pilot, thus allowing adaptation to changing fish behaviors. The video also provides a means for characterizing habitat, prey abundance, etc.; for example, one can survey the bottom to determine if the seafloor would facilitate egg laying for skates and catsharks. The tether, unfortunately, also restricts motion of the vehicle by limiting its range to the length of the tether. Monitoring fish with longer ranges using an ROV is simply not feasible. Because the vehicle is not traveling long distances and power is provided, ROVs are designed not so much for endurance as they are for maneuverability (e.g., their thruster configuration allows motion in all directions). They can be used for situations requiring up-close, interactive navigation.

Figure 6.1 Examples of underwater robots: (A) Deployment of SPURV, the first autonomous underwater vehicle (AUV) (photograph courtesy of the Applied Physics Laboratory, University of Washington, Seattle). (B) A VideoRay underwater remotely operated vehicle (ROV). (C) This robot is a ClearPath Robotics Kingfisher ASV.

6.2.1.2 Buoyancy-Driven Gliders

Unlike typical AUVs, which are motor or propeller driven, buoyancy-driven gliders provide forward motion by modifying their applied buoyancy force in flight. The gliders are equipped with bladders (often located in the vehicle nose) that can be filled or emptied with water from the surrounding environment. When ballasted correctly, the vehicle will change between being positively and negatively buoyant as the bladder is emptied or filled. Wings affixed to the sides of the vehicle transform these vertical forces into horizontal forces, enabling forward motion. Although this type of motion is slower (e.g., 0.35 m/sec) than propeller-driven AUVs (e.g., <2 m/sec), it requires less energy and hence provides longer endurance; for example, the Slocum Glider (Figure 6.2A) can travel a distance of 13,000 km with a maximum deployment time of 18 months. For this reason, the application of such vehicles to fish tracking is limited to conducting more long-range passive surveys than active tracking which requires greater speeds and maneuverability.

6.2.1.3 Wave-Driven Surface Gliders

Similar to buoyancy-driven gliders, wave gliders harness naturally occurring vertical motion and transform it to horizontal motion. As waves carry the vehicle up and down, a

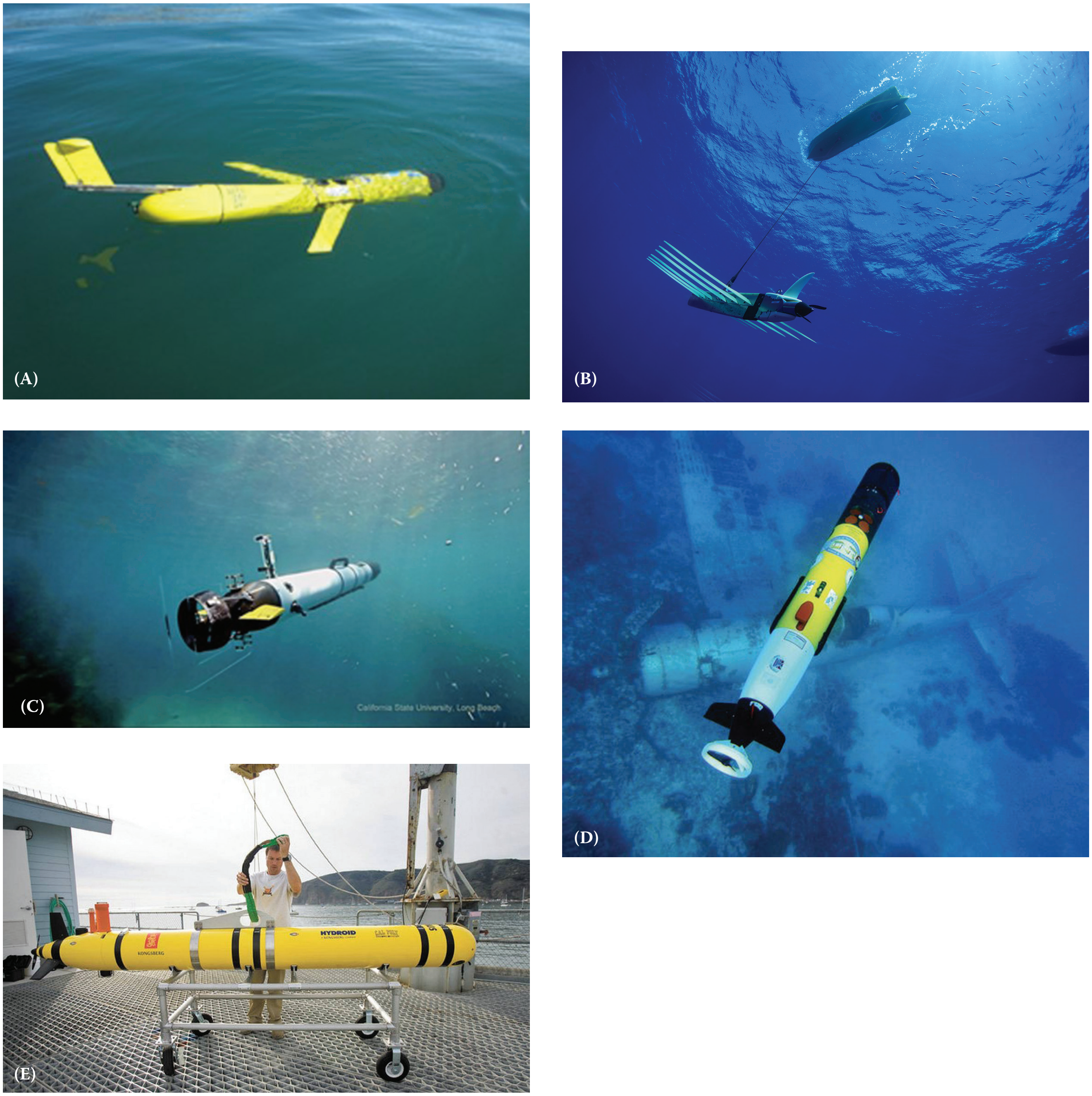


Figure 6.2 Autonomous underwater vehicles: (A) Slocum Glider; (B) underside of Liquid Robotics' Wave Glider (photograph courtesy of Liquid Robotics, Sunnyvale, CA); (C) OceanServer Iver2 AUV; (D) REMUS 100; (E) REMUS 600.

wing system that sits underwater (see Figure 6.2B) provides a force in the forward direction. Also similar to buoyancy-driven gliders, wave gliders have longer endurance but lower maneuverability and speed, making them applicable to long-range passive tracking as opposed to active tracking. Because their primary hull is surface oriented, these vehicles can offer real-time radio connectivity and the use of solar panels to provide the power required to support longer missions.

6.2.1.4 *Propeller-Driven AUVs*

Propeller-driven AUVs are common, and most take on a form factor similar to the SPURV, in which the body is a long cylinder with a cone-shaped nose and actuation at the tail (e.g., the REMUS vehicles shown in Figure 6.2C–E). The motor-driven propellers located at the AUV tail provide forward and reverse locomotion, and a range of steerable control surfaces act as rudders to set the yaw, pitch, and roll angles of the vehicle. Several propeller-driven AUVs also have configurations with thrusters facing in multiple directions for increased maneuverability. Note that several hybrid buoyancy/propeller-driven AUVs are under development that aim to obtain the advantages of both approaches to locomotion. Examples of off-the-shelf, propeller-driven AUVs include OceanServer's Iver vehicles (Figure 6.2C) and Kongsberg's REMUS vehicles (Figure 6.2D,E). Notably, the REMUS 600 (Figure 6.2E) is larger, has a greater depth rating (up to 1500 m), and has greater endurance (24 hr) than the more typical REMUS 100 (Figure 6.2D), which has a 100-m depth rating and 12-hr battery life at 1.5 knots. In research projects, both the Iver and REMUS vehicles have been outfitted with hydrophone–receiver systems that allow not only passive tracking of tagged fish but also active tracking.

6.2.1.5 Navigation

Autonomous underwater vehicles come equipped with path-following capabilities such that users can simply upload to the vehicle a series of longitude, latitude, and depth points that the vehicle can be deployed to follow autonomously. Such path following requires a navigation system that iteratively (1) estimates the vehicle's state (three-dimensional position and orientation) in georeferenced coordinates, (2) determines actuator signals, and (3) sends the signals to the actuators to realize path following. A key to this iterative process, which can run at rates of 10 Hz to several 100 Hz, is providing the state estimation step with accurate sensor data. The sensor payload of an AUV used for navigation typically includes a GPS receiver (that only provides data when the vehicle is surfaced), a compass with three degrees of freedom (3DOF), a pressure sensor for depth, and an altimeter that measures the distance from the seafloor. When the vehicle is underwater (and GPS denied), state estimators will often predict position states using additional sensors, such as inertial measurement units (IMUs), which measure accelerations and rotation rates, or Doppler velocity loggers (DVLs), which measure the velocity of the vehicle with respect to the seafloor. Unfortunately, state estimates can "drift" using such techniques, resulting in positioning error (see Figure 6.3A). However, when the AUV has surfaced and reacquired a GPS location, the course can be corrected and the preplanned mission path resumed. Notably, acoustic

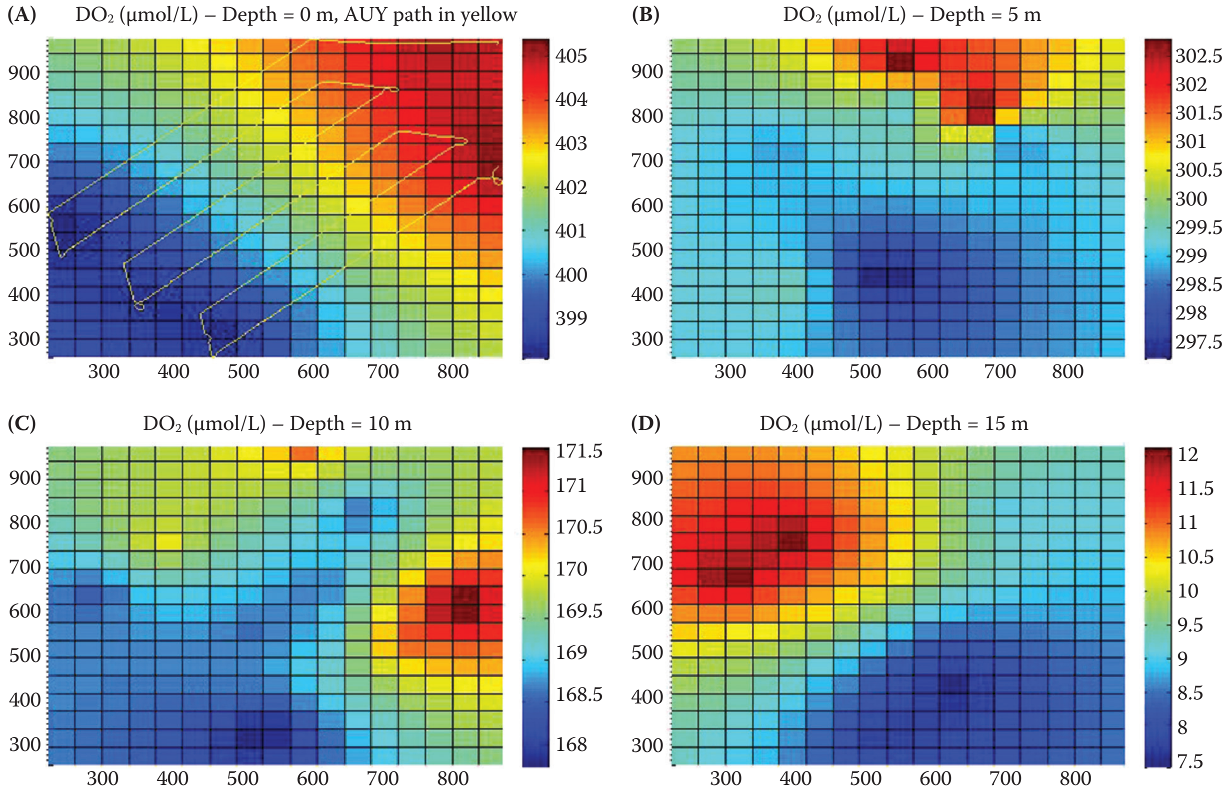


Figure 6.3 Dissolved oxygen concentration map (*x*,*y*-coordinates) constructed by fusing measurements from an AUV deployment within a Denmark fjord. An example of several "jumps" in state estimates can be observed in (A). Consider the AUV's path in yellow at location (200, 100). A jump in the state estimate occurred because the vehicle was drifting off course without realizing it. When the vehicle surfaced at approximately (200, 100), the vehicle obtained a GPS measurement to enable a more accurate position state estimate, thereby allowing the vehicle to make a course correction, turn back to the desired path, and correct the path tracking error.

positioning systems may also be used for absolute, drift-free underwater position measurements but with additional cost and infrastructure. Improving a vehicle's state estimation improves the ability of the vehicle not only to track paths but also to geolocalize sensor measurements. This is especially challenging when localizing tagged fish relative to a moving AUV. The relative localization problem is difficult due to inaccurate time-of-flight measurements in the variable underwater environment, such as changing water density and sound reflections, and such issues will be compounded by inaccurate AUV state estimation.

6.2.1.6 Sensor Payloads and Applications

Sensors are important for navigation, but most AUVs also have a sensor payload dedicated to sampling the underwater environment. Sensors in this payload section allow for measurements of oceanographic variables including salinity, temperature, chlorophyll, and dissolved oxygen (DO_2) at different depths during a mission (Figure 6.3). Sonar and video camera systems are other typical sensors found on AUVs, and they can be used in downward- and forward-facing orientations. They are often used for characterizing seafloor parameters, such as constructing bathymetry maps, terrain classification (Figure 6.4), or fish school quantification. It is important to note that, although video systems may have higher resolution when compared to sonar systems, they are typically shorter range and require sufficient lighting and water clarity. Although sonar and video data can be used for research data collection purposes, these data streams can also be used for navigation and obstacle avoidance. A major advantage of taking environmental sensor measurements when tracking fish is that the fish's behaviors can be tracked while simultaneously characterizing the fish's habitat, providing context for possible state changes in behavior. With the ability to obtain environmental measurements at sampling rates on the order of 1 Hz and geolocalized to within a few meters, AUVs have changed the way passive sampling of the underwater environment is conducted. However, there is potential for AUVs to have even greater impact on the scientific community through active sampling, where the AUVs adapt their trajectories in real time to optimize information gain. For example, some AUVs have been programmed to track steep thermal gradients (Zhang et al., 2010). As described below, this ability of an AUV to modify its behavior in response to live measurements of oceanographic or biological information can be invaluable when tracking marine life that is highly dynamic and can travel long distances.

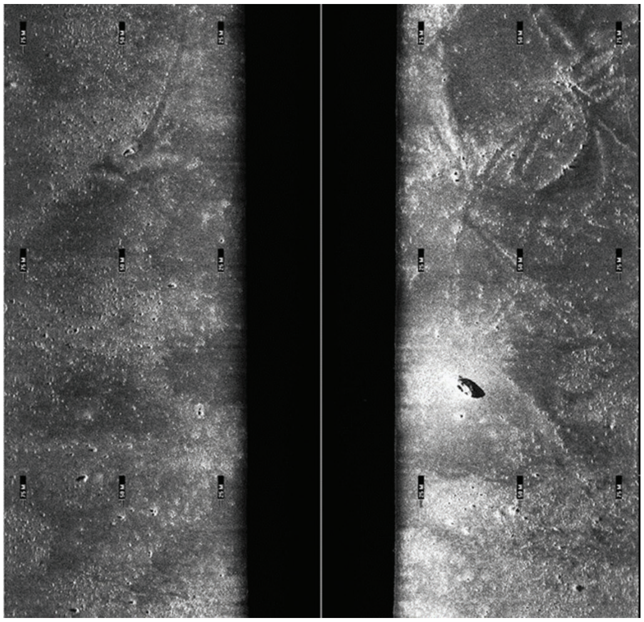


Figure 6.4 Example of side-scan sonar data illustrating a potential shipwreck site (C.M. Clark, unpublished data).

6.3 USE OF AUTONOMOUS UNDERWATER VEHICLES FOR STUDYING ELASMOBRANCHS

6.3.1 Passive Tracking and Surveying with AUVs and ASVs

A variety of commercially available autonomous underwater and surface vehicles (e.g., Slocum Gliders, Wave Gliders, REMUS AUVs, Iver AUVs) have been used to survey oceanographic parameters and map the seafloor of coastal and open-ocean environments over the last 20 years. However, more recently researchers have been equipping these autonomous mobile platforms with a variety of acoustic telemetry receivers to survey for marine animals instrumented with acoustic transmitters (Grothues, 2009; Grothues and Dobarro, 2010; Grothues et al., 2010). For survey applications, AUVs and ASVs are primarily tasked to listen for fish tagged with coded transmitters typically used for passive tracking via stationary receivers, while following a programmed mission path. Because most elasmobranchs are highly mobile, passive tracking methods are constrained by the size of stationary receiver arrays. Mobile acoustic receiver platforms such as AUVs and ASVs provide the ability to autonomously survey a wider range of habitats and areas beyond stationary arrays, and they can simultaneously provide measures of environmental conditions and the benthos in the vicinity (±250 m) where tagged individuals are detected. Because the cost of maintaining large-scale acoustic receiver arrays can be considerable, augmenting area coverage with autonomous mobile acoustic receiver platforms can potentially reduce long-term monitoring costs and provide greater area coverage than expanded stationary receiver arrays. Because of their diving capability, AUVs can provide greater vertical detection capabilities and coverage, as well as oceanographic measurements of the water column, and they achieve better transmitter detection efficiency than surface-oriented platforms alone (Grothues, 2009; Grothues and Dobarro, 2010; Grothues et al., 2010). Autonomous surface vehicles (e.g., wave-driven gliders), however, can provide real-time data via cellular or satellite communication, but they are more limited in terms of their water column characterization and detection efficiency due to sea surface conditions and surface shadows (e.g., acoustic dead spots created when the transmitter and hydrophone are at the surface during rough seascape conditions). Performance of these systems will vary depending on the telemetry system used, habitats and regions surveyed, and duration of deployment.

6.3.1.1 Acoustic Detection Systems

Early attempts to integrate telemetry receiver systems into autonomous mobile platforms varied depending on the acoustic telemetry passive tracking system being used in certain areas and on particular species. In addition, different acoustic telemetry systems may provide different encoding strategies for ID and sensor data. Different transmitter coding schemes have different costs and benefits, often trading off battery life against the number of individuals that can be identified simultaneously. For example, VEMCO coded transmitter systems use a pulse interval coding (PIC) scheme, whereby all transmitters operate at the same frequency, but the code ID is conveyed in a unique pulse train output of varying intervals. This coding scheme only allows a single transmitter to be detected at one time, but it consumes less power than alternative schemes, allowing for longer lived transmitters. The Lotek WHS 3000 series uses a code division multiple access (CDMA) scheme that conveys unique ID and sensor information via frequency spreading and allows for multiple transmitters to be detected simultaneously (Grothues, 2009). This coding scheme is more power consumptive, resulting in a decrease in the battery life of the transmitters.

Typically, coded transmitters have been designed for passive, coarse, spatial-scale tracking or fine-scale tracking using gridded stationary acoustic receiver arrays. Most passive acoustic tracking uses omnidirectional receivers organized in grids and lines (gates) and provides measures of presence/absence within the detection radius of the receiver (Heupel et al., 2006; see also Chapter 8 in this volume). If receiver arrays are organized in a grid formation and close enough that three or more receivers can detect a transmitter as it moves through the array, then a trilaterated position can be obtained by measuring time of arrival to each receiver (Espinoza et al., 2011). These systems include the VEMCO Positioning System (VPS) and Radio-Linked Acoustic Positioning (VRAP) system, Lotek MAP 600 and WHS, and HTI Model 290 + 291 systems, which have been deployed to provide fine-scale movements of fishes, some over larger areas (e.g., up to 10 km2) (Baktoft et al., 2017; Wolfe and Lowe, 2015).

Early integration and comparison of telemetry systems on AUVs were trialed and described by Grothues et al. (2010), who integrated a Lotek WHS 3050 system onto a REMUS 100 AUV to survey for Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) fitted with CDMA-type transmitters in a riverine habitat. They also equipped a REMUS 100 AUV with a VEMCO VR2 receiver to survey another riverine habitat for shortnose sturgeon (*Acipenser brevirostrum*) tagged with VEMCO coded transmitters. Several other project-specific missions were run to survey for and position other fish species using similar systems or setups. Although many of these were proof-of-concept trials, they helped establish the efficacy of using AUV technology coupled with acoustic telemetry systems in quantifying fish movements.

One of the first published studies using an AUV to survey for acoustically tagged elasmobranchs was done by Haulsee et al. (2015), who integrated two VEMCO VR2C acoustic receivers into a Slocum Glider. The glider was programmed to survey along the Delaware coastline and listen for migrating sand tiger sharks (*Carcharias taurus*) previously implanted with VEMCO V16 coded transmitters. Stationary acoustic receiver gate arrays deployed across the study area provided additional coverage of this migration route. Using detection data from the AUV, questions about habitat selection could be addressed because the AUV was also programmed to measure water depth, temperature, colored dissolved organic matter (CDOM), and chlorophyll *a* as it moved through the water column. Because the AUV could provide an estimated position of a tagged shark within ±250 m of the AUV at the time of detection, mesoscale habitat characteristics could be measured at those times and compared with locally available conditions to determine habitat selection. The 19-day mission allowed the AUV to cover 337 km, covering depths from 7 to 22 m (Figure 6.5). Using this methodology, Haulsee et al. (2015) concluded that southward migrating sand tiger sharks are likely selecting habitat features that are influenced by distance from shore (water depth), salinity, and CDOM. There are clearly other environmental and biological factors influencing migratory path, but this study demonstrated the efficacy of this technology for offshore research.

Although none is currently published, studies are under way using Wave Glider platforms to autonomously survey for tagged elasmobranch over larger spatial scales. For example, VEMCO VR2C-equipped Wave Gliders are currently being deployed off central California to survey acoustically tagged adult white sharks while simultaneously gathering oceanographic information along programmed survey paths. Similar missions are being conducted off more

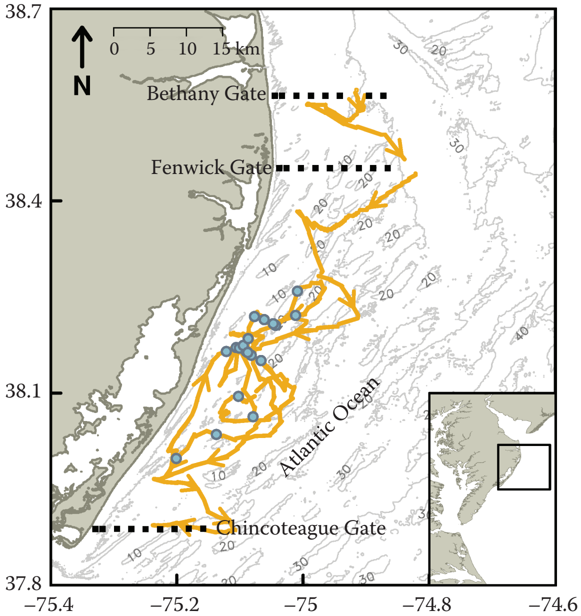


Figure 6.5 Programmed survey path of Slocum Glider in yellow. Location of stationary acoustic receiver gate arrays are shown as black squares, and blue circles indicate locations where tagged sand tiger sharks were detected by the VR2C-equipped glider. (From Haulsee, D. et al., *Mar. Ecol. Prog. Ser.*, 528, 277–288, 2015.)

coastal waters along southern California to survey for acoustically tagged elasmobranchs and food fishes (M. Cimeno, pers. commun.). Because of the greater endurance of Wave Gliders, fewer navigational hazards, and considerable wave energy found in open ocean habitats, these glider missions can run for months and provide periodic or real-time data.

6.3.1.2 Survey Path Planning

As autonomous mobile tracking platform technology becomes more common, developing appropriate surveying methods will be essential for searching for highly mobile or migratory elasmobranchs that have been tagged. For long-endurance gliders (buoyancy-driven or wave-driven), survey paths could be designed for systematic or random surveying across habitats. In Haulsee et al. (2015), the Slocum Glider was programmed to move in a sawtooth pattern surveying across depth and habitat contours; however, it was also missioned to return to an area where a tagged shark had been previously detected. This survey plan was necessary to address their particular question, but it might not be the most effective way to survey a large area. Similar paths are often planned for Wave Glider missions, where these platforms are missioned to survey across depth contours and may yield the best opportunity to encounter and detect migrating elasmobranchs that move along coastal shelves. Other considerations for survey path planning vary depending on knowledge of the species tagged, the platform being used, and degree of boat activity in the areas to be surveyed. For example, buoyancy-driven and wave-driven gliders require a depth of at least 6 m to operate effectively and avoid “dredging,” or grounding (Haldeman et al., 2014). In addition, these vehicles are less maneuverable and more likely to be struck by passing vessels operating at high speeds in survey areas. Propeller-driven vehicles can operate in much shallower water (~1 m) and are far more maneuverable if adequately equipped and programmed for obstacle avoidance.

6.3.1.3 Habitats and Species Surveyed

Autonomous survey vehicles may not be appropriate for certain habitats, conditions, or species. Navigational hazards, rapidly changing bathymetry, and strong tides found in estuarine, coastal river, or lagoon habitats would preclude the use of most commercially available buoyancy- and wave-driven gliders for surveying tagged elasmobranchs due to the minimum depth requirements and relatively poor maneuverability in restricted habitats. Smaller propeller-driven AUVs (e.g., Iver2 and Iver3, REMUS 100) or ASVs may offer the best options for surveying in these types of habitats; however, they are much more limited in endurance. Nonetheless, surveying in complex shallow habitats still poses considerable challenges for path planning and successful navigation. Robust obstacle avoidance systems must be implemented to avoid grounding and entanglements with moorings, fishing gear, and kelp/seagrass, as well as negotiating channels with high vessel activity and strong tidal currents. Autonomous vehicle acoustic surveys for tagged elasmobranchs are less problematic for coastal or offshore habitats than inshore waters or embayments due to deeper waters and fewer navigational obstructions. There are also opportunities for much longer missions using less power consumptive buoyancy- and wave-driven vehicles.

6.3.2 Active Tracking Elasmobranchs with AUVs

Acoustic detection data from passive stationary acoustic receiver arrays (see Chapter 8 in this volume) and autonomous mobile acoustic receiver platforms (Section 6.2.1) can be effective in quantifying movements of individuals over large spatial and temporal scales. Yet, these methods often lack sufficient positional accuracy and localization frequency of the same individual to adequately characterize how animals respond to microscale or mesoscale environmental conditions. Thus, limited information on their movements is obtained for animals that move at scales smaller than the typical passive omnidirectional receiver detection ranges (<500 m). Positioning systems such as VEMCO VRAP or VPS, Lotek MAP 600 or WHS, or HTI 3D tracking systems can provide high-resolution estimates of location, but these systems are constrained by the size and location of the stationary arrays of receivers (Hedger et al., 2008; Heupel et al., 2006). This poses major challenges in obtaining high-frequency, high-spatial-resolution measurements for highly mobiles species of elasmobranchs, especially those that show minimal site fidelity to areas (Hussey et al., 2015).

To study aquatic animal movements at higher frequencies and finer spatial scales, researchers have traditionally turned to active tracking. This practice consists of a human tracker in a small vessel using a directional hydrophone to estimate the location of an acoustically tagged animal and following it for 24 to 96 hr (Holland et al., 1992). The amplitude of the signal received by the hydrophone is a function of the direction of the hydrophone relative to the direction and distance to the transmitter; that is, amplitude increases as this relative angle decreases and proximity increases. By rotating the directional hydrophone, the tracker can determine the direction in which the signal is strongest and thus the direction to the animal. The tracker can then navigate the vessel toward the signal source (transmitter), using the position of the vessel as a proxy for the position of the animal (Bass and Rascovich, 1965; Nelson, 1978). However, to obtain high positional accuracy, the tracker must be positioned directly over top of the transmitter (tagged individual), which can affect the animal's behavior.

Active tracking is labor intensive and reliant on the proficiency of the tracker, and it provides variable spatial accuracies (<50 m) (White et al., 2016). Hence, the development of AUV technology has led many researchers to envision AUVs as replacing humans as active trackers. This idea was first conceptualized over 20 years ago with a kayak outfitted with an electric trolling motor and a VEMCO VR60 (Goudey et al., 1998). To replace human trackers, AUVs must be equipped with two key abilities: (1) accurately estimate the location of a tagged animal in real time while at a distance, and (2) incorporate this location state estimate into the AUV's control system and thus realize autonomous tracking and following of the animal, which includes attempting to relocate a transmitter signal temporally lost.

6.3.2.1 *Acoustic Positioning System*

The acoustic positioning system is the hardware (hydrophone/receiver) and software combination required to provide an estimate of the location of an acoustic transmitter with respect to a georeferenced Cartesian coordinate system (e.g., x, y, z space). A location can be determined when two or more hydrophone/receiver systems are able to derive a distance and bearing to a transmitter, with the tag transmitting information on its depth (z-dimension). This information, when combined with the current position and heading of the AUV, allows for an estimate of the geolocation of the transmitter. Acoustic position systems rely on the fact that sound travels at predictable speeds based on the water density (e.g., temperature and salinity). Thus, accurate measurements of time (microsecond), water density, and temperature allow for precise estimates of location of a transmitter. Two main strategies have been used for acoustic position systems for the active tracking of animals: short baseline (SBL) and ultrashort baseline (USBL).

Short baseline systems can derive a distance and bearing estimate if at least two hydrophones are fix-mounted at least 2 m apart (Clark et al., 2013; Forney et al., 2012; Lin et al., 2013). When both hydrophones detect a tag transmission, the time difference of arrival (TDOA) between the hydrophones is converted to an angle measurement. The TDOA is multiplied by the speed of sound in water, given current environmental conditions, to form one side of a triangle, and the distance between the hydrophones represents the hypotenuse of the triangle. By taking the arc-cosine of the difference in time of arrival over the distance between the hydrophones, the bearing to the transmitter is calculated. When using transmitters that transmit at fixed intervals, this system can be expanded to incorporate a range measurement by estimating the time of flight (how long it would take the acoustic signal to travel a particular distance through water of known density) (Lin et al., 2013). The AUV can keep track of the estimated time the transmitter should transmit, then, by subtracting the time when the AUV detected the transmission, the time of flight (TOF) can be estimated. The time of flight is multiplied by the speed of sound in seawater based on water density at that location to produce a range measurement. The transmitted depth, estimated bearing, and range can be used to estimate a position of a moving transmitter while the AUV is moving.

For such two-hydrophone configurations, there is a sign ambiguity, and the AUV cannot determine if the tag is on its left or right side from a single detection (Figure 6.6); however, the AUV can be programmed to move in a circular or sigmoidal path until several detections are made, which enables the AUV to differentiate a sign (or side) the transmitter is on relative to its path. To further refine accuracy and sign of position estimates using this TOA and TOF approach, a particle filter state estimation algorithm can be applied, which over several successive detections can improve positional accuracy to ±3

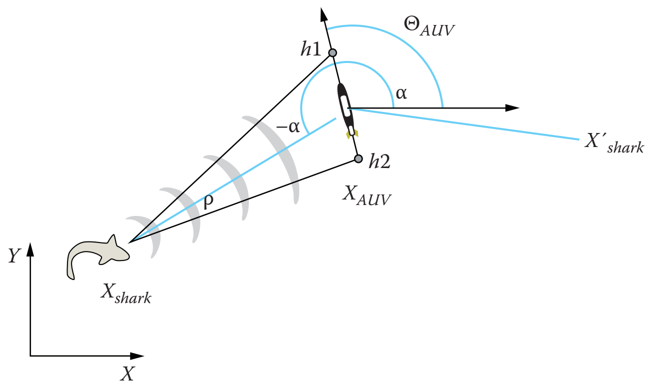
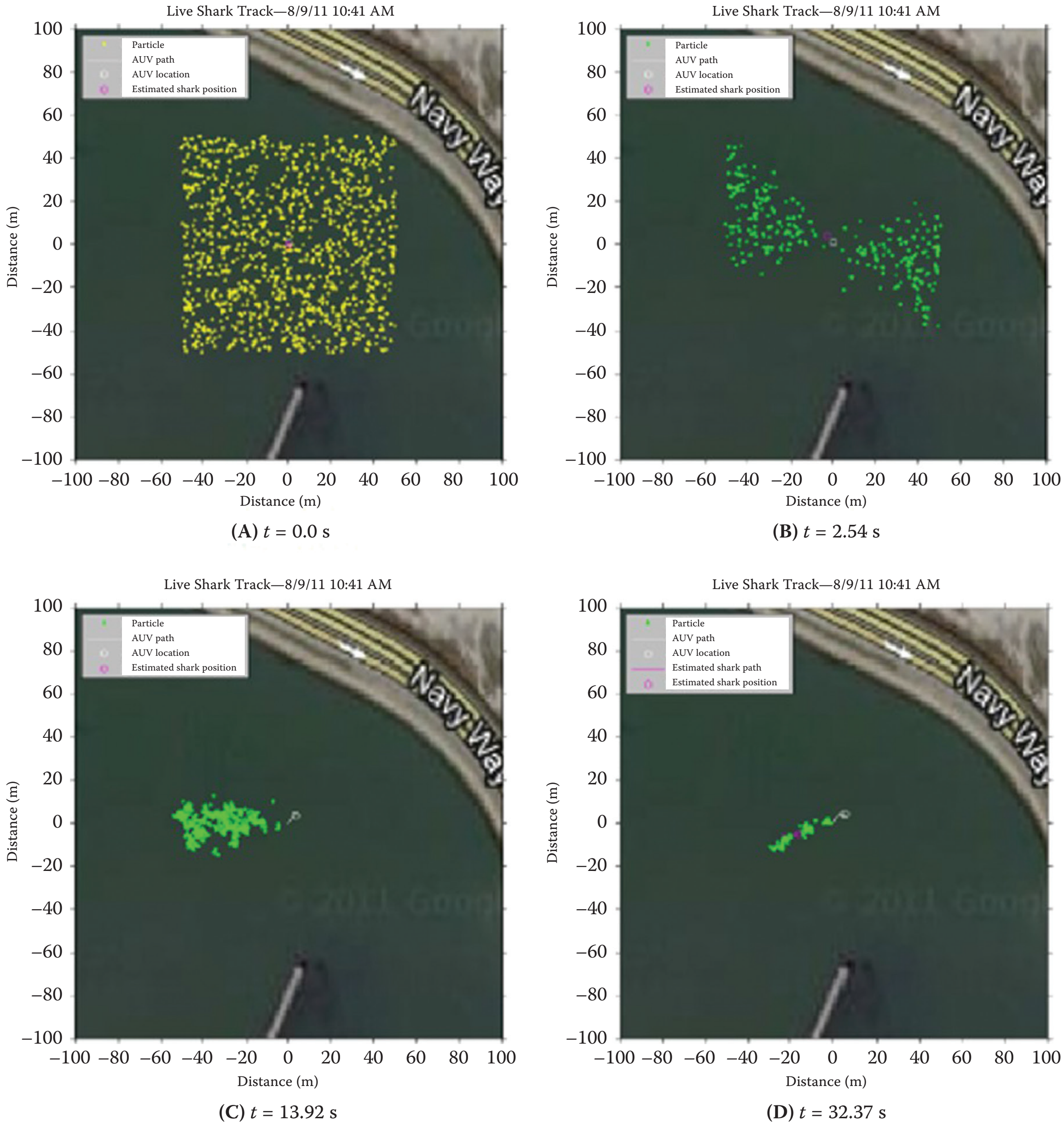


Figure 6.6 Schematic of how a SBL-enabled AUV determines location of a tagged shark. (From Clark, C.M. et al., *J. Field Robot.*, 30(3), 309–322, 2013.)



(A) t = 0.0 s

(B) t = 2.54 s

(C) t = 13.92 s

(D) t = 32.37 s

Figure 6.7 Use of a particle filter with a SBL-enabled AUV to refine a position estimate of a moving transmitter over successive detections. (From Forney, C. et al., in *Proceedings—IEEE International Conference on Robotics and Automation*, Institute of Electrical and Electronics Engineers, Piscataway, NJ, 2012, pp. 5315–5321.)

m while both transmitter and AUV are moving simultaneously (Clark et al., 2013; Forney et al., 2012; Lin et al., 2013; Xydes et al., 2013) (Figure 6.7).

The second type of acoustic positioning system used onboard an AUV for active tracking is the ultrashort baseline system (USBL) (Kukulya et al., 2015, 2016; Packard et al., 2013). In this system, the AUV is equipped with a transceiver with a small array of omnidirectional hydrophones, and the animal is tagged with a transponder that can also transmit depth information. The transceiver onboard the AUV sends an acoustic transmission that is received by the animal-borne transponder, which then sends a reply that is received by the AUV. By measuring the time between when the AUV queried the animal's transponder and when it received the transmission in response, the total time of flight to the animal and back to the AUV is calculated. By dividing this by two and multiplying by the speed of sound, a range estimate can be calculated. The AUV is additionally able to compare the received signal phase difference across the multiple hydrophones within the transceiver to generate a bearing estimate. Because the USBL systems were originally designed for tracking large underwater vehicles and require two-way acoustic communication, the transponder tags are large and subsequently powerful, and they also have significantly better range and bearing estimates than the SBL system, which is limited by the accuracy of time recording across the hydrophones as well as the consistency of tag transmissions over time (Kukulya et al., 2015; White et al., 2016). However, USBL system transponder tags are significantly larger (7.6 × 38 cm) and more expensive and power consumptive, thus limiting their application to large sharks (>3 m) capable of carrying larger tag packages. The SBL system, however, was designed to use existing animal acoustic telemetry infrastructure and standard acoustic transmitters from other acoustic biotelemetry systems (i.e., VEMCO, Lotek, Sonotronics), and it allows for much smaller individuals to be tagged (White et al., 2016).

6.3.2.2 AUV Control System

For fully autonomous active tracking, estimating the location of the tagged animal resolves only half of the problem. The AUV must also incorporate the tagged animal's position estimate into the AUV's control system to enable autonomous following of the animal. The AUV control system can be programmed to incorporate a variety of abilities necessary to track a moving animal, which may stop moving, move in a very small discrete space, or travel in nonlinear paths. So, the AUV must be programmed to adapt its movement path to that of the tagged animal while simultaneously avoiding static obstacles, such as docks and pinnacles, and avoiding grounding or colliding with the shoreline or seafloor. In addition, the AUV must be programmed to determine position from a suitable distance to reduce behavioral interference with the tagged individual but be close enough to maintain continuous detection range (Clark et al., 2013; Forney et al., 2012; White et al., 2016).

The simplest control system might be to just have the AUV drive directly toward the position of the shark. Packard et al. (2013) programmed a REMUS AUV with a USBL system to film sharks under water, which required the AUVs to be very close to the tagged animal (<10 m). The shark's path was interpolated 15 sec into the future, and the AUV was programmed to drive directly at that point and pass to the left, right, above, or below the tagged shark (Figure 6.8). After the AUV passed the shark, it was programmed to turn around and perform this "fly by" again. By repeatedly updating the shark's location relative to the AUV, the AUV could continuously update its path to a new location. This control system was refined by Kukulya et al. (2015), who modulated the speed of the AUV proportional to the distance between the AUV and the shark, so that the AUV would travel faster when it was farther away from the tagged individual and match the animal's speed when it was close to the tagged animal.

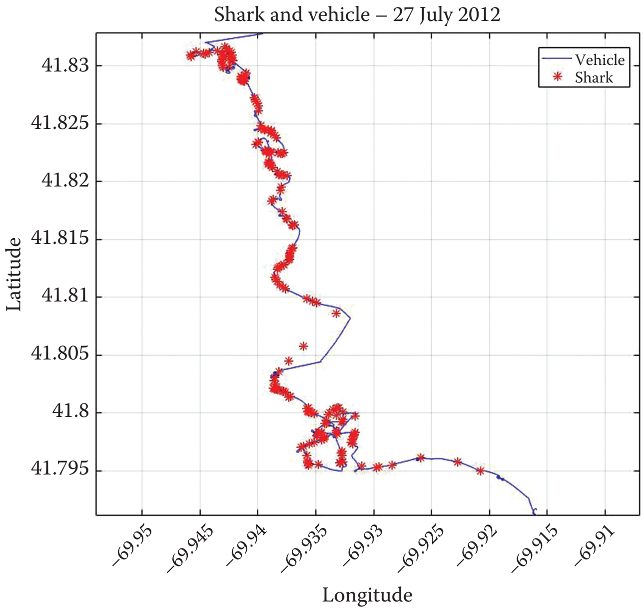


Figure 6.8 The estimated position of a tagged white shark (red asterisk) off Cape Cod using the USBL-enabled system on a REMUS AUV and the path of the AUV (blue line). When frequent detections were obtained, the AUV could accurately predict the shark's path to increase the likelihood of the AUV being close enough to capture video data. (From Packard, G.E. et al., in *MTS/IEEE OCEANS 2013–San Diego*, Institute of Electrical and Electronics Engineers, Piscataway, NJ, 2013, pp. 1–5.)

Such a control system, however, could cause the AUV to influence the tagged animal's behavior by being too close or even colliding with the tagged animal. Because AUVs use propeller-driven propulsion, the vehicles produce low-frequency sounds detectable to the sharks. Sharks have been found to approach or even attack AUVs, following them or staying in close proximity (Skomal et al., 2015; Stanway et al., 2015). A second approach is to have the AUV position itself close enough to the tagged animal to continuously receive acoustic detections but remain far enough away to reduce the likelihood of behavioral interference (>30 m). In this programmed control feature, documented by Lin et al. (2013), an AUV had two different behaviors, depending on the distance to the tagged animal. When the AUV was within detection range, but farther away from the animal, the AUV was programmed to drive directly at the tagged animal. When the AUV was within a user-defined threshold distance of the animal, it switched to nearby circling behavior, such that the AUV circled at a point just outside of the user-defined minimum threshold distance to the tagged animal. Circling allows the AUV to constantly propel itself, which is necessary for stability and to increase the quantity of sensor vantage points, determine bearing and distance to the transmitter, and prevent it from colliding into the tagged animal (Figure 6.9). In addition, if the shark moves toward the AUV and comes within the user-defined minimum threshold distance, the AUV is programmed to move away from the tagged shark. By switching back and forth between point tracking and nearby circle tracking, the AUV can

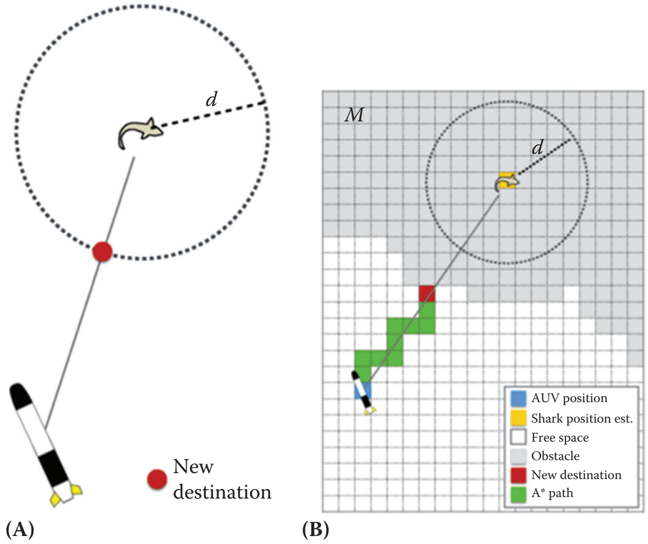


Figure 6.9 Programmed control system for SBL-enabled AUV for predicted obstacle avoidance and nearby circling when in user-defined minimum threshold distance to a transmitter. (From Lin, Y. et al., in *Proceedings of the Unmanned Untethered Submersible Technology Conference (UUST)*, Autonomous Undersea Systems Institute, Durham, NH, 2013.)

continuously follow the tagged individual, remaining within detection range. Using this system, the path of the AUV does not closely reflect the path of the tagged individual. It is also worth mentioning that quantifying shark behavior response to AUVs vs. active tracking surface vessels may be useful for determining minimum threshold distances for AUV tracking.

In addition, control systems for active tracking have been modified and adapted to use multiple AUVs for tracking a tagged shark (Kukulya et al., 2016; Lin et al., 2014, 2017). Having both AUVs simultaneously tracking while in communication with each other allows for incorporation of range and bearing measurements from multiple angles, thereby providing further refined position estimates and reducing the likelihood of losing the animal. These systems are programmed to have one leader and could be expanded to incorporate multiple followers. Future swarm programming of smaller, single-hydrophone AUVs could allow for trilateration (position estimates) of multiple cooperative AUVs surrounding a tagged individual, as long as the AUVs were far enough away from the tagged individual to minimize behavioral disturbance.

6.3.2.3 Environmental and Situational Monitoring.

Traditional uses of AUVs have been in sampling oceanographic conditions. Enabling these duties can provide environmental context for the focal animal being tracked. Most commercially available AUVs can be equipped with a wide variety of sensors (e.g., temperature, salinity, DO2, CDOM, pH, photosynthetically active radiation [PAR], side-scan sonar, image sonar) that can simultaneously sample the environment during tracks within a geospatial context. Measuring these conditions during a track can provide unprecedented resolution of the environment surrounding the animal. This fine-scale environmental information can provide context and insight as to how tracked individuals respond to changing conditions and use gradients as navigational cues.

Environmental sensors can provide valuable information on how tagged individuals respond to changing environmental conditions, but video and sonar imaging can provide insight into how tagged individuals respond when they are in close proximity to other conspecifics, predators, and prey. By outfitting the AUVs with downward- and forward-facing video cameras, or even virtual reality (360° view) video cameras (Figure 6.10), spatially explicit prey and conspecific abundance can be estimated and correlated to changing movement behaviors observed from tracked individuals. Traditional active and passive tracking methods often lack these abilities or require separate teams of researchers to simultaneously collect these data using typical sensor suites, such as sondes; conductivity, temperature and depth recorders (CTDs); or video camera sleds. Although it is a valuable activity, collecting video data is power consumptive and data intensive and often results in a data processing bottleneck, requiring considerable labor-intensive postprocessing. In addition, underwater video data can be hampered by poor visibility or low light conditions (e.g., nighttime periods), and coastal habitats (e.g., lagoons, bays, estuaries) can often have poor visibility conditions, further limiting the use of video in those ecosystems.

Sonar technology has greatly improved and reduced in size and can now provide low-resolution video image quality at distances of less than 50 m (e.g., DIDSON, BlueView). AUVs can be equipped with forward- and downward-facing image sonar, which is capable of recording and identifying unique targets based on their densities and reflective acoustic properties. These systems can operate in poor visibility and zero light conditions, in addition to providing estimates of distances between objects and the AUV and the size of the targets. Digital target recognition and autonomous tracking of sonar-identified objects has allowed short-term tracking of untagged sharks and schools of fishes (McCauley et al., 2016) and holds great promise for augmenting video for identifying conspecifics and prey items surrounding the tagged animal. However, sonar is much more power consumptive in comparison to video, so its application and duration of use would have to be more conservatively applied in comparison to video.

Coupling transmitters and data loggers with environmental sensors attached to focal individuals and having the AUV sample the habitat around the tagged individual can provide insight into how sharks are selecting habitats

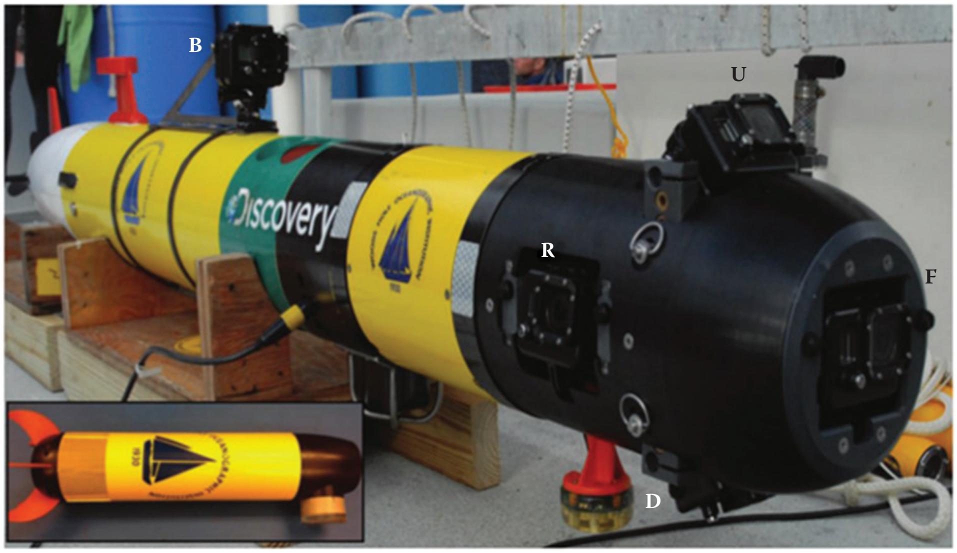


Figure 6.10 REMUS 100 outfitted with six video cameras providing nearly 360° video coverage around the AUV and acoustic transponder tag (inset), used to record white sharks at Guadalupe Island Mexico. (From Skomal, G. et al., *J. Fish Biol.*, 87(6), 1293–1312, 2015.)

and differentiating among environmental gradients. Future AUV control algorithms can incorporate where the AUV has previously sampled and direct the AUV to alternative locations around the moving animals for a more comprehensive characterization of environmental conditions available to the focal animal. This would maximize environmental information gain and provide a more holistic picture of the behavior of the animal.

6.3.2.4 Habitats and Species Tracked

Most of the studies published to date using autonomous active tracking systems have been largely methodological and have focused on the development of the technology and its efficacy. These tracks have taken place on a range of species, including non-obligate ram ventilating species such as leopard sharks (*Triakis semifasciata*) and obligate ram ventilating species such as white and basking sharks (*Cetorhinus maximus*), in shallow coastal areas as well as deeper habitats. Using a modified Iver2 AUV, Clarke et al. (2013) developed an SBL system (Lotek MAP 600) designed for tracking leopard sharks in southern California. Leopard sharks, which are known to aggregate in shallow habitats for thermoregulatory benefits (Hight and Lowe, 2007; Nosal et al., 2014) and exhibit restricted space use during the day, were tracked in embayments ranging from intertidal to 25 m in depth. Tagged leopard sharks were simultaneously actively tracked by a human in a surface vessel and by an SBL-equipped AUV for comparison of positional accuracy and frequency of data acquisition. Comparative tracks (AUV and a human active tracker) indicated that this autonomous system provided similar or better spatial accuracy than a human active tracker, yet provided significantly more accurate locations than a human (White et al., 2016) (Figure 6.11).

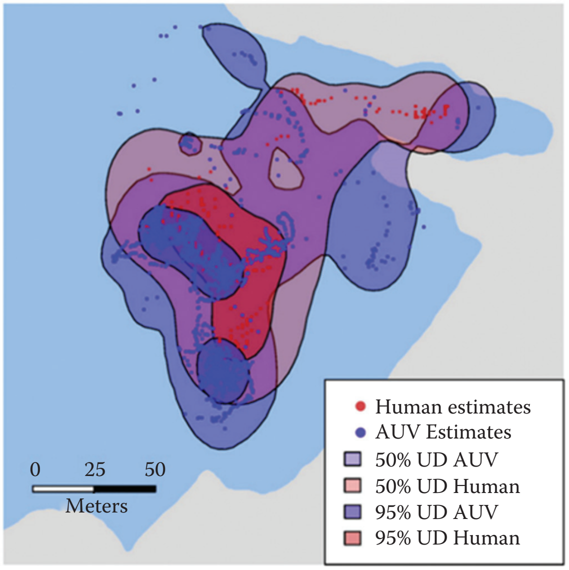


Figure 6.11 Position estimates of a tagged leopard shark tracked in a small cove at Santa Catalina Island. The red dots indicate position estimates made from a human active tracker in a surface vessel using closest estimated range to determine position. The blue dots indicate position estimates from a simultaneous track of the SBL-enabled AUV programmed to remain at least 20 m away from the tagged shark. Colored polygons represent estimated utilization distribution areas of the shark tracked using both methods. (From White, C.F. et al., *J. Exp. Mar. Biol. Ecol.*, 485, 112–118, 2016.)

Individual tracks have lasted longer than 4 hr, and either single or a pair of cooperative AUVs were tested and compared for their accuracy and ability to maintain contact with a tagged leopard shark. These high-resolution spatiotemporal movement data overlaid on high-resolution temperature maps showed leopard sharks spending most of their time in a small temperature range (Bernal and Lowe, 2016). Yet, because the leopard sharks were in shallow (<2 m), rocky, and often narrow habitats, the AUVs would occasionally have to position themselves at a distance (>100 m) from the tagged animal, so detection efficiency and subsequently positional accuracy suffered.

A REMUS 100 outfitted with a USBL system has been used to track basking sharks and white sharks off Cape Cod, Massachusetts (Packard et al., 2013). This study was largely methodological, but the authors were able to show that the tracked white sharks remained closely associated to the benthos while swimming outside seal colonies. Because white sharks were using shallow habitats close to shore, the AUV had difficulties tracking tagged individuals due to periodic loss of transponder detection. White sharks have additionally been tracked off Guadalupe Island, Mexico (Kukulya et al., 2015). Six video cameras mounted to the AUV (forward and reverse) were used to document shark behavior, such as attack events on the AUV (Figure 6.12), as well as shark depth and association with conspecifics (Skomal et al., 2015). White sharks globally are thought to mainly capture prey near the surface by ambushing them, yet the location and the frequency at which these tracking AUVs were attacked by white sharks lead to suggestions that sharks at Guadalupe might be capturing prey at depth (Skomal et al., 2015). Deeper coastal water around Guadalupe Island allowed the AUVs to encounter few obstacles with less ambient noise, so AUVs were more successful in tracking tagged sharks; however, sharks were able to dive deeper than the depth rating of the AUVs (>100 m). The researchers had a second tracking AUV (REMUS 600) that was capable of diving deeper; however, deploying the AUV in a timely manner before the shark was lost was problematic, as well.

6.4 EXPECTATIONS AND DATA

Like most emerging technologies, autonomous tracking systems have the capability of generating considerably larger and more complex datasets than conventional active and passive tracking due to their ability to gather environmental data while tracking; therefore, there may be considerable need for data postprocessing, synthesis, and error checking. Because these data are spatially explicit and often three dimensional, more sophisticated data visualization methods are needed (Martin et al., 2006; Viswanathan et al., 2017). Not only are these accompanying tools necessary for data visualization and display, but they also will be integral in development of new analytical methods for identifying and quantifying behavioral patterns and changes in behavioral state with changing social and environmental conditions.

6.4.1 *Post Hoc* Analysis of AUV Tracks and Movement Predictions

As demonstrated by Haulsee et al. (2015), using autonomous vehicles to survey for tagged sharks can greatly enhance passive tracking arrays by providing greater area coverage

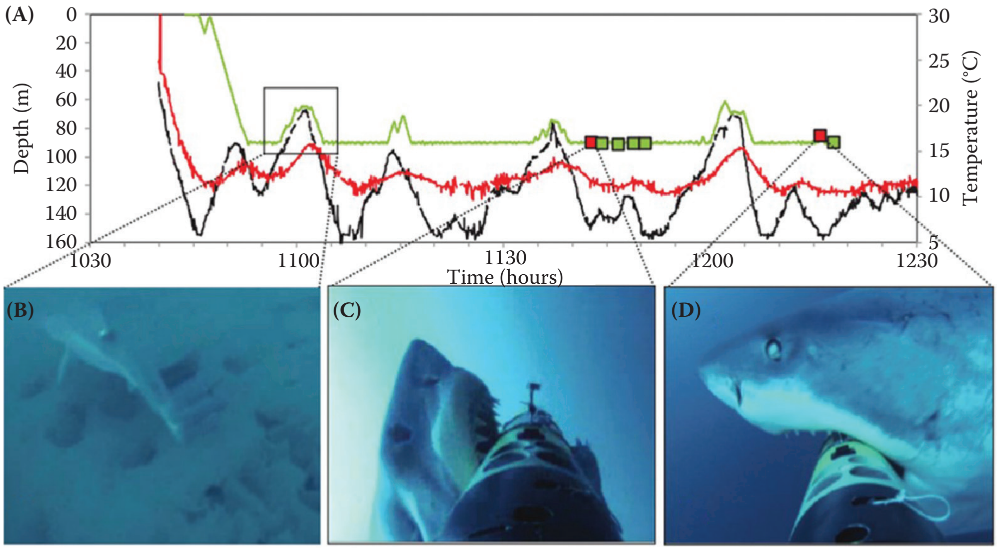


Figure 6.12 The top figure shows the depth of the AUV (green line), and the depth of the shark (black line) recorded onboard a REMUS 100 using an ultra-short base line (USBL) acoustic receiver system. During this span, the shark approached the AUV several times, ultimately biting the AUV twice, while the multiple cameras video recorded the approaches and bites. (From Skomal, G. et al., *J. Fish Biol.*, 87(6), 1293–1312, 2015.)

and simultaneous measurements of environmental conditions. These datasets are quite different from those of conventional stationary acoustic receiver arrays but when analyzed together can provide a much richer understanding of movement and habitat selection than can often be inferred from passive tracking alone. For example, with sufficient sampling and adequate environmental monitoring, habitat suitability models can be developed and used to predict changes in distributions, migrations, and migration routes. Furthermore, these migration routes can potentially be determined from these types of datasets (White, 2016).

One advantage of autonomous vehicle platform active tracking of elasmobranchs is that these systems can provide comparable positional accuracy as human-based active tracking, but at a much higher frequency and while maintaining a distance away from the tagged shark. Using these telemetry systems also provides error measures for each position that can be appropriately filtered to provide more accurate information for assessing habitat association, rate of movement, and fine-scale behaviors.

In addition to obtaining high-resolution position data from autonomous tracking platforms, the ability to overlay these movements over high-resolution, three-dimensional (3D) environmental data (often interpolated from stationary sensors) provides the opportunity to quantify habitat selection and potentially preference. This can allow for development of 3D habitat suitability models, which can be used to make predictions of under what conditions individuals should initiate seasonal migrations, select new habitats, and shift distributions under changing climate and rising ocean temperatures. Coupling these high-resolution movement data with spatially explicit baited remote underwater video (BRUV; see Chapter 7 in this volume) and autonomous camera and image sonar surveys provides the ability to quantitatively evaluate influences such as prey density, intra- and interspecific competition, and presence of mates to predict degree of site fidelity and cues influencing potential emigration. Of course, the utility of autonomous tracking vehicles is still valuable but more limited without corresponding environmental and biological data.

6.4.2 Technical Limitations

While autonomous vehicle and telemetry technology has advanced considerably over the last 20 years, there are still numerous technical limitations that must be considered before attempting to utilize these tools. Although smaller and less expensive AUVs are commercially available, they are still quite expensive (base models are equivalent to the cost of a new, fully equipped 8-m research vessel), not including the cost of the telemetry system. ASVs are currently the least expensive option for full autonomous tracking platforms, but these systems are limited by battery life, power, and speed. Battery life poses a distinct challenge for either surveying or active tracking. Most smaller class AUVs (e.g., Iver2, Iver3, REMUS 100) have a depth range of only 100 m and have approximately 12 hr of battery life under low cruising speeds and with conservative use of power-consumptive sensors. Larger, more expensive AUVs (e.g., REMUS 600) can operate at deeper depths (600 m) and offer considerably longer battery life; they are capable of operating at low cruising speeds for up to 24 hr. However, these larger vehicles are heavy, making deployment and retrieval more difficult and requiring larger vessels to support. Continuous multiple-day tracks would require at least two AUVs that could be swapped out during a track while the other is being recharged. This reduces the advantages of autonomy and may only be feasible in protected embayments or for coastal applications. Wave- and buoyancy-driven vehicles have reduced power requirements and therefore can be used for longer deployments, but they may also suffer from shorter battery life if power-consumptive sensors are not used conservatively.

Another technical limitation of AUVs for tracking highly mobile elasmobranchs may be maximum operating speed of the platforms relative to the detection range of the transmitters being applied. Most AUVs have a maximum operating speed of 4.5 knots (2.3 m/sec) and may not be able to stay within the detection range of faster swimming species such as shortfin mako shark (*Isurus oxyrinchus*) or gray reef shark (*Carcharhinus amblyrhynchos*). Even though these highly mobile species of elasmobranchs cannot maintain these speeds for long periods of time, they may be able to lose the AUV by rapidly moving outside the AUV's detection range. In addition, much like while active tracking, acoustic receiver performance decreases with increased speed due to cavitation around the hydrophone. This makes it more difficult for the AUV to maintain contact with the tagged shark while it is traveling at higher speeds. This may also be problematic when tracking smaller elasmobranchs which requires smaller acoustic transmitters that inherently have lower power output and shorter battery lives.

Another major technical limitation required for full autonomous tracking or surveying is the ability to avoid stationary obstacles such as shore lines, seafloors, docks, and reef markers—features for which there are discrete geospatial references. All AUVs have the capabilities to be programmed to remain within coordinate boundaries or to move around a coordinate position; however, their ability to make these movements correctly is based on the accuracy of the geoposition estimates of these features and the AUV's accuracy of its position while moving. The altimeter can help prevent the AUV from running aground, but steep vertical walls can pose navigation challenges; the situation is further complicated because the AUV's ability to estimate its geolocation is reduced the longer it remains underwater. Therefore, operating in complex and enclosed spaces can be challenging for even the most maneuverable AUVs. Moving and small-profile obstacles such as boats, moorings, kelp, and people in the water pose additional challenges for avoidance, as their geopositions are dynamic. To address these challenges, forward-facing sonar or video systems can be used and programmed to enable the AUV to avoid moving and potentially entangling obstacles; however, these systems are power consumptive, which may further reduce tracking duration. Despite these limitations, engineers and programmers are developing new sensors and detection algorithms to improve obstacle avoidance, improve battery technology, develop in-water recharging stations, and control planning for AUVs.

6.4.3 Potential AUV System Configuration and Planning Abilities

The use of AUVs for tracking marine animals is not limited to a single AUV tracking a single animal. Recent research has demonstrated the advantages of using multiple AUVs to track an animal (e.g., Clark et al., 2013; Kukulya et al., 2016; Lin et al., 2013, 2017; Shinzaki et al., 2013; Tang et al., 2014). The combined sensor footprint is increased, and there is an increase in sensor vantage points, which reduces positional errors. There is also the possibility of tracking multiple animals simultaneously. If acoustic CDMA-type transmitters are used (e.g., share the same time slot with a time division multiple access protocol), then even a single AUV can detect and track multiple tagged individuals simultaneously as long as they all remained in the same area. To accomplish this, more sophisticated AUV path planning algorithms may be required that direct vehicles to optimal locations, such as the locations that when visited yield the highest likelihood of the AUV being in range of and detecting all animals. With such applications in mind, algorithms for the autonomous vehicle tracking of multiple targets has been an active area of research that is providing the AUV community with several starting points for such future work.

6.4.4 Future Sensor Integration and Autonomy Capabilities

Autonomous vehicle technology (AUV and ASV) has the potential to completely change the way marine life is surveyed and tracked. Work in the last decade has provided several examples of successful tracking experiments, and the technology has matured to the point where it can be used for systematic tracking deployments. Image sonar offers potentially one of the greatest additions to sensor integration for AUV operations and enhanced tracking capabilities. Forward-facing image sonar could be used not only for AUV obstacle avoidance but also for visualizing the tagged sharks and its associated surroundings. This technology can also be used to measure the size of tagged sharks and any other associated individuals within the sonar window.

Moving from SBL to USBL hydrophone arrays not only improves position estimates but also significantly reduces drag and the power consumption of tracking AUVs and increases the mobility and utility of ASVs. The USBL hydrophone arrays can also be used to detect one-way PIC-type transmitters, which will allow for a greater selection of telemetry systems for integration into autonomous tracking platforms and tracking of much smaller transmitters (Rypkema et al., 2017). AUVs could be equipped with transponder technology and programmed to search out elasmobranchs instrumented with archival transponding tags. Once located, the AUV would be programmed to follow the tagged shark until all the archived data from the shark's transponding tag has been downloaded to the AUV. Because transponding tags are quite large, this technology might only be feasible for larger elasmobranchs in the near future.

The future of this technology will provide greater positioning accuracy, increased temporal resolution, reduced labor intensity, and simultaneous sampling of the environment, as well as access to new datasets that were previously unachievable. Automatic identification of habitat type, quantification of aggregation sizes and densities, and intelligent inference of near-future animal behavior are possible, but these are only a subset of the new capabilities that will provide marine biologists with new data and hence new findings.

6.5 SUMMARY AND CONCLUSIONS

While historically, autonomous vehicle technology was used and developed for remote open ocean exploration, the need for coastal autonomous oceanographic monitoring has increased, which has driven the development of a range of autonomous vehicle platforms (AUV and ASV) that are smaller, more maneuverable, and more affordable. In addition, acoustic telemetry companies have begun to recognize the growing market for autonomous vehicles and need for adapting their technology for application on these robotic platforms. The expectation is that the development and use of autonomous tracking platform will expand greatly in the next decade and will require biologists to work more closely with oceanographers, computer scientists, and engineers in order to produce the systems and tools necessary to address more complex questions about the behavior and ecology of elasmobranchs. In addition, there is a growing need for higher resolution positioning and simultaneous environmental monitoring in order to quantify habitat use, migration cues, migration pathways, and drivers of movement strategies of elasmobranch fishes. The continued development of these tools will help address questions regarding habitat recolonization of recovering populations; the effects of climate change on distributions, migrations, and habitat selection; and the evaluation of essential habitat for highly mobile shark and ray species.

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