Chapter 6
Foraging Ecology and Behavior

W. Don Bowen and Ian D. Jonsen

Contents

Abstract Phocid seals exhibit a range of body sizes and life-history traits. They forage at a wide range of spatial scales from long-distance oceanic movements (e.g., northern elephant seals) to short local trips of resident coastal species (e.g., harbor seals). Our current understanding of the foraging behavior of phocids comes mainly from northern and southern elephant seals, gray seals, harbor seals, ringed seals, and Hawaiian monk seals. Foraging tactics appear to develop rapidly within the first year of life, but the effect of age on the foraging of older animals appears to be weak. Sex differences in seasonal foraging distribution and diving behavior are evident in several dimorphic species but less evident or absent otherwise. Body size, condition, and reproductive status also influence foraging trip characteristics and dive effort. Recent studies reveal the consequences of foraging on mass gain and reproductive success and how those consequences vary with interannual and longer-term environmental change. More accurate location tags, improved dataloggers, and new analysis tools are being used to measure and infer in-situ patterns of foraging behavior and foraging success. Animal-borne instruments can also collect data on the ocean environment, which have proven useful in describing foraging behavior.

Keywords Phocids · Intrinsic and environmental drivers · Movement · Diving · Foraging success · Life-history consequences · New tools · Analysis methods

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6.1 Introduction

Phocids are large-bodied and long-lived species. Their large size means they tend to be wide-ranging predators that encounter habitats differing in quality, which may, in turn, influence their foraging behavior. Their longevity suggests that foraging performance may benefit from experience gained over a long life, as prey in the marine environment are often spatially aggregated and temporally variable (Mann and Lazier 1996). This may lead to the evolution of foraging behaviors that benefit individual reproductive output and survival at interannual and longer timescales.

These and several other factors are likely, therefore, to influence the foraging behavior of phocids. These factors may be intrinsic to the individual (e.g., age, sex, physiological condition), whereas others are expressed through changes in the environment at a range of spatial and temporal scales (e.g., seasonal and longer-term changes in prey availability, competitors, and predators). Although the effects of single factors are often evident, multiple factors generally interact to shape the behavior we observe. For example, gray seals (*Halichoerus grypus*) exhibit seasonal sex segregation in at-sea foraging distribution (Breed et al. 2006) and sex-specific seasonal differences in diving characteristics at the level of individual dives and bouts of diving (Beck et al. 2003a, b). Males and females also differ in feeding frequency (Austin et al. 2006a), seasonal patterns of energy storage and expenditure (Beck et al. 2003c), and seasonal diet (Beck et al. 2007). Foraging tactics develop rapidly with age, presumably reflecting the effects of experience (Breed et al. 2011). Variables that predict gray seal foraging success differ across temporal scales indicating that environmental variation becomes important at some scales and not others (Austin et al. 2006b). The results of studies on the foraging behavior of other phocid species also provide evidence for the interaction of intrinsic and environmental factors (Hassrick et al. 2013; Dmitrieva et al. 2016; Hindell et al. 2016; Yurkowski et al. 2016a, b, c; Rodriguez et al. 2017; Crawford et al. 2019; Chap. 5).

Foraging is critical to survival. More successful foragers may increase their fitness by surviving longer and passing their genes to the next generation. Thus, foraging ecology is an important driver in the evolution of behavior, life histories, and population dynamics. In securing food, phocid seals face several decisions. The first is where and how to search for food. Second, among the many possible species that could be consumed, which ones should be eaten to maximize energy gain. Third, how to balance the risk of predation with the need to find and capture food. Fourth, how to distribute foraging effort seasonally to meet the demands of reproduction and other components of an annual life cycle, and finally, how to deal with intra- and inter-specific competition. Thus, foraging behavior emerges as individuals respond to changes in their environment, with the response directed by their physiological state and navigational capability (Nathan et al. 2008).

Optimal foraging theory, formulated by MacArthur and Pianka (1966), sought to provide a predictive model to address some of the decisions foragers make. The theory stated that natural selection favors animals whose behavioral strategies maximize their net energy intake per unit time spent foraging (i.e., searching for prey and handling it) and sought to explain why, of the wide range of foods available, animals often consume just a subset of prey species. The theory predicted that animals should balance two contrasting strategies: spending a long time searching for highly "profitable" food items (so-called energy maximizers) or minimizing the time spent searching by consuming more common but less profitable food items (so-called time minimizers). Profitability here is expressed as the energy gained by consuming a prey item relative to energy expended during searching and handling the prey item. Many factors cause animals to deviate from foraging optimally. For example, predation risk may cause an animal to forage in a relatively safe location where food is less available or of lower quality, rather than opting for a more efficient but riskier feeding strategy where predator density may be higher. Foraging decisions may also depend on the physical state of the individual and the presence of other foragers (Ydenberg et al. 2007). Optimal diving (Kramer 1988; Thompson et al. 1993; Thompson and Fedak 2001; Houston 2011), optimal search strategies (Zollner and Lima 1999), and the marginal value theorem (Charnov 1976) are related concepts that predict how individuals should behave to maximize net energy intake. Davidson and Hady (2019) attempted to develop a more realistic model of the patch-leaving problem, in which a forager must decide to leave a current resource in the search for another, by considering how the imperfect and noisy information constrained by neurobiological mechanisms influences individual foraging decisions. Although animals may not always forge optimally, these concepts serve to remind us that foraging strategies are embedded within life histories and evolve by natural selection.

Foraging decisions of individuals also play a role in determining how the energetic cost of reproduction and provisioning of young are financed (Chap. 8). Animals are capital or income breeders based on their capacity to store energy during feeding for use in future reproduction (Sibly and Calow 1986). This capacity is largely a function of body size as mass-specific metabolic expenditure decreases with body mass. In contrast, fat storage increases with body mass to the power of 1.1 (Prothero 1995). In capital breeders, the energy and nutrients needed for reproduction are stored during foraging prior to the breeding season and then used during the breeding season. Income breeders, on the other hand, continue to forage during the breeding season. These two strategies should be regarded as either end of a continuum and markedly influence foraging behaviors (Stephens et al. 2009; Chaps. 7 and 8). Among phocids, capital breeders include elephant seals (*Mirounga leonina*, *M. angustirostris*), Hawaiian monk seals (*Neomonachus schauinslandi*), gray seals, hooded seals (*Cystophora cristata*; Schulz and Bowen 2004), and most likely the crabeater seal (*Lobodon carcinophgus*; Boyd 2000; Southwell 2004). In four species, (Weddell, *Leptonychotes weddellii*; bearded, *Erignathus barbatus*; harp *Pagophilus groenlandicus*; and harbor seals, *Phoca vitulina*), females initially support lactation from body stores but supplement energy expenditure by foraging as lactation progresses. In Weddell seals, this supplemental energy is nominal, and they are fundamentally capital breeders (Wheatley et al. 2006, but see Chap. 13). The ringed seal (*Pusa hispida*) is an income breeder, and given their similar small body sizes, presumably, the Caspian (*Pusa capsica*), ribbon (*Histriophoca fasciata*), spotted (*Phoca largha*), and Baikal (*Pusa sibirica*) seals are as well, but this has not been established.

Not enough is known about the leopard (*Hydrurga leptonyx*), Ross (*Ommatophoca rossii*), and Mediterranean monk seal (*Monachus monachus*) seals to classify them along the capital-income continuum. However, their long lactation period strongly suggests that Mediterranean monk seals are income breeders.

Except for the crabeater seal, phocids are generalist predators (Bowen et al. 2002a), with foraging behavior variable in time and space. This means that to make inferences about the factors (intrinsic and extrinsic) influencing foraging behavior, a large sample of individuals should be studied to have any confidence that population variability has been reasonably identified. As the number of individuals studied increases, the probability that recorded data will reveal individual variability in the behavior also generally increases such that ecologically valuable inferences about populations become feasible (Hindell et al. 2003; Sequeira et al. 2019). The appropriate sample size is dependent on the question and the level of between-individual variation in the study population. Hindell et al. (2003) showed that the relative increase in the relationship of adult female southern elephant seals between area occupied and sample size diminished substantially after 25 seals had been tracked. Because foraging behavior may often differ in males and females by age, and in response to environmental variability, large sample sizes are generally needed to make reliable inferences. Studies on small numbers of individuals can be informative where a combination of instruments (e.g., satellite tags combined with accelerometers, oceanographic sensors, or animal-borne video) is used to gain insight into individuals' foraging behavior (see Sequeira et al. 2019 for examples). Nevertheless, inferences from such studies should be viewed as tentative as they might not be representative of the population.

6.2 Statistical Approaches for Inferring Foraging Behavior

The foraging behavior of aquatic animals usually cannot be observed directly. Therefore, most insights on the foraging ecology and behavior of phocids have come from biotelemetry devices capturing a variety of in-situ data, including horizontal location, depth, 3D acceleration, and various environmental measures such as temperature, salinity, and light level. These data are often complex, high-volume time-series with varying levels of measurement error. As a result, statistical and/or heuristic approaches are often employed to summarize the data (Heerah et al. 2014; Photopoulou et al. 2014), account for measurement error (Jonsen et al. 2005; Johnson et al. 2008), and make inferences about behavioral processes hidden within the data (e.g., Thums et al. 2011; Bestley et al. 2013; Schick et al. 2013; Heerah et al. 2019).

There are two key and inter-related areas where statistical modeling has been instrumental in advancing the understanding of phocid foraging ecology. The first is to identify where and when foraging may occur and the environmental correlates of this activity (Chap. 5). The second is estimating the success of inferred foraging activity. Because seal foraging behavior is rarely observed directly (cf. Bowen et al. 2002b; Heaslip et al. 2014), it often can be inferred only from indirect measurements such as changes in horizontal movement pattern (e.g., Jonsen et al. 2005), dive pattern (e.g., Dragon et al. 2012; Heerah et al. 2014), acceleration (e.g., Gallon et al. 2013), or some combination of these (e.g., Adachi et al. 2017; McClintock et al. 2013).

6.2.1 Foraging Inferred from Horizontal Location Data

Horizontal location data are commonly determined by Doppler effect measurements of microwave radio transmissions to polar-orbiting satellites from externally attached tags on individual animals. These transmissions are processed by Service Argos (https://www.argos-system.org/). Several continuous state-space models have been developed to extract behavioral information from Argos data. Jonsen et al. (2005) developed a Bayesian continuous, state-space model to account for measurement errors typical of Argos horizontal location data and estimate switches between movements related to putative foraging behavior and those related to transiting or migratory behavior. Breed et al. (2009) used this approach to infer dynamic networks of intensely used local foraging sites that differed markedly between male and female adult gray seals. The "behaviorally-informed" spatial use maps arising from this approach revealed fine-scale foraging activity that was not obvious from previous analyses of the same location data (Breed et al. 2006). Bestley et al. (2013) built on this approach by incorporating a binomial regression into the state-space model so that the probability of switching between behavioral states could be related to environmental and other covariates to understand factors that influence foraging patterns. McClintock et al. (2012) used a broadly similar but more generalizable Bayesian approach to estimate activity centers (presumably profitable foraging sites) and their strengths of attraction for gray seals foraging in the North Sea.

Hidden Markov models, a class of discrete state-space models, are similarly used to infer behavioral states from animal tracking data (Langrock et al. 2012). These models are generally easier to compute than continuous state-space models, facilitating greater flexibility in estimating behavioral states and resulting in potentially more realistic interpretations of seal foraging and activity budgets. For example, Michelot et al. (2017) used a 4-state hidden Markov model to infer movement behaviors of southern elephant seals on their long, post-molt foraging trips. The model was constructed so that transitions between behavioral states reflected the sequential pattern of elephant seal movements during outbound transit from the breeding colony, repeated switches between searching and foraging (or resting) states, followed by an inbound transit back to the breeding colony (Fig. 6.1).

An alternative approach is to treat movement patterns as a continuum rather than as discrete behavioral states. Jonsen et al. (2019) showed how time-varying autocorrelation (move persistence) in southern elephant seal movements could be related to environmental covariates in a mixed-effects model. The flexible random effects allow relationships between movement patterns and environmental or intrinsic factors to be

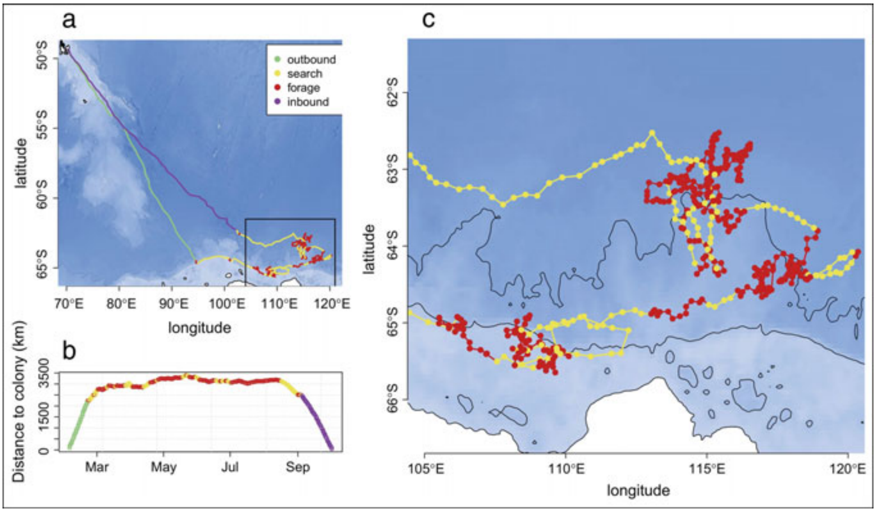

Fig. 6.1 **a** An example track of a southern elephant seal. **b** The distance from the colony (i.e., Kerguelen Island) over time. **c** Expanded view of box in panel A. The four colors correspond to the most probable states from the Viterbi algorithm. **a** and **b** clearly illutrate the phases of fast and directed movement attributed to the outbound and inbound trips. **c** Detailed movement when near the sea ice, with search (yellow) and foraging (red). From Michelot et al. (2017)

estimated so that variability across animals is explicitly quantified, thereby delving deeper into the context of movements that underlie foraging habitat usage. Such an approach may prove particularly advantageous when behavioral sequences (as per Michelot et al. 2017) are unknown.

6.2.2 *Foraging Inferred from Dive Data*

The methods highlighted in the previous section all implicitly assume a reasonably direct relationship between horizontal movement and foraging activity. Because phocids forage at depth, more direct and accurate information about foraging activity likely comes from their dive records. Early attempts to infer foraging behavior from dive data involved the classification of dive shapes on the assumption that shape encoded information on functionality (e.g., Le Boeuf et al. 1988, Chap. 12). Dives were classified visually or using classification algorithms (e.g., Scheer and Testa 1996) into four to seven types depending on angles of descent and ascent, and the fraction of time spent at the bottom of the dive (reviewed in Schreer et al. 2001). Foraging dives were thought to be mainly those where much of the time at depth was spent at the bottom of the dive (often termed U-shape or square-shape) where prey were presumably more frequently encountered. Dive shape analysis has been widely used to describe individual dives or bouts of diving derived from time-depth recorders as a means of inferring behavior (e.g., Boyd et al. 1994; Schreer et al. 2001; Fedak et al. 2001, Beck et al. 2003a).

Validation of the functional inference of dive shapes with respect to foraging has come from stomach temperature data on feeding (Lesage et al. 1999; Kuhn et al. 2009), water flux estimates of food intake (Baechler et al. 2002), animal-borne video (Bowen et al., unpublished data; Yoshino et al. 2020), and jaw accelerometers (Naito et al. 2013). Despite these validations, caution is needed when making inferences about behavior from dive shape alone, as these shapes may also be exhibited during behaviors unrelated to foraging. For example, animal-borne video of adult male harbor seals revealed that U-shape (i.e., bottom-time dives) dives also were performed during transiting and while making reproductive vocalizations (Boness et al. 2006). Similarly, Kuhn and Costa (2006) found that only 28% of feeding events based on stomach temperature data from northern elephant seals were associated with bottom-time dives, whereas some 65% were associated with V-shaped dives.

Shape is simply a two-dimensional representation of behavior performed in three dimensions, so studies have taken the next logical step by investigating the three-dimensional properties of diving behaveor (Harcourt et al. 2000; Simpkins et al. 2001; Davis et al. 1999, 2003; Adachi et al. 2017; Le Bras et al. 2017). Although three-dimensional analysis is informative, inferences about the function of dives still needed to be validated by video (Davis et al. 2003). More recently, Heerah et al. (2014, 2019) quantified southern elephant seal and Weddell seal dive behavior using an automated broken-stick algorithm to identify two behaviors, with highly sinuous segments indicating "hunting" and less sinuous segments indicating "transiting". They verified these functions using accelerometry data during prey capture attempts. A key finding was that hunting time in these species differed from bottom time, which was previously used as a proxy for time spent foraging in a dive.

Several studies have simultaneously used information from horizontal and vertical dimensions to infer foraging behavior. Bestley et al. (2015) used five common dive metrics as covariates of the rate of switching into foraging (or resident) behavioral state as estimated from a state-space model (Bestley et al. 2013). Heerah et al. (2017) used a heuristic approach based on a combination of movement data expressed as First Passage Time (Fauchald and Tveraa 2003) and a hunting time index derived from dive profiles to investigate foraging behavior. Recently, van Beest et al. (2019) combined horizontal GPS locations and summarized dive data in a multivariate hidden Markov model to infer the spatial foraging activity of gray seals. Together, these studies indicate the value of simultaneously using the information on horizontal movements and diving behavior to gain deeper insight into the foraging behavior of phocids.

6.2.3 Inference of Foraging Success

Statistical modeling of Argos and GPS location data from tagged phocids has provided insight into movement and foraging behavior's spatial and temporal characteristics. However, the identification of behavior without an indication of energy

Table 6.1 Methods used to infer overall foraging success or individual prey capture attempts and success. Methods are often used in combination or with other methods such as time-depth location tags. References in text

Method	Resolution	Prey capture	
		Attempts	Success
Mass gain	Integrated over entire trip	No	No
Buoyancy changes/drift diving	Integrated over entire trip	No	No
Body composition—isotope dilution	Integrated over short or partial trips	No	No
Water turnover (food intake)—isotope dilution	Integrated over short or partial trips	No	No
Accelerometry	Individual events, short duration of data collection	Yes	Sometimes
Stomach temperature telemetry	Individual feeding events/meals, short duration of data collection	No	Yes
Animal-borne video/stills	Individual feeding events, short duration of data collection	Yes	Yes
Coded acoustic tags in prey, acoustic transceiver on predator	Individual feeding events	No	Yes

gain provides an incomplete picture. Several approaches have been used to fill this gap (Table 6.1). Some integrate success over an entire or part of a foraging trip (e.g., mass gain). In contrast, others provide resolution of behavior at the level of individual events (i.e., prey capture attempt or success) at timescales of only hours or a few days (e.g., animal-borne video) due to limited battery life. The approaches listed in Table 6.1 have been used alone but more often are used in combination with other instruments, particularly time-depth and location tags.

Mass gained during foraging trips is commonly used to measure overall foraging success (e.g., Coltman et al. 1998; Le Boeuf et al. 2000; Beck et al. 2003c; Crocker et al. 2006). Mass gain ultimately must reflect foraging success, but what it really measures is the fraction of energy stored from food intake. Differences in the diet (e.g., prey size and energy content) and cost of foraging (e.g., prey behavior) influence the relationship between mass gain and foraging success. The advantage of mass gain is that it is easy to measure. However, the disadvantage is that the most accurate and informative data come from repeated measurements of the same individual, which can be difficult to acquire.

Two approaches use changes in body composition to infer foraging success. The first uses characteristics of drift dives to infer foraging success based on an individual's change in buoyancy (Biuw et al. 2003). Changes in rates of descent during elephant seal drift dives can be inferred from high- and low-resolution (i.e., broken-stick dive summaries) dive data (Arce et al. 2019). These data can be used to identify how much energy seals acquire while at sea, and where profitable foraging regions are located and how these may vary in space and time (Biuw et al. 2007). Several modeling studies have integrated drift-dive-estimates of foraging success with movement patterns/behaviors to infer rates of lipid gain along individual elephant seal foraging trips (Schick et al. 2013; New et al. 2014). Pirotta et al. (2019) adapted the Bayesian state-space model of Jonsen et al. (2005) to include feeding and body-condition components that change over time. The amount of feeding on each day was assumed to be a function of the behavioral state (transiting vs. foraging) and daily averaged dive metrics. Daily change in body condition was a function of previous body condition, informed by drift dive rates, and amount of feeding estimated for that day.

In the second method, changes in body composition (e.g., percentage of fat) of an individual are estimated by use of a hydrogen isotope dilution at departure and again on return from a foraging trip or series of trips (e.g., Coltman et al. 1998; Beck et al. 2003c; Thums et al. 2011; Hassrick et al. 2013). This provides more information on foraging success than mass gain alone because it estimates the total and individual components of energy gain during foraging. Closely related to body composition changes are estimates of food intake based on water flux measurements from isotope dilution (Costa 1987; Coltman et al. 1998; Bowen et al. 2001; Muelbert et al. 2003; Lidgard et al. 2005). An estimate of food intake, combined with data on changes in body composition, enables inferences about the net energy gain from foraging success. Disadvantages of these methods include the requirement for the recapture of the same individual, which may not be possible, and that water turnover measurements must be made at timescales (a few days to several weeks) that are often much shorter than individual foraging trips.

The methods discussed above integrate foraging success over a trip or portion of a trip. Therefore, they fall short of providing information on the spatial and temporal pattern for prey encounters and of foraging success as a function of prey species or other prey characteristics. To fill these gaps, ecologist have fitted seals with accelerometers (Naito et al. 2010, 2013; Volpov et al. 2015), stomach temperature tags (Austin et al. 2006a; Kuhn and Costa 2006), coded acoustic tags (Lidgard et al. 2014), and cameras (stills—Hooker et al. 2002; video—Parrish et al. 2000, 2002; Yoshino et al. 2020).

Accelerometers provide indirect data on foraging behavior, but if calibrated (e.g., simultaneous animal-borne video or observation) can be used to estimate prey capture attempts (e.g., Naito et al. 2010, 2013; Volpov et al. 2015; Wilson et al. 2017a; Adachi et al. 2018). However, accelerometry data alone cannot confirm if attempts were successful. Goulet et al. (2019) fitted a miniature biomimetic sonar and movement tag to a southern elephant seal to partially deal with this shortcoming. The sonar detection of prey and movement sensors provided information to determine if the predator attempted to capture the detected prey. Stomach temperature tags operate on the principle that the ingestion of prey will lower stomach temperature (Wilson et al. 1992). Although these instruments can accurately record meals, it is doubtful that individual prey captures within a meal can be reliably resolved (Bekkby and Bjørge 1998; Austin et al. 2006a; Kuhn and Costa 2006). A challenge to be overcome with respect to stomach telemetry is the difficulty in keeping the stomach temperature transmitter from being passed by the animal. Kuhn et al. (2009) obtained an average of 8 days of records (range 2–21 days) from northern elephant seals. By placing the transmitter within an ethofoam "fish", Austin et al. (2006a) obtained data for 2–40 days with a mean of 16 days from adult gray seals.

Coded acoustic tags have recently been used to study predation in gray seals (Lidgard et al. 2014). Seals were fitted with a Vemco Mobile Transceiver (VMT) and a GPS tag to determine the spatial and temporal pattern of interactions between gray seals and several fish species that had previously been surgically implanted with coded acoustic transmitters. The coded transmitters allowed the identification of individual fish. Prey encounters could be distinguished from predation by the pattern of acoustic detections recorded by the VMT. Depending on the size used, acoustic fish tags transmitted for several years, and VMT recorded transmissions for about 12 months, providing data over an ecologically relevant period.

Camera images, both still but more commonly video, provide information on prey encounters, capture attempts, and capture success. However, sampling durations are typically short (hours to days) because of limitations of battery life and instrument weight (Parrish 2000; Bowen et al. 2002b; Davis et al. 2013; Krause et al. 2015). However, this limitation was overcome by triggering the video camera to record only during periods when the animal was at depth and or triggered by jaw movements (Yoshino et al. 2020). Given the large size of cameras relative to most other externally-mounted instruments, there has been concern about the potential for adverse effects on instrumented animals' behavior or energetics. For camera deployments of about three days, Bowen et al. (2002b) found no evidence for increased rate of mass loss and dive duration in male harbor seals that were equipped with the camera compared to those in previous years that wore a small time-depth recorder. Littnan et al. (2004) also found no evidence for adverse effects on diving behavior and trip duration of short-term camera deployments on subadult monk seals. Although short-term deployments may not have measurable adverse impacts, their large size has limited the use of cameras to larger species and age classes.

6.3 Foraging Behavior

6.3.1 Spatial and Temporal Scales of Foraging

Environmental variation at different temporal and spatial scales often affects the survival and reproductive success of individuals through its impact on foraging success. Thus, to understand the ecology of phocid seals in large marine ecosystems, we need information on the scales at which foraging decisions are made (e.g., Block et al. 2011; Sequeira et al. 2018).

Conceptually, a foraging trip entails transit to a prey patch or cluster of patches, movement within and between those prey patches, and then typically a return transit to land or ice (e.g., Breed et al. 2009). Spatial and temporal scales of foraging are nested within the ranging behavior of individuals from mesoscale coastal species (harbor seal) to large-scale and oceanic ones (hooded seal, elephant seals, Table 6.2). Although data are not available for all species, enough species have been studied to provide a reasonable understanding of the spatial and temporal scales involved while foraging. Nevertheless, the values in Table 6.2 should be regarded as a rough guide, as studies use different metrics to report the spatial scales of movement, and usually report considerable individual variation as well as season and sex effects (e.g., Breed et al. 2009; Sharples et al. 2012; Hindell et al. 2016; Yurkowski et al. 2016a).

Movement associated with travel to and from foraging areas is usually at the largest scale. The magnitude and duration of those movements vary greatly among phocid species. For example, large body size and the ability to store large amounts of energy in the form of blubber enables some species (e.g., harp seals, hooded seals, northern and southern elephant seals) to exploit foraging areas 1000 s of km from their breeding colonies. Harp and hooded seals exhibit a single foraging trip consisting of return migration of >4000 km to the eastern Canadian Arctic and Greenland in Northwest Atlantic populations (Sergeant 1965; Andersen et al. 2013a, Chap. 14). Northern and southern elephant seals make just two foraging trips involving long-distance migrations each year between breeding and molting sites (McConnell et al. 1992; Stewart and DeLong 1995; Le Boeuf et al. 2000; Hindell et al. 2016; Chap. 11). During these extended trips, some foraging occurs along transits in northern elephant seals (Kuhn et al. 2009) as well as at distant prey patches. Thus, it appears that the spatial and temporal scales of foraging are more complex than had been assumed in the conventional view of a foraging trip. There is no reason to imagine that similar complexity will not be found in the other species. Presumably, this complexity is primarily driven by the availability of prey and the trade-off associated with increased transit time versus time spent in more profitable prey patches, but this remains to be studied.

Rather than undertaking long migrations, most other phocids seasonally disperse throughout their range to forage. In the United Kingdom, gray seals use offshore areas (up to 100 km) connected to their haul-out sites by prominent corridors. In contrast, harbor seals primarily stay within 50 km of the coastline (Fig. 6.2, Jones et al. 2015). In the northwest Atlantic population, gray seals exhibit seasonal and sex-specific changes in foraging distribution within the continental shelf limits, and therefore, outbound transits are typically 50–80 km or less (Breed et al. 2006, 2009). There is also evidence from stomach temperature telemetry (Austin et al. 2006a) and coded acoustic tags (Lidgard et al. 2014) that gray seals forage along transits in addition to times where movements indicate area-restricted searching behavior (an indicator of increased likelihood of foraging), underscoring the complexity of foraging. Relatively short outbound transits to foraging areas are also evident in Hawaiian monk seals (Stewart et al. 2006; Wilson et al. 2017b) and Weddell and crabeater seals foraging in fjords or along the inner continental shelf of the Antarctic Peninsula (Costa et al. 2010).

Foraging trip duration also varies greatly among species, with the longest trips generally observed in long-distance migratory species and the shortest trips exhibited by coastal species. For example, trip durations of Hawaiian monk seals and harbor seals average less than a day to one week. In contrast, elephant seals may spend

Table 6.2 Representative temporal and spatial scales characteristic of foraging trips in adult phocid species. Values represent means range of seasonal means and are separated by sex (F = female, M = male) when applicable. N is the number of individuals studied

Species	N	Location	Trip duration (days)	One-way straight-line distance (km)	Dive depth (m)	Source
Northern elephant seal	37, 40	North Pacific	73, 243 F 125 M	18,000 F[a] 21,000 M	486–522 F 366 M	Stewart and Delong (1995), Le Boeuf (2000)
Southern elephant seal	287, 42	Southern Ocean	77	1,372, 2975	~430	Hindell et al. (2003, 2016)
Hooded seal	21, 51	North Atlantic		~2,600 (14,142)[a]	255	Andersen et al. (2013a, b)
Hawaiian monk seal	19	Main Hawaiian Islands	0.6	18	12–32	Wilson et al. (2017b)
Gray seal	84, 81	Scotian Shelf, NW Atlantic	7–13	50–80	50–150	Breed et al. (2009), Lidgard et al. (2020)
	11	Baltic Sea	1.5		<40	Sjoberg and Ball (2000)
Harbor seal	115	United Kingdom	<1.0–3.5	10–60	25–65	Sharples et al. (2012)
	49	Prince William Sound, Alaska		61		Lowry et al. (2001)
	37	Moray Firth, Scotland	<1.0–10.7	30 (F) 61 (M)		Thompson et al. (1998)
Ringed seal	130	Canadian Arctic		3–50	30–100	Yurkowski et al. (2016c)
	26	Baltic Sea		254	13	Oksanen et al. (2015)
Caspian seal	75	Caspian Sea			80% <15	Dmitrieva et al. (2016)
Bearded seal	7	Svalbard			24	Hamilton et al. (2018)

[a] Estimated total distance traveled

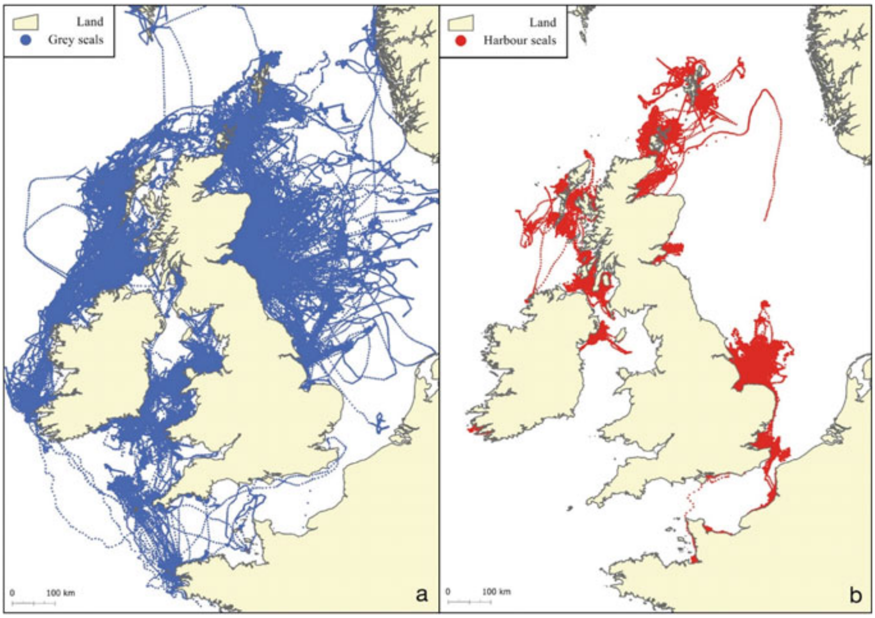

Fig. 6.2 Movement tracks of 259 Gy seals (**a**) and of 277 harbor seals (**b**) from different colonies around the United Kingdom from 1991 to 2013 and 2003 to 2013, respectively. From Jones et al. (2015)

months on a single foraging trip (Table 6.2). Both intrinsic and extrinsic factors can influence trip duration in some species. In harbor seals, males undertake longer and more distant trips than females (Thompson et al. 1998; Sharples et al. 2012). Although both sexes made trips of similar duration in gray seals, average trip duration varied seasonally from about one week in summer to two weeks in fall and winter (Breed et al. 2009). Despite shortened trips in summer, both sexes gain body mass (Beck et al. 2003a), suggesting prey may be more accessible during summer than at other times of the year.

Although there is some evidence that foraging may occur along transits, most foraging is thought to occur during periods of area-restricted search (ARS), where movements are characterized by frequent turning such that the animal stays within an area for an extended period. These areas are putative prey patches and are now routinely identified using behavioral switching state-space models (see Sect. 6.2.1). The spatial and temporal scale of ARS again varies widely among species, presumably reflecting the type and density of prey being consumed and the number of competing predators. Estimates of the spatial extent of ARS are difficult to compare across species as the methods used are often not comparable. Breed et al. (2009) used convex polygons to show that adult gray seals foraged over areas of 200–400 km^2 during ARS for periods of 3–7 days. The spatial extent of ARS differed by sex and season, being most significant in the fall and smallest in winter. Males foraged over larger areas than females in all seasons. Although regions of ARS along movement tracks are evident in all phocid species, few studies have quantified the size, number, and residence time per putative prey patch. Analysis of ARS behavior could provide insight into the characteristics of seasonal, inter-annual, and longer-term variations in prey availability.

6.3.2 Intrinsic Factors

6.3.2.1 Sex

The foraging behavior of males and females differs in many taxa (Clutton-Brock et al. 1982; Boinski 1988; Petit et al. 1990; Lewis et al. 2002; Neuhaus and Ruckstuhl 2002; Bearhop et al. 2006). Among the explanations for these differences, the three most prominent hypotheses are sexual body-size dimorphism, reduced intersexual competition for food, and the differential roles of each sex during reproduction and parental care. Among phocids, relatively few species have been studied in enough detail to test for sex differences robustly. Still, sex differences in foraging behavior have been found in northern and southern elephant seals, gray seals, and hooded seals (Table 6.2). These four species exhibit body-size dimorphism whereby males are larger and heavier than females. By contrast, sex differences in movement behavior, and therefore presumably foraging, are not evident in harbor (Russell et al. 2015) or ringed seals (Luque et al. 2014); species exhibiting little or moderate body-size dimorphism (males are about 25% heavier than females) or are monomorphic, respectively.

Foraging behavior of males and females may differ in spatial distribution, characteristics of diving, seasonal effort as manifested by changes in body energy storage (e.g., Biuw et al. 2007), and differences in diet (Beck et al. 2003b, 2007). The effect of sex on the spatial distribution of foraging is evident in several body-size dimorphic phocids. In northern elephant seals, males appear to primarily forage benthically along the west coast of North America from Oregon to the Gulf of Alaska. In contrast, females predominately forage pelagically in the mid-Pacific Ocean between the latitudes of about 35–50° N (Stewart and DeLong 1995; LeBoeuf et al. 2000; Robinson et al. 2010, 2012). This segregation pattern is evident in individuals during both the post-breeding and post-molt foraging trips (Stewart and DeLong 1995, Chap. 11), presumably indicating a level of predictability of profitable foraging areas. Sex segregation of foraging distribution is less evident in southern elephant seals as both sexes forage in shelf habitats. However, with the advance of sea ice in late autumn or early winter, female seals move northwards, resulting in some degree of sex segregation (Hindell et al. 2016).

In the northwest Atlantic, adult gray seals, another size-dimorphic species, exhibit strikingly different foraging distributions during the three months following the winter breeding season and again during several months leading up to the breeding season (Fig. 6.3). Males are more likely to undertake long-distance foraging trips (Austin et al. 2004). The result is that males have larger home ranges than females

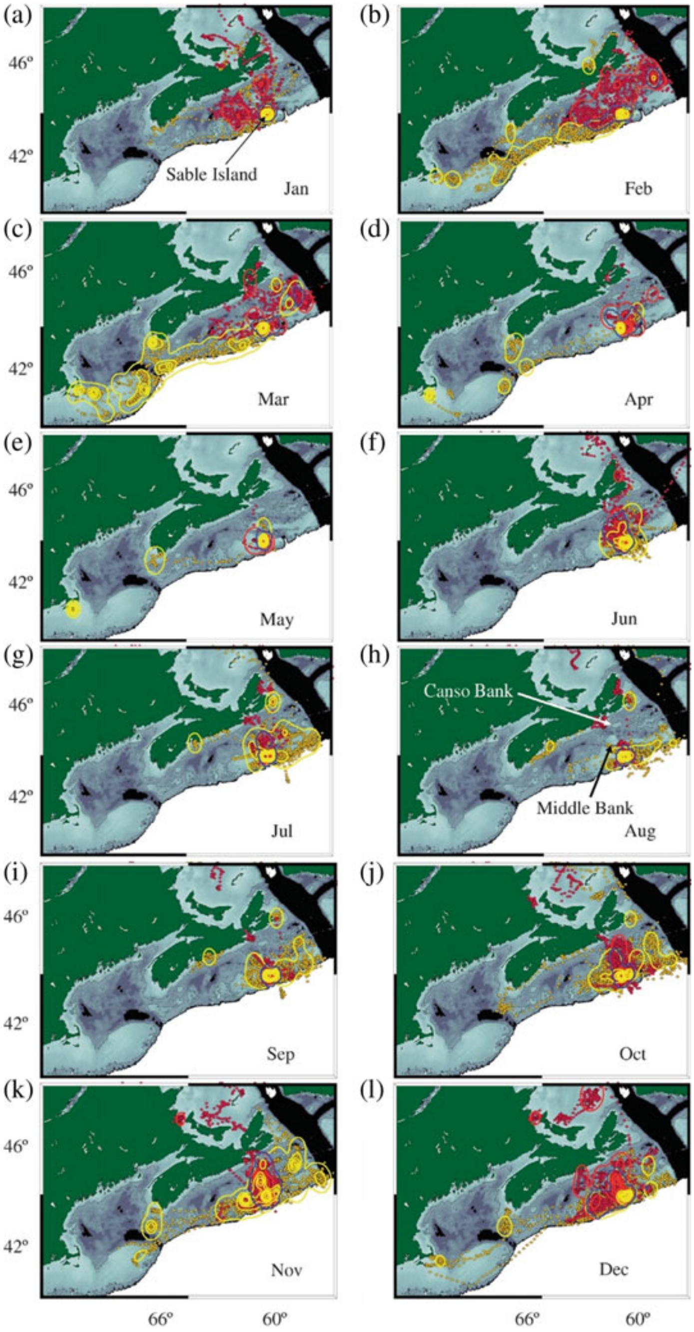

Fig. 6.3 Monthly sex segregation in adult gray seals on the Scotian Shelf. Red symbols are females, and yellow symbols are males. From Breed et al. (2006)

throughout the year (Lidgard et al. 2020). These differences in movement characteristics and foraging distribution are reflected in diet and patterns of body energy storage and expenditure (Beck et al. 2003c, 2007). Based on stomach telemetry data, adult gray seals fed on only 58% of days at sea, but when feeding occurred, males fed on average twice per day, whereas females fed only once (Austin et al. 2006a). Sex-specific, seasonal differences in the proportion of time spent foraging and traveling are also evident in juvenile and adult gray seals in the Northeast Atlantic (Russell et al. 2015). Less is known about the body-size dimorphic hooded seal, but Andersen et al. (2013b) found that males and females were spatially segregated within the same overall range based on regional differences in intensity of habitat use.

Based on current information, species exhibiting sex differences in at-sea distribution also show sex differences in diving behavior. Sex-specific diving behavior is evident in gray seals at the level of individual dives, bouts of diving, and dive effort (Beck et al. 2003a, b), and in both species of elephant seals (Le Boeuf et al. 2000; Hindell et al. 2016). Although female gray seals are smaller than males, they dived longer (5.5 vs. 4.9 min) and spent more time at depth (3.4 vs. 2.7 min), whereas males dived deeper (57 vs. 49 m; Beck et al. 2003b). Males dived consistently to near the seafloor throughout the day. In contrast, females showed strong diurnal patterns in dive depth, duration, and frequency, consistent with feeding on prey in the water column that vertically migrates. Similar findings have been reported in southern elephant seals where males had shorter dives than females, but there was no sex difference in dive depth (Hindell et al. 2016). However, in hooded seals, the effect of sex on diving characteristics was weak compared with geographic location, water depth, and season (Andersen et al. 2013a).

Sex differences in movements and foraging behavior appear to develop early in life based on studies of gray and elephant seals. Breed et al. (2011) found that although foraging in the same habitats, male and female gray seal pups showed small but significant differences in movement behavior and trip structure. However, in the UK, Carter et al. (2017) found no significant difference in trip duration between males and females in either region. However, sex differences in dive depth were apparent in pups from Celtic\Irish Seas colonies, with males diving significantly deeper than females. Similarly, sex differences in diving behavior are evident in northern elephant seals, where by their third foraging trip males exhibited more flat-bottom dives than females suggesting greater use of near-bottom foraging. Sex differences in foraging location, similar to those seen in adults, are evident before the seals reach 2 years of age (Le Boeuf et al. 1996).

Phocid species that do not exhibit sex differences in at-sea distribution also appear not to differ in diving characteristics. Sex was not a predictor of diving behavior in harbor seals (Frost et al. 2001) or ringed seals (Oksanen et al. 2015; Crawford et al. 2019). However, Luque et al. (2014) found an interaction between sex and ice concentration in ringed seals. Adult males were more likely to forage in areas with greater ice concentration than females, but the effect was relatively weak.

Based on studies to date, sex differences in seasonal patterns of at-sea distribution, dive behavior, and diet, are associated with differences in the seasonal patterns of energy storage and expenditure of males and females. These differences, in turn, reflect differences in life-history trade-offs associated with the reproductive strategies of each sex rather than the influence of body-size dimorphism alone.

6.3.2.2 Age

As long-lived species, age may influence the foraging behavior of phocids through experience. Age-related variation in foraging behavior has been reported for seabirds, which have some similar life histories as phocids (Riotte-Lambert and Weimerskirch 2013; Votier et al. 2017). However, physiology also plays an essential role in diving ability as oxygen stores in blood and muscles are needed to support aerobic diving, both of which scale with age and body size (Burns et al. 2007). The rapid development of body oxygen stores is crucial for phocid young to transition from nursing to independent foraging. Studies on phocids reveal a general pattern of increasing blood oxygen stores as a function of age until maturity (Burns 1999; Burns et al. 2005, 2007; Noren et al. 2005; Bennett et al. 2010). This increase is associated with an increase in diving ability with body mass (a general proxy for age) measured by dive depth and duration in phocids (Schreer and Kovacs 1997).

Despite its importance, the influence of age on foraging behavior in phocids has only recently begun to emerge from studies on the ontogeny of at-sea behavior. As phocid fathers provide no parental care, and mothers generally terminate parental care at weaning, newly weaned offspring receive no parental instruction on where and how to forage. The rapid development of foraging ability is critical to survival as newly weaned young have little time to learn how to capture prey before their blubber reserves are depleted (McConnell et al. 2002; Muelbert et al. 2003). Studies of phocid pups on their first and subsequent trips to sea, therefore, provide an insight into how foraging behavior develops in naïve animals during the transition to independence. Harbor seal pups, tagged during lactation, exhibited rapid increases in diving depth and duration and in the amount of time spent diving post-weaning; they exhibited an abrupt shift in movement patterns near 50 days of age, after which longer, deeper dives gradually became the norm (Blanchet et al. 2016). Gjertz et al. (2000) observed a rapid increase in diving depth of bearded seal pups, such that by 60 days of age, pups dived deeper than 448 m. Hooded seal pups began diving within days of weaning. Both dive depth and duration increased rapidly such that by 3 weeks of age, pups were diving to >100 m and for >15 min per dive, and by the fall maximum dive depths and durations had increased to 700 m and 30 min, respectively (Folkow et al. 2010).

Characteristics of foraging trips also appear to develop quickly. The initial direction of migration appears to be established during the first foraging trip in male and female northern elephant seals, but the differential migration and sexual segregation characteristic of adults do not develop until puberty when growth rates of males are substantially greater than those of females (Stewart 1997). By contrast, temporal and spatial segregation in at-sea distribution develops over the first 4 years of life in the southern elephant seal, which is thought to reduce intra-specific competition for resources (Field et al. 2005). The initial foraging trip of newly weaned southern elephant seals exhibits elements of such trips in adults. This initial trip is characterized by a rapid outbound movement (>100 km/d), slower travel rates for several months during which foraging is believed to occur, followed by a rapid inbound leg back to the birth colony (McConnell et al. 2002). Naïve southern elephant seal pups also performed shallow (100 m) and short (5.7 min) dives without a diurnal pattern during the first 60–80 days at sea. However, on the return phase of the trip, diving behavior changed abruptly with deeper and longer dives exhibiting a diurnal pattern like that of adults (Hindell et al. 1999). Together, these studies suggest that some aspects of foraging are primarily innate, but that foraging behavior develops with experience.

A comparison of the movement behavior of young phocids with that of adults provides further insight into the ontogeny of foraging tactics. Breed et al. (2011) compared the movement behavior of 5-month-old pups with subadult and adult gray seals. Tortuosity and speed of outbound travel on foraging trips were not different in pups, subadults, and adults, suggesting that pups, even at this young age, navigate as well as older animals. However, pup trips lasted 1.2–3.5 days longer. They required up to twice as much transit time to reach foraging areas that were 1.5–3 times farther from haul-out sites than those of subadults and adults. This suggests a higher foraging effort for pups than older animals. In all groups, apparent foraging effort decreased in the summer. It increased in the winter, which is consistent with seasonal changes in prey distribution and energy content. Adult foraging patterns showed complex seasonal patterns influenced by reproductive cycles and seasonal environmental variation. In contrast, annual foraging patterns of pups and subadults, neither of which invest in reproduction, were simpler and appeared more closely tied to seasonal changes in prey availability and condition.

Recently, Bowen, Nowak, Lidgard, and den Heyer (unpublished data) studied the movement patterns of naïve gray seal pups over the first 60 days at sea. Unlike older pups, the movements of naïve pups were not well defined, such that a behavioral switching model was unable to identify discrete behavioral states. Few pups made return trips characteristic of adults in this population, a striking contrast to naïve pups' behavior in the UK (Carter et al. 2017), perhaps suggesting that geography may play a role in shaping early behavior. Pups from North Sea colonies undertook a prolonged exploratory phase shortly after leaving the colony, with 69% of pups spending >20 days offshore without returning to the coast (Fig. 6.4). Some pups had trips exceeding 60 days, which is greater than typical trip durations seen in adults (McConnell et al. 1999). After this initial period of exploration, pups exhibited a pattern of return trips like that observed in adults.

Fewer studies have examined the effects of age on foraging behavior of adults. Hassrick et al. (2013) used data from post-breeding and post-molt females to investigate the extent to which intrinsic (body mass and age) and environmental factors influence foraging tactics, foraging efficiency, and foraging success in northern elephant seals. Age (4–14 years) had little impact on behavior, except for the structure of dives during the post-molt foraging trip. Age-related variation in dive structure suggested that older females were more efficient foragers as measured by rates of energy gain

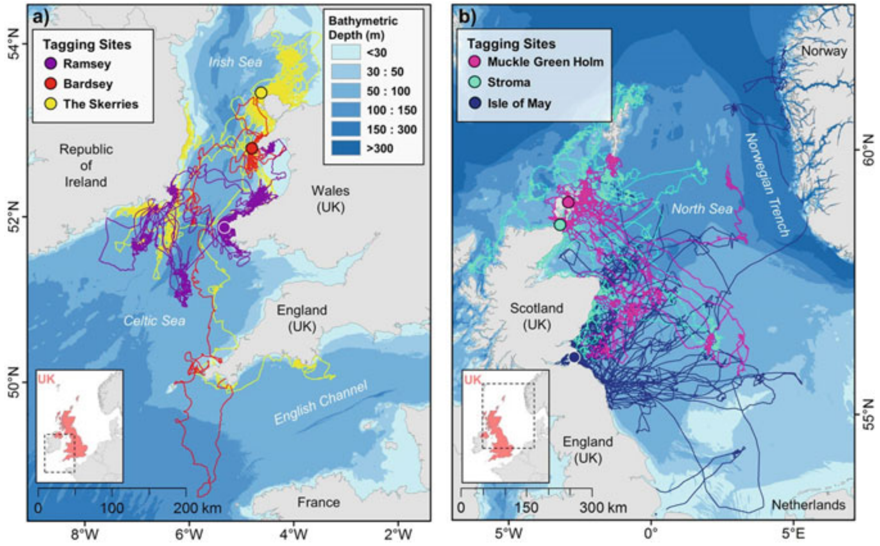

Fig. 6.4 Tagging locations. **a** Celtic and Irish Seas. **b** North Sea and trips at sea of 52 Naïve gray seal pups during the initial four months after leaving their colonies. From Carter et al. (2017)

(Hassrick et al. 2013). Recent work on a large sample of southern elephant seals from six colonies suggests that an effect of age on foraging is manifest through spatial memory (Rodriguez et al. 2017). Although the effect of age was not explicit in their analysis, the authors argue that foraging decisions are likely associated with prior experience of prey location (i.e., memory) as tracking data showed clear evidence of directed movements to areas of high use. Fine-scale analysis of gray seal GPS locations revealed differences in the frequency and duration occupancy of areas within the home range (Lidgard et al. 2020). Regions between haulout locations and apparent foraging areas were used infrequently and for short periods and thus were characterized by rapid directional movement, which may reflect memory of the location of profitable foraging areas.

Although a comparison of the movements of individuals of different ages may be the most direct means of probing the effects of age on foraging performance, age-related changes in the physiological condition of individuals can also provide insight. For example, any decline in oxygen handling or muscular performance with advancing age in a diving animal could reduce foraging ability. Hindle et al. (2011) compared oxygen stores and aerobic dive limit (ADL) of prime (9–16 years) and beyond peak-reproductive age (17–27 years) Weddell seals and found no evidence of reduced ADL late in life that would imply a decrease in foraging ability. However, Hindle et al. (2009) found that increased collagen deposition and decreased muscle myocyte suggested a probable effect of aging on sprint capacity and contractile efficiency, decreasing foraging efficiency. Nevertheless, evidence that muscular senescence reduces the foraging ability of free-ranging seals remains to be studied.

Although we have gained some insight into the ontogeny of foraging behavior in phocids, much remains to be learned. We still have little understanding of the influence of environmental variability or population size on the development of foraging behavior or how stable foraging tactics are over the life of these long-lived species (but see Sect. 6.3.2.4).

6.3.2.3 Body Size

Body size can influence the foraging behavior of phocids, presumably through its effect on energy requirements and physiological capacity. Thompson et al. (1998) found positive relationships between adult body size, trip duration, and distance in harbor seals. These findings supported the marginal value theorem's theoretical predictions that variation in the total duration of foraging trips should be positively related to the distance traveled to feed. In Prince Willian Sound, Alaska, larger harbor seals exhibited a broader isotopic niche than smaller ones, suggesting that larger seals exhibit more diverse foraging through much of the year. Smaller individuals were more likely to forage in tidewater glacial habitat throughout the year (Smith et al. 2019). In northern elephant seals, body mass was the sole predictor of residence time in foraging zones, which was the strongest behavioral predictor of foraging efficiency and success during the post-breeding foraging trip (Hassrick et al. 2013). Lidgard et al. (2020) found that heavier male and female gray seals had smaller core areas (30% home range isopleth). One possible explanation for this pattern is that heavier individuals might have competitively greater access to localized high-quality foraging habitats. However, since core area size was not a predictor of body mass gain during foraging, other explanations may be needed.

The effects of body size are expressed early in life. Dive duration and depth were positively related to body mass departure from the breeding colony in southern elephant seal pups (Irvine et al. 2000). Nevertheless, despite making shorter and shallower dives, foraging success, based on mass gain, was independent of body size. Burns et al. (1997) found that body-size differences explained about one-half of the variation in the diving behavior of yearling Weddell seals. Larger individuals made longer and shallower dives than smaller ones, suggesting that large yearlings foraged primarily on small shallow-water prey items. In contrast, small yearlings concentrated on energy-dense deep-water prey.

Body size also appears to have had strong influences on the evolution of foraging strategies of pinnipeds during the breeding season (Boness and Bowen 1996; Boyd 1998; Chap. 8). Harbor seal females, which are relatively small for a phocid, give birth to a single young that they nurse for an average of 24 days (Chap. 10). Unlike larger phocids, most females cannot support the entire cost of lactation from body reserves (Bowen et al. 1992) and begin to undertake regular foraging trips after about one week of fasting (Boness et al. 1994). However, there is a strong inverse relationship between maternal body mass and time spent foraging and food intake during mid to late lactation. By contrast, adult male harbor seals devote considerable time to foraging early in the season (Coltman et al. 1997). Most males maintain or increase body mass during this period (Walker and Bowen 1993). During the latter part of the season, when estrous females become increasingly available, males reduce foraging and devote more time to reproductive behavior while at sea. As a result, males may lose up to one kg of mass daily (Reilly and Fedak 1991; Walker and Bowen 1993). Given their relatively small body size, Coltman et al. (1998) show that most males could fast for only about 19 days or about 60% of the period when estrous females are available. Thus, males appear to balance foraging and reproductive behavior in such a way as to maximize potential encounter rates with estrous females (Coltman et al. 1997).

6.3.2.4 State-Dependent Foraging

Although body size is an important life-history trait, body condition also influences an organism's ability to survive and reproduce, where condition may include territory quality, energy reserves, foraging ability, parasite load, and the quality of its immune system (McNamara and Houston 1996). Body mass, a useful proxy for body condition, represents a state variable that accounts for much of the variability in the occurrence of pregnancy in capital breeding phocid seals (Boyd 2000). In Weddell seals, females that gave birth the following spring began the winter foraging period with significantly longer and deeper dives, as compared to non-reproductive individuals (Shero et al. 2018). By mid-to-late winter, reproductive females spent a significantly greater proportion of the day in one long daily foraging bout without rest compared to more frequent and shorter bouts by non-reproductive females. The increase in dive activity and reduction in diving metabolic rate were similar to the estimated energetic requirements of supporting a fetus, suggesting that increased foraging effort was associated with successful pregnancy (Shero et al. 2018). In northern elephant seals, Huckstadt et al. (2018) found that dives of pregnant females became shorter (accounting for dive depth) after week 17 compared to non-pregnant females, suggesting that increased fetal demand for oxygen could be the cause.

Mass gain during foraging and the resulting change in body condition can also influence diving behavior. Northern and southern elephant seals perform dives during which they spend a large proportion of time drifting passively through the water column. The rate of vertical change in depth during these "drift" dives is mostly a result of the proportion of lipid tissue in the body, with fatter seals having higher (more positive or less negative) drift rates compared with leaner seals (Crocker et al. 1997; Webb et al. 1998; Biuw et al. 2003). Several studies have used temporal changes in drift dive rate to estimate changes in body composition (a proxy for energy intake) throughout foraging trips as a measure of foraging success (Bailleul et al. 2007; Biuw et al. 2010; Robinson et al. 2010; Arce et al. 2019). In gray seals, a paired comparison of female diving behavior after molting with that just prior to the breeding season showed that the more buoyant pre-breeding females descended less rapidly, made longer dives, and spent more time at the bottom of dives than they had just after the molt when they were in poorer body condition (Beck et al. 2000). Together, these studies demonstrate that body condition plays a significant role in shaping diving behavior and that inferences about foraging success can be gleaned from such changes.

6.3.2.5 Individual Variation

There is growing evidence that individual variation in foraging ability is a critical component of natural selection, driving the evolution of life histories and individual responses to changing environmental conditions (Bolnick et al. 2003). A specialist may be defined as an individual whose niche is substantially narrower than its population's niche for reasons not attributable to its sex, age, or discrete morphological group (Bolnick et al. 2003). Individual specialization indicates that there are multiple ways of making a living. Specialization may allow animals to capture specific prey more efficiently but may also limit their ability to adapt to changes in prey resources. Individual variation can affect intra-specific competition, population persistence, species diversity, and ecological dynamics (Bolnick et al. 2003, 2011).

Although there is wide-spread taxonomic evidence for foraging specialization within populations, including marine mammals (Ford et al. 1998; Estes et al. 2003), the extent to which this occurs within phocids is not well studied. Individuals of several species (harbor seals, gray seals, and Hawaiian monk seals) use different feeding tactics to capture and consume different sizes or types of prey (Bowen et al. 2002b; Gallon et al. 2017; Kienle et al. 2019). However, the extent to which individuals specialize on a subset of prey over time to satisfy their energy requirements is still largely unknown. At a larger spatial scale, Oksanen et al. (2015) found that the number and location of apparent foraging areas of ringed seals were quite variable among individuals, suggesting different foraging tactics within the population. Some individuals foraged locally using only one area or several areas separated by short distances. However, most were long-distance foragers, with foraging areas separated by 150–825 km. Similarly, in a closely related land-locked species, the Caspian seal, Dmitrieva et al. (2016) identified three spatially exclusive types of summer dive behaviors (shallow, intermediate, and deep divers), suggesting that individual variation in behavior may play a role in niche partitioning to reduce intra-specific competition.

Estimates of the diets of individuals provide further evidence of foraging specialization in phocids. For example, Huckstadt et al. (2012) used stable isotope signatures within and between individuals to identify sources of variation in adult southern elephant seals' diet. They found that between-individual variability of δ^{13}C explained most of the total observed variance, suggesting that most individuals were specialists during the year they were studied. Similar findings are suggested by within and between individual comparison of isotopic levels in fur, skin, and blood of a small sample of gray seals (Hernandez et al. 2019).

Interannual repeatability in foraging behavior may be another expression of foraging specialization, although at a somewhat larger spatial and longer temporal scale. Long-term fidelity to foraging regions in variable environments may confer ecological benefits to individuals, such as familiarity with resources, even when energy gain is not consistently high in all years. Foraging site fidelity has been studied in several species where repeated tagging of the same individual has been possible. The most extensive data come from elephant seals, where individuals differ in the extent to which they show fidelity, while fidelity appears to be a fixed trait within individuals (Bradshaw et al. 2004; Costa et al. 2012; McIntyre et al. 2017; Abrahms et al. 2018a). Based on overlap among years in kernel density utilization distributions of 30 adult female northern elephant seals, Abrahms et al. (2018a) found that those individuals exhibiting the highest fidelity had a more consistent mass gain. In contrast, those showing lower fidelity had more variable mass gain among years. Repeated tracking of 21 adult gray seals also suggests that individuals exhibit strikingly similar movements and foraging distributions among years (W. D. Bowen and C. E. den Heyer unpublished data). Evidence of foraging site fidelity in observations of the same individual made up to 19 years apart suggests that, like elephant seals, this behavior is relatively fixed. Further studies are needed to determine at what age fidelity is developed and how fidelity to foraging areas responds to environmental variation.

Variation in foraging ability also may represent differences in the quality of individuals, where quality here is often thought to capture characteristics that are indicative of differences in fitness (e.g., Cam et al. 2002; Hamel et al. 2008). There is every reason to expect that phocids will show heterogeneity in foraging ability, given evidence of heterogeneity in reproductive performance (Weddell seal, Chambert et al. 2013; gray seals, Badger et al. 2020), but this has not been studied. Therefore, in addition to foraging specialists, there may also be heterogeneity in the foraging ability of individuals. Both specialization and heterogeneity of foraging ability may influence diet, how individuals respond to environmental variation, and, in turn, reproduction and survival. Nevertheless, for the most part, these are research questions that remain to be studied in phocids.

6.3.3 Extrinsic Factors

6.3.3.1 Environmental Variability

Physical and biological oceanographic features are dynamic over a range of spatiotemporal scales (Simpson and Sharples 2012, Chap. 5). This results in some areas having disproportionately high levels of primary productivity (Sathyendranath et al. 1995; Muller-Karger et al. 2005) that support assemblages of species at higher trophic levels (Richardson et al. 2000; Platt et al. 2003; Stevick et al. 2008; Benoit-Bird et al. 2013; Davoren 2013). The heterogeneous nature of oceanographic conditions results in a three-dimensionally patchy distribution of prey species available to upper-trophic level predators (Cox et al. 2018).

Phocids often have broad geographic ranges, providing the opportunity for within and among-population differences in foraging behavior that reflect regional environments. Regional environments may differ in geographic complexity, prey characteristics, potential competitors, and predators. There is ample evidence that the diets of phocids are influenced by environmental variation among populations, seasons, years, and over longer temporal periods (Bowen 1997; Brown and Pierce 1998; Bowen et al. 2002a; Wilson and Hammond 2019; Brown et al. 2001). Much of this variation likely reflects differences in the prey assemblages encountered spatially and temporally that may affect the way individuals forage.

Studies on several phocid species have revealed within-population differences in foraging behavior presumably driven by regional environmental conditions (e.g., Muelbert et al. 2013). In Prince William Sound, Alaska, Iverson et al. (1997) found mesoscale partitioning of harbor seal foraging habitats among different regions of the Sound (about 80 km) and finer-scale differences among sites 9–15 km apart based on differences in fatty acid profiles of harbor seals sampled at haulout locations within the Sound. These differences in fatty acid signatures undoubtedly reflected differences in the composition of diets and indicate a level of habitat partitioning that was unexpected as individual harbor seals could forage throughout the Sound. Satellite telemetry studies of harbor seals within the Sound have confirmed the scale of foraging activity indicated by the fatty acid signature analysis (Frost et al. 1998). Similar partitioning in foraging habitats also is evident among harbor seal populations in the UK. This suggests that harbor seals may benefit from increased foraging success through knowledge of local prey distribution or reduced risk of exposure to predators such as killer whales (Sharples et al. 2012; Russell et al. 2015).

The behavior of another circumpolar species provides further evidence of the influence of environmental factors on foraging behavior. At Svalbard, Norway, during years of late formation and the limited extent of land-fast ice, ringed seals made longer dives and spent less time at the bottom of dives compared to almost a decade earlier, suggesting increased foraging effort in response to environmental conditions (Hamilton et al. 2016). In the Canadian Arctic, Yurkowski et al. (2016b) found strong support for among-population differences in foraging characteristics using movement data from six tagging locations. Regional ice coverage had a significant effect on movements and foraging behavior in these populations, underscoring the need to study large numbers of individuals throughout the species range to draw reliable conclusions. As sea ice phenology may affect prey distribution, these data suggest plasticity in foraging decisions across the variable Arctic. Among-population differences in foraging behavior are supported by the results of a companion study, where the isotopic trophic position of ringed seals generally decreased with latitude and isotopic niche size increased over time, likely due to recent circumpolar increases in subarctic forage fish distribution and abundance (Yurkowski et al. 2016a).

Because many phocids are generalist predators, local changes in relative prey abundance are reflected in their foraging behavior. This is apparent for harbor seals, a generalist predator, where interannual variation in winter abundance of clupeid fishes such as Atlantic herring (*Clupea harengus*) and spratt (*Sprattus sprattus*) resulted in changes in the composition of harbor seal diets (Thompson et al. 1991, 1996). In years of high clupeid abundance, there was an increase in the proportion of these species in the diet. This change in diet was associated with a significant difference in the condition of seals caught in the spring following good and bad clupeid years, suggesting that there are energetic advantages and disadvantages to foraging on certain prey types (Thompson et al. 1996).

Large-scale variability in ocean conditions that presumably affect food supply also influences foraging behavior of pinnipeds (Field et al. 2001; Guinet et al. 2001; Dragon et al. 2010; Kuhn 2011; Hazen et al. 2013; O'Toole et al. 2015; Heerah et al. 2017; Abrahms et al. 2018b; van Beest et al. 2019; Nowak et al. 2020). For example, the period from 1975 to the late 1990s in the North Pacific Ocean was characterized by a large-scale, basin-wide warm regime that included multiple strong or long-duration El Niños, with a return to cooler conditions in the late 1990s. Le Boeuf and Crocker (2005) found that adult female northern elephant seals increased foraging effort and decreased body mass gain during this warm period compared to females foraging during the cool period. Comparing the foraging behavior of northern elephant seals during the strong 1997–98 El Niño to earlier non-El Niño years, Crocker et al. (2006) found that although the spatial behavior of females did not differ, the rate of mass gain was lowest during the El Niño year. Females attempted to compensate for decreases in foraging success by increasing trip duration. During the severe 1998 El Niño, diving data also suggested reduced residence time in prey patches and increased travel time between patches. Hassrick et al. (2013) found that age and body mass affect different components of foraging behavior in adult female northern elephant seals, both of which were influenced by environmental variation. Age influenced dive shape and dive bout characteristics, while body mass influenced the amount of time allocated to foraging zones. Interannual and seasonal impacts on distance (vertical and horizontal) that females traveled, thought to be a measure of annual variation in prey availability, influenced the rate and magnitude of foraging success.

Consequences of large-scale oceanographic variability on foraging success and demography are also evident in Hawaiian monk seals. The Transition Zone Chlorophyll Front (TZCF) is a large-scale oceanographic feature separating low surface subtropical chlorophyll waters and the high chlorophyll Transition Zone waters of the North Pacific Ocean. The TZCF annually migrates over 1000 km in latitude, and its southern extent in winter varies. Baker et al. (2007) hypothesized that movement of the front southward would bring more productive waters into monk seal foraging range, resulting in measurable positive effects at seal populations situated farthest north and nearest the TZCF. They found a nonlinear relationship between the winter position of the TZCF and survival of monk seals through 4 years of age at the most northerly atolls. This relationship did not extend to subpopulations located farther south or among adult animals at any site. They concluded that variation in ocean productivity might mediate prey availability in monk seal foraging habitat and consequently influence juvenile survival in the northern portion of their range. In a follow-up study, Baker et al. (2012) found that periods of growth and decline in monk seal abundance at four subpopulations were associated with positive and negative phases, respectively, of the Pacific Decadal Oscillation (PDO). They proposed that the PDO was a proxy for varying productivity in the northern NWHI, which propagated vertically through the food web and reflected in top predators such as the monk seal. As a result, the long-term dynamics of monk seal populations may be primarily driven by climate-ocean variability and its effects on foraging success.

At a finer scale, in-situ measurements of oceanographic properties collected at high temporal resolution by animal-borne data loggers provide insight into the conditions encountered that directly or indirectly influence behavioral decisions. Bailleul et al. (2007) used changes in the sinuosity of movement, diving frequency, and changes in body condition to show that estimated foraging success of juvenile and adult southern elephant seals was associated with different water temperatures depending on the habitat used. Dragon et al. (2010) showed that southern elephant seals preferentially exhibited foraging behavior in the presence of eddies. In northern elephant seal females, sea surface temperature was the best single predictor of estimated foraging areas (Simmons et al. 2007). In addition to water temperature, estimates of chlorophyll-a concentration have improved predictions of the spatial and temporal pattern of foraging behavior in several phocid species (Guinet et al. 2014; Vacquié-Garcia et al. 2015; Nowak et al. 2020). Vacquié-Garcia et al. (2015) studied 12 southern elephant seal females simultaneously equipped with accelerometers and with a range of physical sensors. They found that foraging environments were structured according to the primary frontal systems of the Southern Ocean and were characterized by different combinations of temperature, depth, and light level, suggesting the use of different prey communities. Nowak et al. (2020) found that chlorophyll-a concentration, estimated from animal-borne light level attenuation, varied seasonally and was positively associated with the chances of observing apparent foraging behavior in adult male and female gray seals, particularly during fall phytoplankton blooms when spatial variation in chlorophyll-a concentration was greater.

The presence of ice is another environmental factor that can influence the foraging behavior of phocids. Breed et al. (2018) found that sea ice concentration was highly predictive of juvenile bearded seal habitat use, with juveniles preferring intermediate concentrations and areas closer to the ice edge. Seasonal movements of bearded seals appeared to result from tracking the sea ice edge as it seasonally expanded and receded over the Bering and Chukchi continental shelves. Southern elephant seals making foraging trips to Antarctic sea ice consistently reduced move persistence as sea ice coverage increased but had highly variable responses to chlorophyll-a concentration. In contrast, seals foraging in the open ocean generally reduced move persistence where circumpolar deep water shoaled (Fig. 6.5, Jonsen et al. 2019).

Overall, these studies indicate that oceanographic features at various scales influence the behavior of phocids, presumably through their influence on the availability of prey. However, this presumption remains to be confirmed in most cases as simultaneous in-situ measurements of the spatial distribution of prey are generally not available.

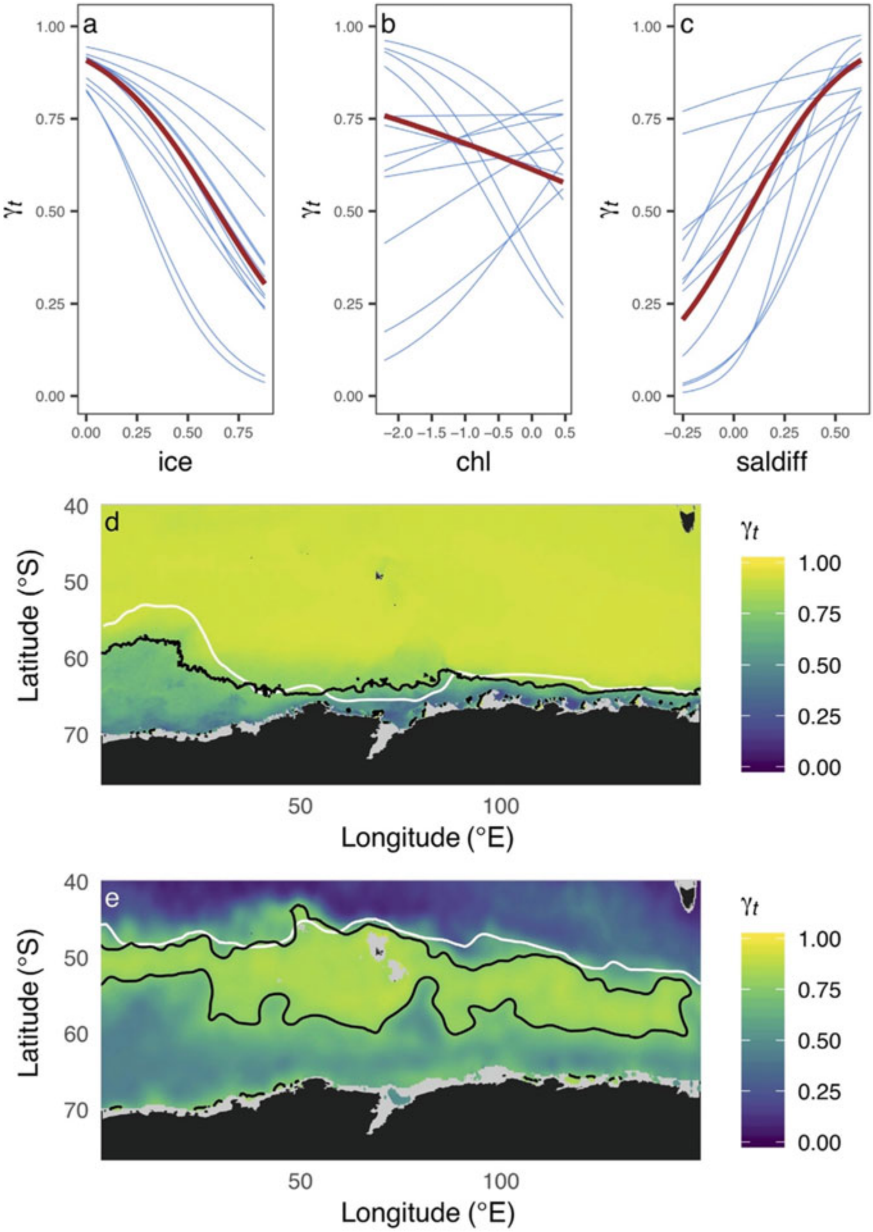

Fig. 6.5 Fixed (the mean response, red) and random (individual seals, blue) effects relationships between move persistence γ_t and (**a**) the proportion of ice cover (ice) and (**b**) chlorophyll *a* concentration (chl) for ice-foraging seals and (**c**) between γ_t and the salinity difference (saldiff) between 600 and 200 m for pelagic foraging seals. The models were used to generate spatial predictions of move persistence for ice (**d**) and pelagic (**e**) foraging seals. Areas of high move persistence (ie. $\gamma_t > 0.75$) are delineated by the black lines. The southern boundaries of the Antarctic Circumpolar Current (**d**) and the Subantarctic Front (**e**) are indicated as white lines. From Jonsen et al. (2019)

6.3.3.2 Predators and Competition

Predators can have important effects on foraging behavior and success of individuals by influencing where and when feeding occurs (Lima and Dill 1990; Peacor and Werner 2000; Preisser and Bolnick 2008; Wirsing et al. 2008). The direct effects of predation are widely recognized as a strong selective force; however, non-lethal impacts of predators may often have greater effects on their prey's behavior (Preisser et al. 2005). Relatively little research has been conducted on either the direct or indirect effect of predators on the foraging behavior of phocid species. One predator–prey interaction has provided some insight—killer whales, *Orcinus orca,* and harbor seals. Transient (Bigg's) killer whales from the US/Canada Pacific Northwest feed primarily, if not solely, on marine mammals, and harbor seals are the most frequently consumed (Baird and Dill 1995; Ford et al. 1998). The occurrence and residence time of transient killer whale pods peaked during harbor seal pupping when the energy intake by whales (mainly seal pups) also peaked. Exposure to transient killer whales can influence harbor seal behavior, such as activity budgets. In Hood Canal, Washington, harbor seals exposed to high levels of killer whale predation exhibited an increased probability of hauling out on land over a 2-year period when the whales were present compared to years before and after the whales had left the area (London et al. 2012). Increased time spent hauled out presumably reduced time available for foraging, although harbor seal foraging behavior was not explicitly studied.

A modeling study of several harbor seal predators (killer whales and Pacific sleeper sharks, *Somniosus pacificus*) provides further insight concerning non-lethal effects on harbor seal foraging behavior. Killer whales hunt near the surface, overlapping with Pacific herring (*Clupea pallasii*). In contrast, sleeper sharks primarily use depths of >100 m, overlapping with walleye pollock (*Gadus chalcogrammus*), a less energy-dense prey than herring. Both species are prey of harbor seals (Frid et al. 2006). Frid et al. (2007) predicted net energy gain and predation risk per foraging dive, parameterizing an analytical model with field data on the diving behavior of harbor seals, prey distributions, and use of depth by sleeper sharks and killer whales. Their analyses suggested that net energetic gain was highest when seals foraged for pollock in deep waters (>70 m). Nevertheless, plots of the individuals' predicted energy gain against predicted predation risk showed that seals underutilized relatively abundant prey found in deep waters where encounters with sleeper sharks were greater.

There is an increasingly accurate resolution of the movements and diving behavior of phocid seals. However, we still have relatively little understanding of how conspecifics and competitors may influence the foraging behavior of individuals. Nevertheless, we can gain some insight concerning the effects of intra-specific competition on behavior from the spatial distribution of different age classes. Patterns of habitat use and behavioral time budgets suggest that gray seal pups are likely displaced from foraging areas near the Sable Island, Canada breeding colony by adult females (Breed et al. 2013). This displacement was most pronounced in summer (Fig. 6.6). As young seals are less capable divers than adults, this may limit the habitat available to them. Juveniles born between 1998 and 2002 at Sable Island had reduced survivorship compared with cohorts born in the late 1980s, while adult survivorship

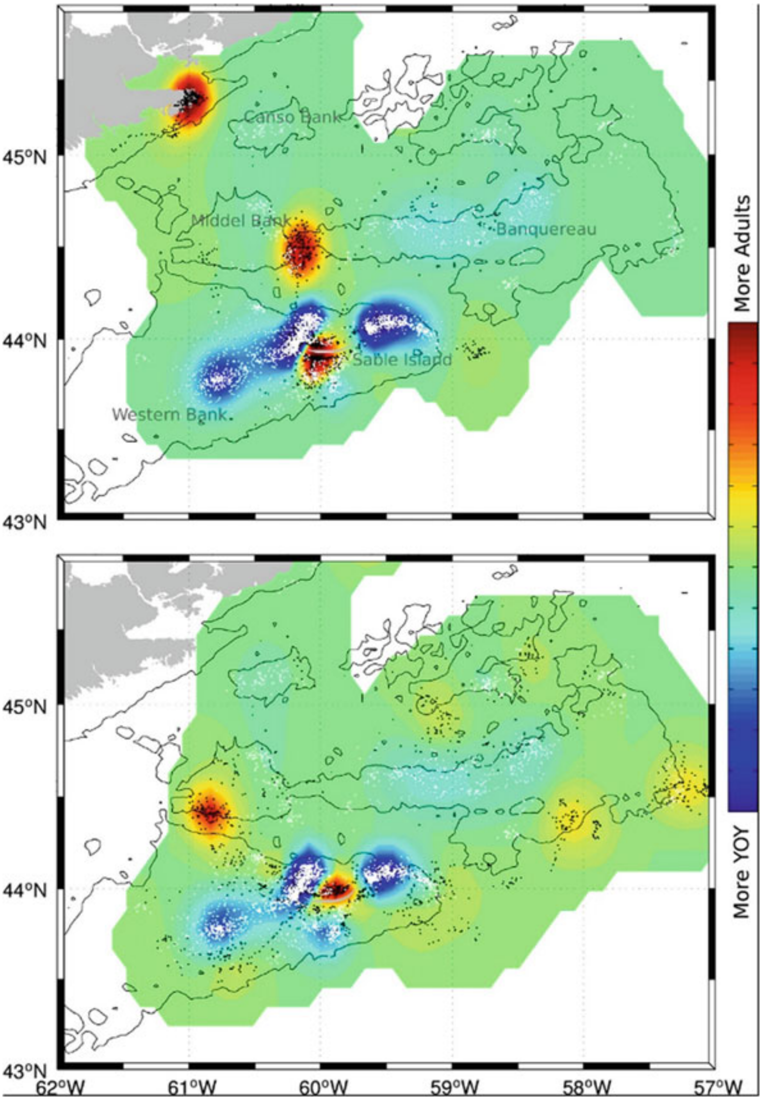

Fig. 6.6 July to September kernel density anomaly for **a** adult females versus young of the year gray seal (YOY) and **b** adult males versus YOY. White points are foraging locations of YOY, and black points are foraging locations from adults. Blue areas indicate regions used more heavily by YOY, while yellow and red areas indicate those used more heavily by adults. Green areas were used equally, while white areas were not used. From Breed et al. (2013)

has remained steady (den Heyer and Bowen 2017). Combined with behavioral observations, these survivorship data suggest that the foraging distribution of gray seals in their first year of life may be influenced by intra-specific competition from adults. Similar segregation of juvenile and adult ringed seals has been observed at glacial fronts in Svalbard (Hamilton et al. 2016). In Hawaiian monk seals, adults have smaller home ranges than younger seals, suggesting that adults may outcompete younger seals in areas of low prey abundance (Curtice et al. 2011). Age segregation among juvenile southern elephant seals (ages 1–4 years) has been interpreted as a way of reducing intra-specific competition for food (Field et al. 2005), but such segregation could also result from ontogenetic differences in diet. Although they are informative, the results of these studies provide only circumstantial support for how intra-specific competition may influence foraging behavior.

6.3.3.3 Foraging Success

Predators face decisions about which prey to include in their diet to maximize fitness. Many theoretical models attempt to explain and predict the behavior of air-breathing divers that exploit a food resource underwater. Telemetry and data-logging instruments, either alone or in combination with other instruments, have provided fine-scale (i.e., at the level of individual dives) resolution of foraging behavior of several species, which provide ways to test model predictions. Bowen et al. (2002b) fitted adult male harbor seals with an animal-borne video system and dive recorders to investigate prey-dependent foraging tactics and prey profitability in a free-ranging pinniped. They found that foraging tactics differed among and within prey types based on differences in prey behavior. Sand lance (*Ammodytes dubius*) was both a cryptic prey when in the bottom substrate and a conspicuous schooling prey when in the water column. Seal swimming speed, handling time, and capture success differed between cryptic and conspicuous sand lance. The highest capture success and handling time was recorded for flounders (family Pleuronectidae). Estimated profitability, i.e., net energy intake per unit time, also differed with prey type and prey size. Using the same data at the level of individual dives, Heaslip et al. (2014) tested nine predictions from optimal diving theory. They found support for seven of the nine predictions. As predicted, prey encounters increased with bottom duration; dive duration increased with dive depth; and travel duration, bottom duration, and percent bottom duration decreased over a wide range of travel durations. Descent duration increased with dive depth, and seals terminated dives earlier when prey were not encountered or when prey were encountered later in a dive. However, contrary to prediction, bottom duration did not increase and then decrease for short travel durations, and dives were not terminated earlier when travel durations were short, and the prey encounter rate was low.

The effect of prey density (or prey patch quality) on foraging behavior has been studied in several species. Sparling et al. (2007) conducted experiments in a large pool where gray seals had to swim horizontally to simulate diving to depth, to test the effect of prey patch density and distance from the surface on diving behavior. As predicted from theory, seals responded to prey density, leaving low-quality patches earlier. This pattern was still evident when seals had to travel far to reach the patch (simulating diving to deeper depths), contrary to the prediction that during deep dives, seals should stay at a patch regardless of prey density. Seals maximized dive durations at high prey densities, and longer distance traveled (again simulating longer dive durations), but they did not do so at short distances (simulating shallower dives). The giving-up strategy of the seals always produced higher profitability than would have been achieved if they had remained at the foraging site up to their aerobic dive limit on every dive. Thums et al. (2013) tested predictions of several optimal diving models in free-ranging, deep-diving southern elephant seals. Dive durations and bottom times varied with patch quality, but seals did not schedule their diving to maximize time spent in the foraging zone in patches of relatively higher quality. This observation is consistent with the predictions of the marginal value theorem (Charnov 1976), which states that animals foraging in a patch with better-than-average resources should spend relatively less time there. They also found higher descent and ascent rates in high-quality patches, suggesting that seals minimized travel time to the foraging patch when quality was high. Jouma'a et al. (2016) used time-depth recorder and 3D accelerometer data on southern elephant seals to test four predictions. Almost three-quarters of prey capture attempts detected by accelerometry occurred at the bottom of the dive. For dives <300 m, seals spent more time at the bottom of dives where prey were encountered. Seals had shorter bottom times and higher swimming speeds for dives where prey were encountered at deeper depths. When only dives associated with prey encounters were considered, the time spent at the bottom increased with the number of encounters. Body density, that is buoyancy, was a critical factor in controlling variations in dive duration. Finally, as predicted, post-dive surface intervals increased with dive duration and swimming effort in the previous dive. This study revealed a complex adjustment of foraging behavior relative to body density, prey encounter rate, and prey accessibility.

Fine-scale data from the combined use of animal-borne cameras and tri-axial accelerometers have permitted further tests of optimal diving theory. By integrating data from accelerometers with video and GPS, Wilson et al. (2017a) were able to identify variables associated with each foraging dive of Hawaiian monk seals. Dive depth, body motion (mean overall dynamic body acceleration during the dive), and proximity to the seafloor were the best predictors of prey searching. Search events typically occurred on long and deep dives, with more than 50% of the dive spent at the bottom.

Stomach temperature telemetry has revealed the spatial and temporal pattern of feeding in several free-ranging phocids. Austin et al. (2006a) studied feeding frequency in gray seals to test if previously reported sex differences in diving, movement, and diet were reflected in the temporal pattern of foraging success. Over 500 feeding events were recorded in 21 gray seals over periods of up to 40 days. Overall, seals fed on about 58% of days sampled with an average of 1.7 meals per day, but there were sex-specific differences and a high level of individual variability. Kuhn et al. (2009) used stomach temperature telemetry to show that northern elephant seal females fed within hours of departure and about 60 km from the rookery. Bouts of feeding began about 8 days into their foraging trip. Although associated with all dive types, they occurred most often during deep bottom-time dives. Females successfully fed only 18–24% of the time when they displayed the foraging type dive shape. This study showed that females feed extensively during early migration and that there was considerable individual variation in foraging locations and success.

Lidgard et al. (2014) used a combination of acoustic tags (Vemco Mobile Transceiver, VMT) and GPS locations to determine the spatial and temporal pattern of interactions between gray seals and potential prey that had been surgically implanted with a coded acoustic tag (Fig. 6.7). During a year study, the VMTs on 9 of 64 adult gray seals recorded detections from three species of fish, namely adult Atlantic cod *Gadus morhua*, Atlantic salmon *Salmo salar*, and American eel *Anguilla rostrata*. An examination of these seal-fish acoustic detections' temporal and spatial pattern suggested that predation on salmon and cod might have occurred. This study provided proof-of-concept that the foraging behavior of seals fitted with VMT and GPS tags can provide new insights into the nature of interspecies interactions in otherwise inaccessible environments.

Animal-borne cameras on a small sample of leopard seals have provided evidence of previously unknown foraging behavior of phocids. Video imagery showed that leopard seals mainly consumed Antarctic fur seals (*Arctocephalus gazella*, older animals and pups), demersal notothen fishes, and Pygoscelid penguins (Krause et al.

Fig. 6.7 A 30-year-old female gray seal fitted with a satellite-linked/GPS, time-depth recorder tag, a VHF radio tag, an accelerometer (head-mounted) and an acoustic transceiver (back) to study temporal and spatial encounters with acoustically tagged prey species. Photo by W. D. Bowen

2015). Seals used both chase and ambush tactics when hunting fur seals. However, successful hunting was driven by a subset of individuals using an ambush tactic, suggesting that individuals may specialize (see Sect. 6.3.2.4). Capture success was high for both Antarctic fur seal pups (76.5%), the most frequently targeted prey, and nototthen fishes (64.3%). Video data also recorded kleptoparasitism, whereby other females stole 6 of 10 fur seal pups captured by one female, and food scavenging/caching of carcasses on the seafloor. These behaviors are not known to occur in other phocid species, but may be profitable in leopard seals because of the relatively large prey that are routinely captured compared to that consumed by other phocids.

6.4 Life History Consequences

Tagging of adult seals has dramatically increased our understanding of the factors that influence the inferred foraging behavior of phocid species. However, less is known about the life-history consequences of foraging behavior. We know that body mass plays a critical role in reproductive performance in male and female phocids (e.g., Iverson et al. 1993; Crocker et al. 2001; Lidgard et al. 2005; Haley et al. 1994). However, we still know relatively little about how foraging behavior influences mass gain and, thus, the amount of energy available for reproduction and survival. Studies on elephant seals and several other phocids are beginning to fill this gap. In southern elephant seals, despite relatively strong fidelity to foraging areas across years, the relative mass gain of individual seals was highly variable (Bradshaw et al. 2004). Seals returned to forage in the same regions even when they did relatively poorly in the previous year. The authors concluded that returning to the same foraging area may not necessarily provide short-term benefits because seasonal variation in ocean productivity is high. However, fidelity to regions that show higher productivity on average over an individual's lifetime may maximize net energy gain over the longer term. This finding is consistent with the results of Thums et al. (2011), whereby females did not appear to regulate broadscale movement in response to foraging success, suggesting that movement patterns represent a response to the prior expectation of the location of predictable and profitable resources. Schick et al. (2013) used a state-space model to infer daily body lipid content from drift dives of foraging northern and southern elephant seals. Estimates of body condition in individual elephant seals at fine time scales allowed inferences to be made about the areas and times in which these predators profitably exploited their environment. They found that southern elephant seals performed fewer drift dives and gained lipid at a lower rate than northern elephant seals (Fig. 6.8), but that physiological condition and foraging location were significantly associated with lipid gain in both species. In northern elephant seals, Abrahms et al. (2018a) found that despite exhibiting alternative patterns of site fidelity among females, strong and weak fidelity performed equally well in terms of body condition over a 10-year period, but the success of each strategy varied interannually and was mediated by climate conditions. While these

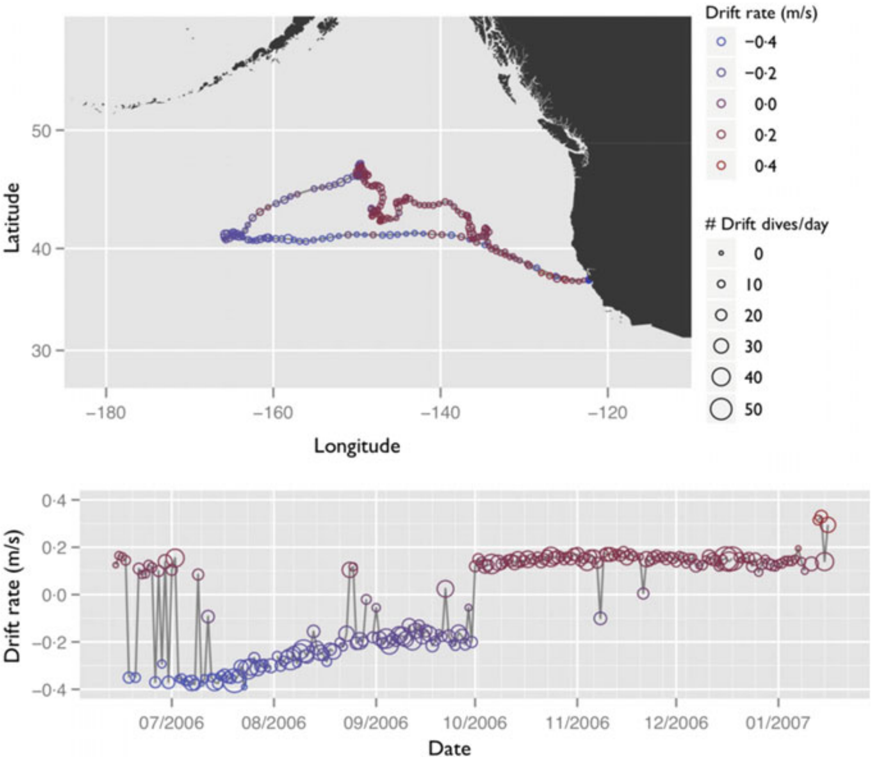

Fig. 6.8 Foraging trip map and drift rate time-series for one northern elephant seal tagged at Año Nuevo, California in 2006. The large shift to positive buoyancy occurs in early October 2006. From Schick et al. (2013)

studies provide insight on the relationship between foraging and body condition, they did not evaluate the life-history consequences of differences in foraging behavior.

A few studies have attempted to link reproductive performance and population dynamics to foraging behavior. Le Boeuf and Crocker (2005) took advantage of the fact that the weaning mass of northern elephant seal pups is strongly linked to maternal condition to examine the effects of decadal changes in prey availability and foraging success in pregnant northern elephant seal females in deep waters of the northeastern Pacific. They found evidence for a declining trend in the mean annual weaning mass of pups from 1975 to the late 1990s, a period characterized by a large-scale, basin-wide warm decadal regime that included multiple strong or long-duration El Niños. During a return to a cool regime from about 1999–2004, pup weaning mass then increased, reflecting improved foraging success of females. Robinson et al. (2012) analyzed diving, tracking, foraging success, and natality data for 297 adult female northern elephant seal migrations from 2004 to 2010. Seals focused their foraging effort along a narrow band corresponding to the boundary between the subarctic and subtropical gyres throughout the year. They found that mass gain during foraging migrations varied seasonally, but not among years. Annual mean rates of energy gain during post-molting foraging trips were good predictors of pregnancy status, but were not significant predictors of natality, perhaps due to the generally high natality rate in this population.

Several studies on southern elephant seals have provided further insight into the consequences of foraging behavior on reproductive performance. Authier et al. (2012) modeled pup weaning mass using blood stable isotope ratios to discriminate between maternal foraging behavior previously identified from movement studies. The carbon isotope ratio was a strong predictor of weaning mass, but there was an interaction between weaning mass and where females foraged. Females foraging in the inter-frontal zone weaned pups with a smaller mass compared with females foraging in Antarctic waters. McMahon et al. (2017) used the relationships between Southern Annular Mode and maximum sea-ice extent (both linked to foraging success) and maternal mass in southern elephant seals to infer consequences of changes in foraging behavior on pup weaning mass and subsequent survival. Maternal condition varied by as much as 59 kg among years. Environmental conditions increased predicted survival of pups with small mothers by 7% in ‘good’ versus ‘bad’ years compared to 1% for female pups of large mothers. New et al. (2014) used a modeling approach to simulate the effect of environmental change on the long-term fitness of female southern elephant seals. Simulations implied that single “bad” foraging years result in a relatively small (0.4%) population decline but that persistently poor foraging conditions (over 30 years) result in up to 10% population decline. Modeled reduction in maternal mass resulted in lighter pups at weaning, which in turn resulted in reduced pup survival. Using data from northern elephant seals, Pirotta et al. (2019) modeled the fitness implications of different foraging tactics. Their model simulated realistic patterns of environmental variation at different stages of a foraging trip, examined how the accumulation of lipid reserves would vary as a result of changes in foraging success, and the consequences for body condition, which in turn would affect offspring growth and survival.

6.5 Conclusions

Our understanding of foraging behavior of phocid seals has advanced considerably in the past decade or so. Most of this improved understanding results from studies on several of the more accessible species (i.e., land-breeders). More studies are needed on ice-breeding species to provide a more firm basis for generalization about phocid foraging ecology. The foraging behavior of phocids is influenced by multiple intrinsic factors (e.g., age, sex, body size, reproductive status) modified by environmental variability at various spatial and temporal scales (season, annual, interannual). We are just beginning to understand the ontogeny of foraging behavior and how spatial foraging patterns are influenced by early experience, individual heterogeneity, and environmental variation. Recent studies illustrate the power of statistical process-based models for integrating diverse information gleaned from animal-borne telemetry and data loggers to shed new light on phocid foraging behavior, foraging success, and, ultimately, potential fitness implications. However, more studies are needed to validate estimates of the spatial and temporal patterns of foraging success derived from statistical models of movement and diving behavior and understand the life-history consequences of changes in foraging behavior.

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