

# SEXUAL SEGREGATION IN MARINE FISH, REPTILES, BIRDS AND MAMMALS: BEHAVIOUR PATTERNS, MECHANISMS AND CONSERVATION IMPLICATIONS

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## Abstract

Sexual segregation occurs when members of a species separate such that the sexes live apart, either singly or in single-sex groups. It can be broadly categorised into two types: habitat segregation and social segregation. Sexual segregation is a behavioural phenomenon that is widespread in the animal kingdom yet the underlying causes remain poorly understood. Sexual segregation has been widely studied among terrestrial mammals such as ungulates, but it has been less well documented in the marine environment. This chapter clarifies terms and concepts which have emerged from the investigation of sexual segregation in terrestrial ecology and examines how a similar methodological approach may be complicated by differences of marine species. Here we discuss the behavioural patterns of sexual segregation among marine fish, reptile, bird and mammal species. Five hypotheses have been forwarded to account for sexual segregation, largely emerging from investigation of sexual segregation in terrestrial ungulates: the predation risk, forage selection, activity budget, thermal niche–fecundity and social factors hypotheses. These mechanisms are reviewed following careful assessment of their applicability to marine vertebrate species and case studies of marine vertebrates which support each mechanism recounted. Rigorous testing of all hypotheses is lacking from both the terrestrial and marine vertebrate literature and those analyses which have been attempted are often confounded by factors such as sexual body-size dimorphism. In this context, we indicate the value of studying model species which are monomorphic with respect to body size and discuss possible underlying causes for sexual segregation in this species. We also discuss why it is important to understand sexual segregation, for example, by illustrating how differential exploitation of the sexes by humans can lead to population decline.

## 1. INTRODUCTION

There is a burgeoning literature documenting sex differences in animal behaviour. These differences range from divergent foraging strategies (e.g., feeding rates) to gross differences in the geographical distribution of the sexes. Investigating sex differences in habitat use is of particular relevance, because understanding the mechanisms governing how and why the sexes differentially distribute themselves in nature is important in attempts to predict population processes and dynamics. It also has resonance in the successful management and conservation of animal populations since spatial dynamics of the sexes influences overlap with area-focused human activities such as hunting and fishing.

Sexual segregation can be defined as the separation of members of a species such that the sexes live apart, either singly or in single-sex groups. Sexual segregation is widespread in the animal kingdom. This is particularly so for the class Mammalia; it is almost ubiquitous among ungulate populations (for reviews, see [Bowyer, 2004](#); [Main \*et al.\*, 1996](#); [Ruckstuhl and Neuhaus, 2002](#)) and it also occurs in cetaceans ([Brown \*et al.\*, 1995](#); [Martin and da Silva, 2004](#)), carnivores ([Beck \*et al.\*, 2003c](#); [Wielgus and Bunnell, 2000](#)), bats ([Altringham and Senior, 2005](#)), elephants ([Stokke and du Toit, 2002](#)), marsupial mammals ([Broome, 2001](#)) and primates ([Pellegrini, 2004](#)). However, sexual segregation is a behavioural strategy which is not confined to mammals. It is seen in reptiles ([Shine \*et al.\*, 2000](#); [Wikelski and Trillmich, 1994](#)), fish ([Croft \*et al.\*, 2004](#); [Robichaud and Rose, 2003](#); [Sims \*et al.\*, 2001](#)) and birds ([Gonzalez-Solis, 2004](#); [Gonzalez-Solis \*et al.\*, 2000](#); [Lewis \*et al.\*, 2002](#)).

Yet, despite the widespread nature of sexual segregation, the underlying causes remain poorly understood. Investigative studies to date have tended to focus on sexual segregation in terrestrial vertebrates and on ungulates in particular. These species typically exhibit pronounced sexual dimorphism with respect to adult body size. Sex differences in body size are likely to confer significant sex differences in attributes such as predation risk, nutritional requirements and activity budgets, all of which are likely to influence spatial and temporal habitat use of the sexes. This is important to consider because it may be equally likely that individuals from each sex would segregate, regardless of their sex, simply due to differences in their body size. Therefore, sexually size-dimorphic species may not be the most appropriate behavioural models for examining differences due to sex per se since body-size differences represent a principal confounding effect.

Within the marine realm, no systematic investigations have been conducted into the underlying causes of sexual segregation in any vertebrate to date, but there have been several descriptive studies and potential causes have been proposed. Hence, there is a need to bring together the literature on marine vertebrates generally with respect to patterns of sexual segregation, and relate these findings to observations made for terrestrial, aquatic and aerial species. This chapter, therefore, reviews the evidence for and assesses the implications of sexual segregation in marine vertebrates (fish, reptiles, birds, mammals). The aims of this chapter are to clarify terms and concepts, to appraise current hypotheses that have emerged from the study of a diverse range of species and to assess their applicability to marine species in particular. A principal motivation here is to identify the similarities and differences in sexual segregation behaviour and its causes between terrestrial and marine vertebrates; are general features apparent or does a watery world confer key differences not present elsewhere?

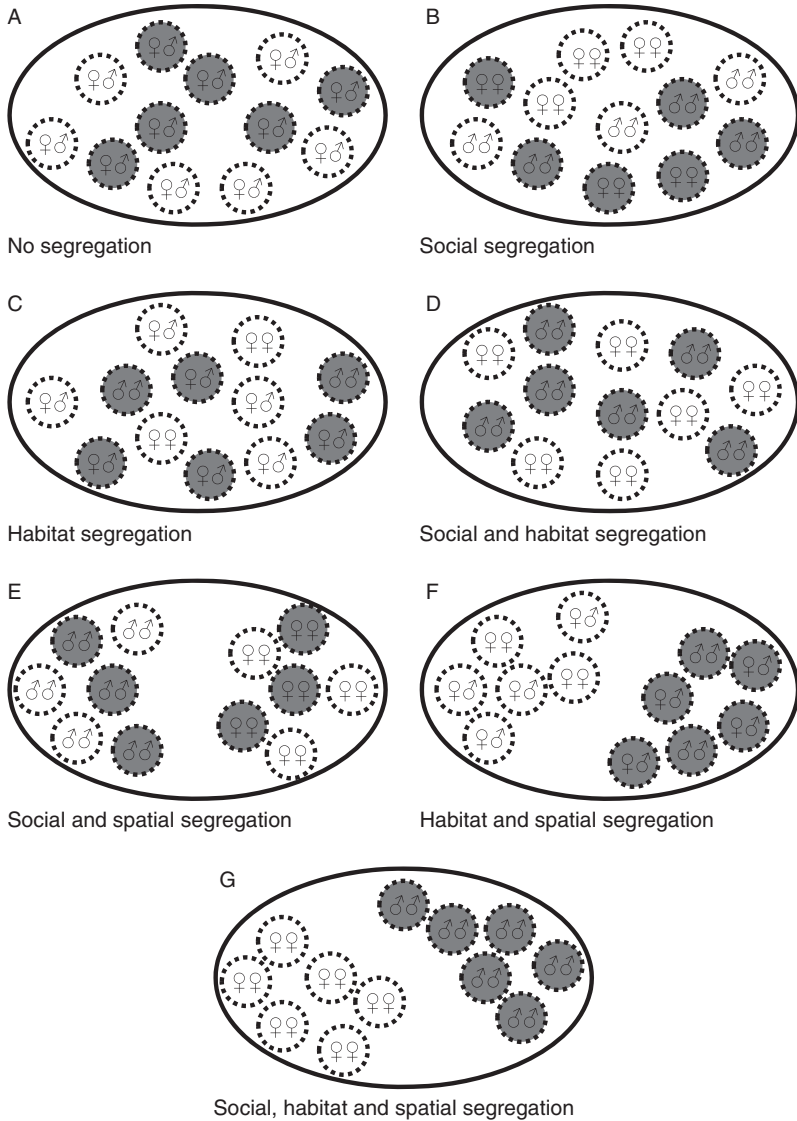
## 2. TYPES OF SEXUAL SEGREGATION

### 2.1. Habitat versus social segregation

Sexual segregation can be broadly categorised into two types: habitat segregation and social segregation. Habitat segregation occurs where the sexes differ in their use of the physical environment, whilst social segregation is the tendency for a species to form single-sex groups. However, socially segregating species may also exhibit sex-specific habitat use (social and habitat segregation). In addition, habitat- and socially segregating species may or may not separate spatially (Fig. 2.1). For example, in the marine flatfish known as dab, *Limanda limanda*, both sexes are captured by trawl on the same grounds (i.e., no spatial segregation), but social segregation is evident in the foraging behaviour of the sexes: The proportion of females with full stomachs is higher in the morning than in the afternoon, whereas the reverse appears the case for males (Temming and Hammer, 1994). In contrast, habitat segregation in male and female northern elephant seals, *Mirounga angustirostris*, leads to spatial separation of the sexes: Males forage on the continental margin and generally feed on benthic prey, whereas females range more widely over deep water and feed on vertically migrating pelagic prey (Le Boeuf *et al.*, 2000).

Sexual segregation is a behavioural pattern that is likely to be influenced by both social and ecological factors, such as the temporal pattern of mating opportunities, population density and the availability of resources. Within terrestrial mammals such as ungulates, sexual segregation is generally seen only outside the breeding season (when the sexes aggregate to mate) and therefore should be more pronounced in species with a discrete breeding season. However, this general observation does not appear to be the case for species in the marine environment. For example, sexual segregation is only seen in breeding populations of green turtles (G. Hays, personal communication). High population densities generally facilitate group fission, as the availability of suitable group mates should be sufficient for new group formation. However, in socially sexually segregating species which co-occur within the same habitat, high population densities may make sexual segregation difficult to identify as inter-group distances will be reduced. The effect of resource abundance on animal distributions will depend on whether the sexes exploit similar or diverging habitats, and, equally, whether habitats are homo- or heterogeneous.

The underlying causes of social segregation are likely to differ from those of habitat segregation. Habitat segregation results from sex differences in a species' responses to variability in factors such as resource availability, predation and environmental conditions, whereas social segregation results from inter-sexual asynchrony or aversion, or intra-sexual affinity. It is therefore



**Figure 2.1** The distribution of 12 social groups (dashed circles) across habitats (grey and white) under different sexual segregation scenarios. The diagrams depict: (A) No segregation: the sexes associate at random and are equally distributed between habitats; (B) Social segregation: unisexual groups are equally distributed between habitats; (C) Habitat segregation: the majority of groups are mixed sex but most males utilise the grey habitat ( $n = 8$ ), whereas females prefer the white habitat; (D) Social and habitat segregation: unisexual male groups utilise the grey habitat, unisexual female groups utilise the white habitat; (E) Social and spatial segregation: unisexual groups are equally distributed between habitats but occupy different areas; (F) Habitat and spatial segregation: the sexes associate at random but males prefer the grey habitat which is spatially separated from the white habitat preferred by females; (G) Social, habitat and spatial segregation: unisexual male groups utilise the grey habitat which is spatially separated from the habitat utilised by female groups (the white habitat).

useful to try and identify the type of segregation which occurs as it may help determine the underlying causes of the behaviours. The two types of sexual segregation are, however, not mutually exclusive. If a species exhibits sex-specific preferences over spatially separated habitats, the sexes may well live in different social groups (Conradt, 2005). Similarly, social segregation may also result in habitat segregation (Bon *et al.*, 2001; Conradt, 1999). Thus, identifying the proximate cause of sexual segregation is not straightforward.

## 2.2. Detecting types of sexual segregation

In an attempt to overcome the apparent dilemma of what causes sexual segregation, Conradt (1998b) developed the segregation coefficient. Unlike measures of ecological overlap (e.g., the percentage of animals in unisex versus mixed-sex groups), the segregation coefficient is not stochastically dependent on animal density, group sizes and sex ratio (Conradt, 2005). By estimating the product of the proportion of males which segregate and the proportion of females which segregate, the segregation coefficient (SC) measures the degree of segregation in an animal population (see Box 2.1). If males and females are found in completely separate groups (complete segregation), SC takes a value of 1. If there is no segregation (males and females meet randomly in groups), SC will be 0. Values of SC between 0 and 1 reflect partial segregation (where only a proportion of animals in the population segregate).

The segregation coefficient can be used to quantify the degree of social, habitat or spatial segregation exhibited by a population, thus enabling identification of the type(s) of segregation exhibited. For example, if the sexes use spatially separated habitats, but socialise randomly within habitats (i.e., social segregation is a by-product of habitat segregation) then  $SC_{\text{social}} = SC_{\text{habitat}}$ . On the other hand, if animal classes segregate socially within habitats, additionally to segregation between habitats, then  $SC_{\text{social}} > SC_{\text{habitat}}$  (Conradt, 2005). In addition, the segregation coefficient can be used to quantitatively compare the degree of segregation within and between species and populations.

The segregation coefficient has been successful in some cases for identifying degrees of sexual segregation in relation to various factors in social animals within particular taxa (i.e., ungulates). However, this measure can only be used effectively for group-living animals. This appears to overlook the need to identify sexual segregation in solitary animals. The issue is further complicated because it has been stated that '*in the case of solitary animals, the concept of inter-sexual social segregation does not apply*' (Conradt, 1998b), '*since a single animal is not social*' (Neuhaus and Ruckstuhl, 2004a). The implication is that solitary animals are not likely to exhibit social segregation, even if they occur in the same habitat. Nevertheless, where solitary animals actively avoid members of the opposite sex, as has been suggested in the river

**Box 2.1** The segregation coefficient (after [Conradt, 1998b](#))

Conradt's segregation coefficient (SC) determines the degree of sexual segregation in animal populations using the following formula:

$$SC = \sqrt{1 - \frac{X + Y - 1}{X \cdot Y} \cdot \sum_{i=1}^k \frac{x_i \cdot y_i}{x_i + y_i - 1}} \quad (1)$$

where for  $SC_{\text{social}}$ :  $x_i$  is the number of males in the  $i$ th group;  $y_i$  is the number of females in the  $i$ th group;  $k$  is the number of groups with at least two animals (i.e., solitary animals are excluded);  $X$  is the total number of males in all  $k$  groups;  $Y$  is the total number of females in all  $k$  groups.

$SC_{\text{habitat}}$ :  $x_i$  is the number of males in the  $i$ th habitat type;  $y_i$  is the number of females in the  $i$ th habitat type;  $k$  is the number of habitat types which are used by at least two animals;  $X$  is the total number of males in all  $k$  habitat types;  $Y$  is the total number of females in all  $k$  habitat types (the measure is sensitive to the classification of habitat types).

$SC_{\text{spatial}}$ :  $x_i$  is the number of males in the  $i$ th grid square;  $y_i$  is the number of females in the  $i$ th grid square;  $k$  is the number of grid squares which are used by at least two animals;  $X$  is the total number of males in all  $k$  grid squares;  $Y$  is the total number of females in all  $k$  grid squares (the measure is sensitive to grid square size, i.e., spatial scale). It is important that sample sizes are large.

The resulting segregation coefficient or degree of segregation ranges from 0 (no segregation) to 1 (all males and females segregate).

dolphin or boto (*Inia geoffrensis*; [Martin and da Silva, 2004](#)), they appear to exhibit social segregation. Therefore, Conradt's indices of sexual segregation do not apply to numerous species that are principally solitary in their behaviour.

### 2.3. Measurement problems for marine species

Determining the underlying causes of sexual segregation in the marine environment presents a particular challenge. This is mainly due to the fact that studying marine vertebrates in their natural surroundings is complicated by the fact that they live in a relatively inaccessible and concealing environment ([Sundstrom et al., 2001](#)). Additionally, unlike most terrestrial ungulates, marine vertebrates live in a strongly three-dimensional environment and, whilst it may be relatively simple to observe the behaviour of shallow

reef-dwelling species which may also be held in captivity, other species may move or migrate both horizontally and vertically on a regular basis and sometimes across large spatial scales. In such circumstances, it is extremely difficult to determine which individuals constitute a population. In addition, there is often a lack of information on the sex of the individual, which may be attributable to a general difficulty in identifying the sex of individuals based on external morphology (Catry *et al.*, 2005; Gilardi, 1992). Therefore, in an environment where it is difficult to determine which individuals constitute a group/population and where it is virtually impossible to distinguish the sex of all individuals, Conradt's indices are largely inappropriate.

Understanding the underlying causes of sexual segregation in marine vertebrates is further complicated by their foraging behaviour. Whereas terrestrial ungulates are herbivorous and foraging can be observed directly and food type and quantity can be determined (or at least estimated with some accuracy), many marine vertebrates are predatory and forage on mobile prey. This makes identification of foraging behaviour and forage type very difficult since to fully understand individual foraging behaviours one must first have some knowledge of the behaviour, abundance and availability of the prey species. Much of our current knowledge of marine vertebrate diet comes from the analysis of scats or the stomach contents of dead animals. However, dietary analyses using scats may underestimate foraging niche breadth as only hard parts (e.g., fish otoliths and bones, squid beaks) are identifiable (Pierce and Boyle, 1991). In addition, these techniques only provide an indication of forage selection over a narrow time period (governed by digestion rates: Sims *et al.*, 1996), and as moribund animals are unlikely to exhibit normal foraging behaviour, stomach content analyses may also be unrepresentative. Information on diet is needed over temporal scales relevant to life-history characteristics. With the application of new techniques, such as mammal-blubber fatty acid profiles which reflect prey consumed over a period of weeks or months (Beck *et al.*, 2005), this information gap is being closed in some taxa.

Pinnipeds, marine birds and marine reptiles, with few exceptions, breed on land. Consequently, much of our understanding of the behaviour of representatives from these three groups stems from observations made at or near breeding colonies. The development of remote telemetry systems for tracking movements of individuals and the environment they move through is now extending our understanding of pinniped, bird and reptile behaviour into the non-breeding seasons (Hays *et al.*, 2004; Ropert-Coudert and Wilson, 2005). These remote monitoring techniques also provide insights into the habits of cetaceans and fish, which are wholly marine. In the case of fish, acoustic telemetry has been widely used to investigate habitat choice in marine species. Attaching an acoustic pinger to an individual fish enables its movements to be tracked in real-time.



Initially, acoustic signals were tracked manually using a directional hydrophone (e.g., [Carey and Scharold, 1990](#); [Sims \*et al.\*, 2001](#)), a labour-intensive and expensive technique that has yielded only short-term tracks when used continuously (from days to up to 2 weeks). More recently, remote monitoring of acoustically tracked fish has been facilitated by the development of radio-acoustic positioning systems (a triangle of three moored hydrophones which radio-link to a base station on land where the location of the fish is calculated and displayed in real-time) (for a review, see [Klimley \*et al.\*, 2001](#)). In addition, using acoustic pingers with sensors, where depth or ambient temperature is encoded within the acoustic pulse sequence, has enabled reconstruction of an animal's three-dimensional trajectory and provided information on the abiotic conditions at an animal's location.

Acoustic telemetry techniques are spatially constrained by the distance sound energy travels in seawater and this distance can be dramatically reduced if the environment is acoustically noisy (e.g., strongly tidal areas) and/or bathymetry is not uniform in the local area. More recently, satellite-linked archival transmitters incorporating a data-logging (termed 'archival') tag with a satellite transmitter for relaying stored summary data have been used widely to track large marine fish such as sharks ([Sims \*et al.\*, 2003](#)) and tuna ([Block \*et al.\*, 2001](#)). Similarly, satellite transmitters have been attached directly to the dorsal fin of sharks to enable direct tracking of movements. Here, transmissions to over-passing satellites are made when fish surface and the transmitter becomes dry, which is necessary since ultra-high frequency radiowaves will not penetrate seawater ([Weng \*et al.\*, 2005](#)).

Archival tags record data from onboard sensors that allow, for example, post hoc track reconstruction and detailed diving behaviour analysis ([Shepard \*et al.\*, 2006](#)). These tags can collect data such as light level, direction heading and sea temperature which can be used determine an animal's geographical location using light-level geolocation (see [Sims \*et al.\*, 2006b](#)) or dead reckoning (see [Wilson \*et al.\*, 2008](#)), record environmental conditions at the animal location (such as temperature, salinity and light) and monitor energy acquisition that is, feeding (using stomach/oesophageal temperature or inter-mandibular angle sensors) and expenditure (motion sensors and heartbeat frequency). Indeed, archival tags have been developed to record almost every aspect of an individual's daily life, including gut evacuation rates via a cloacal opening/closing sensor (for a review, see [Wilson, 2004](#)).

Furthermore, early acoustic pingers, satellite transmitters and archival tags were cumbersome, but increases in memory have been coupled with decreases in component sizes and power consumption, and therefore also unit size. Thus, the periods over which animals can be monitored have increased from hours to months whilst the sampling frequency has decreased from minutes or seconds to fractions of a second ([Wilson, 2004](#)). Despite this, the sophistication of electronic tags available for tracking or estimating geographic location and other activities, deployment times have so far been

too short for tags capable of recording variables of use in assessing the potential causes of sexual segregation, for example, prey type (Wilson *et al.*, 2002). This then represents a key deficiency in studies attempted so far: A detailed picture of movements and behaviour is singularly lacking for the majority of marine species. Moreover, despite the utilisation of state-of-the-art technology, one vital piece of information is frequently lacking from many investigative studies: the sex of the animal. This may be due to the difficulty in distinguishing (by non-invasive means) the sexes in many species (Magurran and Garcia, 2000).

Nonetheless, whilst detailed behavioural information is not always available, sexual segregation has been documented in many species of marine vertebrate to date. Here we review the evidence for and patterns of sexual segregation in marine mammals, birds, reptiles and fish.

### 3. SEXUAL SEGREGATION IN MARINE VERTEBRATES

#### 3.1. Sexual segregation in marine mammals

Like their terrestrial counterparts, sexual segregation is widespread in mammals that inhabit marine environments. There are five groups of marine mammals: sireneans (manatees and dugongs); cetaceans (whales, dolphins and porpoises); and, within the Order Carnivora, there are the pinnipeds (seals, sea lions and walruses), polar bear (Family Ursidae) and the European and South American sea otters (Family Mustelidae). This section of this chapter will examine sexual segregation in cetaceans and pinnipeds, the best studied and most speciose marine mammal groups.

##### 3.1.1. Sexual segregation in Cetacea

The order Cetacea comprises 90 species and all except 5 (the freshwater dolphins) are marine. Many cetacean species socially segregate into same age or sex groups. In 1968, Gaskin described the composition of schools of sperm whale, *Physeter macrocephalus*, the cetacean species that shows the greatest body-size dimorphism between the sexes (females 9.5–11 m, males 13–18 m: Whitehead and Weilgart, 2000). Six major social categories were identified for *P. macrocephalus*: solitary males, male pairs, schools of bachelor males, mixed-sex schools (immatures), harems (predominantly female with 1–4 large males) and nursery groups (females and their dependent offspring) (Gaskin, 1968). Subsequent studies have enhanced our understanding of the composition of these social groupings. Female sperm whales appear to maintain long-term social bonds, associating in matrilineally related units (Lyrholm *et al.*, 1999; Whitehead *et al.*, 1991). In contrast, males disperse from natal family units into bachelor schools (Whitehead and Weilgart, 2000). With increasing age and size, male sociality decreases

(Lyrholm *et al.*, 1999) and male pairs are thought to represent the final stage in the break-up of bachelor male schools into solitary animals (Gaskin, 1968). However, strong and persistent social bonds among females of a species do not form the basis for all cetacean social groupings. Female and immature northern bottlenose whales (*Hyperoodon ampullatus*) form only a loose network of associations and show no preferential associations or long-term bonds, whereas mature and subadult males form stronger associations with individuals in their own age and sex class, with associations between some males lasting for several years (Gowans *et al.*, 2001, 2008). In contrast, some species do not appear to segregate socially: Both male and female resident killer whales (*Orcinus orca*) remain in their natal group for life (Connor, 2002; Fig. 2.2).

Spatial segregation of the sexes is common in cetacean societies. Indeed, whilst male and female killer whales do not segregate socially, there is evidence to suggest that, within these natal groups, the sexes may segregate by water depth with larger males diving deeper or avoiding shallow water (Michaud, 2005). Similarly, male sperm whales are generally found in deep water, whereas females are found only rarely in waters more than 1000 m deep (Whitehead and Weilgart, 2000). Humpback whales exhibit both social and spatial sexual segregation: Maternal humpback whales (*Megaptera novaeangliae*) segregate from all other humpback whale groups, preferentially occupying shallower, nearshore waters (Clapham, 2000; Smultea, 1994). Similar patterns are also seen in the river dolphin or boto (*Inia geoffrensis*) with females and their calves moving away from rivers and into floodplain habitat as seasonal water levels increase, whereas males remain in rivers (Martin and da Silva, 2004). As well as sex differences in 'local' distribution, large-scale (e.g., latitudinal) spatial separation of the sexes is also seen.



**Figure 2.2** Resident killer whales (*Orcinus orca*) do not segregate socially: Both males and females remain in their natal groups for life. Photo courtesy of J. Eveson (Ardnamurchan Charters), with permission.

Female and juvenile groups of sperm whale are mainly found at low latitudes, remaining close to tropical breeding grounds throughout the year (Gaskin, 1973; Lyrholm *et al.*, 1999; Whitehead and Weilgart, 2000). Adolescent males disperse from these low-latitude natal family units, initially into bachelor schools, but show decreased sociality as they mature and move to higher latitudes (Whitehead and Weilgart, 2000). In addition, as breeding males (~25 years old) must migrate from high-latitude feeding grounds to tropical breeding grounds, sex differences are evident in the annual home ranges of mature individuals (Whitehead and Weilgart, 2000). Sex differences in home range size are also seen in bottlenose dolphins (*Tursiops truncatus*). In the Gulf of Mexico, females were found to utilise small core areas which they shared with other females, whilst males frequently ranged to either end of and even beyond the 40-km long study area (Wells *et al.*, 1987, 1996, cited in Connor *et al.*, 2000).

Sex differences are also seen in cetacean migration patterns. The humpback whale breeds in low-latitudes in winter, then migrates to high-latitude polar or sub-polar waters to feed in summer. Commercial whaling catches of humpback whales near winter-breeding colonies were highly skewed towards males (Brown *et al.*, 1995), yet sex ratio at birth is 1:1 (Clapham, 2000). From this, Brown *et al.* (1995) inferred that around 50% of Antarctic females remain in feeding areas throughout winter. There is even evidence of sexual segregation within migrating individuals, with males appearing on breeding grounds earlier and having longer residence times than females (Stevick *et al.*, 2003).

Finally, sex differences in foraging patterns have been documented. Stable isotope analysis has revealed that the trophic position of male beluga whales in the Estuary and Gulf of St. Lawrence, Canada, is higher than that of females: Males were more  $^{15}\text{N}$ - and  $^{13}\text{C}$ -enriched than females (Lesage *et al.*, 2001). Similarly, stomach content analysis revealed sex differences in the diet of common dolphins (*Delphinus delphis*) captured in Natal, South Africa. During the annual migration or 'run' of sardine (young South African pilchards, *Sardinops ocellatus*), male dolphins tended to concentrate on this single prey species, whereas the diet of females was more diverse: Mature females were the only individuals which fed on flying fish, and consumed larger, heavier prey with a greater reliance on squid (Young and Cockcroft, 1994). However, differences were also seen between females. Lactating females consumed more squid than pregnant females and a greater proportion of larger, faster-swimming fish (mackerel, *Scomber japonicus*; and elf, *Pomatomus saltatrix*) (Young and Cockcroft, 1994). Similarly, dietary differences occur between pregnant or non-lactating and lactating female harbour porpoise (*Phocoena phocoena*) and spotted dolphin (*Stenella attenuata*), with lactating females ingesting more fish in both cases (Bernard and Hohn, 1989; Recchia and Read, 1989). Lactating harbour porpoises also had a significantly higher total caloric intake than non-lactating females or mature males (Recchia and Read, 1989). In addition, there was evidence of

differences in stomach fullness between pregnant and lactating spotted dolphins (Bernard and Hohn, 1989). These latter studies suggest that factors such as an individual's reproductive status may have more influence on dietary niche specialisation than sex.

### 3.1.2. Sexual segregation in pinnipeds

Pinnipeds are marine mammals of the order Carnivora, comprising the families Odobenidae (walruses), Otariidae (eared seals) and Phocidae (true seals). Spatial separation of the sexes has been inferred from sightings of South American sea lions (*Otaria flavescens*) from fishing vessels which suggest that males move further offshore than females (Alonso *et al.*, 2000). The occurrence of sex differences in habitat use in this species has been supported by satellite-tracking studies revealing that females remain on the continental shelf, whereas males venture to the shelf break (Campagna *et al.*, 2001). Deployments of data-logging time-depth recorders and/or satellite tracking has revealed similar patterns in grey seals (*Halichoerus grypus*: Breed *et al.*, 2006) and New Zealand fur seals (*Arctocephalus forsteri*: Page *et al.*, 2005). In both cases, females remained on the continental shelf, whereas males foraged along or beyond the shelf break.

These sex differences in habitat use may be related to the breeding system: Offspring provisioning may constrain female habitat use. Indeed, foraging trip length in lactating New Zealand fur seals appears to be dictated by the fasting ability of the pups, as central place foraging females exhibit shorter foraging trip durations than unconstrained males (5 d and 9 d, respectively) (Page *et al.*, 2005). Similarly, adult female Galapagos sea lions (*Zalophus wollebaeki*) with offspring had smaller home range sizes than non-breeding females (Wolf and Trillmich, 2007). By remaining on the continental shelf, female South American sea lions remained close to rookeries (Campagna *et al.*, 2001) whilst female Antarctic fur seals (*A. gazella*) remain close to their South Georgia breeding colony during the post-breeding period when males head south towards the South Orkney Islands (Boyd *et al.*, 1998). Such sex differences in foraging trip locations may result in sex differences in dietary niche. For example, pre-breeding male South American sea lions travelled about twice as far east and into deeper waters than lactating females. Stomach contents analyses were consistent with these results, suggesting that females are coastal, benthic feeders whereas males are pelagic (Campagna *et al.*, 2001). However, dietary niche separation may not be solely attributable to geographic separation of foraging locations as, in some species, the sexes forage in separate regions of the water column. Male Antarctic fur seals dive deeper than lactating females and exploit prey at the bottom of the surface mixed layer of the ocean, whereas females forage within this zone (Boyd *et al.*, 1998). Similarly, male New Zealand fur seals dive deeper and for longer than lactating females (Page *et al.*, 2005).

Not all cases of dietary niche specialisation, however, are related to offspring provisioning; Sex differences occur among non-breeding individuals and in breeding individuals outside the breeding season. These differences appear to start early in life: Sex differences are seen in body composition of suckling Australian fur seal (*Arctocephalus pusillus doriferus*) pups, with females having larger body lipid stores than males (Arnould and Hindell, 2002). Furthermore, juvenile female southern elephant seals spend more time at sea than juvenile males (Field *et al.*, 2005) and post-weaning Antarctic fur seal males forage significantly further away from land and from their natal colony (Warren *et al.*, 2006).

Among mature individuals of a species, the grey seal, *Halichoerus grypus*, has been particularly well studied outside of the breeding season. Austin *et al.* (2004) found that males were more likely to display directed, long-distance travel, only returning to the Sable Island breeding colony just prior to the breeding season, whereas females were more likely to be resident, remaining close to Sable Island and making short return trips to and from a single place. *H. grypus* also exhibits sex differences in foraging behaviour. Whilst males dive deeper during foraging bouts, females spend more time diving and less time hauled-out between trips, undertaking longer bouts with a greater proportion of each bout spent at depth and with more dives per bout (Beck *et al.*, 2003b,c). However, it is likely that these sex differences in dive bout characteristics vary seasonally. Stomach temperature telemetry has revealed that, just prior to the breeding season, the number of feeding events per day was greater in males than females (by 2.2 times), as was the time associated with feeding per day (56.6 vs 43.9 min, respectively) whilst the length of time between meals was significantly less in males than females (541.4 vs 1092.6 min, respectively) (Austin *et al.*, 2006). These results support observations of significant sex differences in the seasonal patterns of total body energy in adult grey seals. Whilst females exhibit greater energy content (after accounting for body mass) throughout the year, with them regaining body energy quickly following the breeding season, males, in contrast, only gained energy just prior to the breeding season (Beck *et al.*, 2003a). Dietary analysis also suggests significant dietary segregation between male and female grey seals, with mature males eating larger and older prey than females and younger seals (<4 year) of both sexes (Hauksson and Bogason, 1997). Stable isotope analysis indicates that males feed more heavily on benthic prey, whereas adult females appear to feed more on pelagic prey (Tucker *et al.*, 2007). Similar analysis has revealed sex differentiation in diet in hooded, *Cystophora cristata*, and harp seals, *Phoca groenlandica*, where males are more  $^{15}\text{N}$  enriched than females and the difference between the sexes increases with age (Lesage *et al.*, 2001).

Pronounced sex differences in foraging location and pattern are a characteristic of northern elephant seal distributions. Whereas males show directed movement to focal foraging areas along the continental margin,

travelling up to 21,000 km in 250 days at sea; females range across a wider area of the northeast Pacific Ocean but cover only about 18,000 km over 300 days (Le Boeuf *et al.*, 2000; Stewart and DeLong, 1995). On reaching the continental margin, males exhibit flat-bottomed dives and feed on benthic prey (Le Boeuf *et al.*, 2000). In contrast, females did not proceed directly to a particular site, but searched for prey whilst in transit and apparently pursued prey when they encountered it, as inferred from jagged bottom dives which tracked the sound scattering layer presumably comprising patchy, vertically migrating, pelagic prey in the water column (Le Boeuf *et al.*, 2000). California sea lions also exhibit geographical segregation during the non-breeding season. Only adult and subadult males are encountered on southern Vancouver Island as females do not venture north of central California (Morejohn, 1968; Orr and Poulter, 1965, cited in Bigg, 1973). Similarly, female harbour seal (*Phoca vitulina*) foraging trip duration and range are significantly shorter than that of males (Thompson *et al.*, 1998).

Sex differences are also seen in the terrestrial habitat use of pinnipeds. The sexes are often segregated during the breeding season, for example, some common seal, *Phoca vitulina*, haul-out groups are male dominated whereas others comprise mostly females with pups (Thompson, 1989). Similarly, ringed seals (*Pusa hispida*) in their fast-ice breeding habitat segregate by age and by sex. Adult females occupy the inner, most stable ice areas, subadults predominate in the outer parts of the fast-ice, where the ice conditions are more unstable, and adult males are scattered across these two areas (Krafft *et al.*, 2007). By contrast, it is male Galapagos sea lions that are found further inshore. In this species, habitat use is influenced by the costs of locomotion and thermoregulation, thus, flat, shady habitats directly adjacent to the sea are preferred over inland habitats which offer only shade. Mature females are generally found in the optimal habitat. Only a small number of large territorial males manage to establish semiaquatic territories, a pattern of sexual segregation which, whilst more pronounced during the reproductive period, still occurs during the non-reproductive period (Wolf *et al.*, 2005). As one might expect, sex differences are also seen in terrestrial habitat use during the pupping season, when female common seals are seen to haul out more frequently than males (Thompson *et al.*, 1997). However, perhaps less expected was that sex differences in the distribution of common seals were evident during the annual moult. This event occurs shortly after weaning and, whereas males haul out every day at the beginning of moult (to increase skin temperature and therefore to speed up the moult), females spend more time at sea (Thompson *et al.*, 1989).

To summarise, sexual segregation is widespread in mammals that inhabit marine environments. In many cetacean societies, social groups are often based around bonds between females, with males breaking off from maternal groups at adolescence to form male coalitions or to remain solitary. However, male-biased social groupings also occur and in some species, the



males remain in the natal group for life. In marine mammals in general, spatial sexual segregation is commonplace. At the local scale, sex differences are seen in attributes such as depth use and distance from the shore. However, spatial segregation also occurs on latitudinal scales, leading to gross differences in the home ranges of the sexes and possibly even sex-specific migrations. These spatial separations of the sexes appear to be largely attributable to offspring provisioning, with females remaining either close to pupping areas or to environments where offspring survival is enhanced (i.e., away from predators or strong currents). Sex differences are also seen in foraging behaviour. As previously mentioned, the sexes may forage in different areas and at different depths, but sex differences are also seen in dive duration and prey species consumed. Reproductive status may be the proximate or ultimate cause of these differences due to the constraints of offspring provisioning on foraging range and the disparity in the time needed for each sex to prepare to the following mating season. However, as sex differences are also seen in the behaviour of immatures, reproductive status cannot explain sexual segregation in all species.

### 3.2. Sexual segregation in marine birds

Despite a general wealth of information on the habits of terrestrial birds, relatively little is known about the behaviour of marine birds. The scarcity of information on sex differences in the behaviour of marine birds may also be partly attributable to a general difficulty in identifying the sex of individuals based on external morphology (Catry *et al.*, 2005; Gilardi, 1992). Indeed, most information which exists on sexual segregation in seabirds concerns the wandering albatross (*Diomedea exulans*) and the northern giant petrel (*Macronectes halli*), two species with particularly marked sexual size dimorphism (Gonzalez-Solis, 2004; Xavier and Croxall, 2005). This section of this chapter starts by discussing sexual segregation in wandering albatross and the northern giant petrel, and then compares and contrasts the behavioural patterns observed in these two species with those patterns documented in several other species of seabird.

The wandering albatross exhibits sex differences in the spatial distribution of foraging locations. By satellite-tracking foraging birds commuting to and from breeding colonies, it has been demonstrated that females, the smaller sex, frequently commute to the shelf edge and feed in oceanic waters, whereas males spend more time on the shelf or shelf slope (Weimerskirch *et al.*, 1997; Xavier *et al.*, 2004). Female wandering albatross make longer foraging trips, travel greater distances and forage further from the colony (Xavier and Croxall, 2005). Thus, it seems the foraging effort of females far exceeds that of males (Salamolard and Weimerskirch, 1993). Nonetheless, males apparently forage more efficiently than females (Weimerskirch *et al.*, 1997). As both sexes feed on the same prey types (squid and other



cephalopods) (Xavier and Croxall, 2005), these results suggest that resource quality differs between the foraging locations of the sexes: It is possible that the habitats exploited by males are more profitable than those used by females. Nevertheless, a more significant relationship between trip duration and mass gain for females suggests that, whilst the female foraging areas may provide lower energy yield, they were perhaps more predictable and less patchy than male foraging areas (Weimerskirch, 1995).

Male and female northern giant petrels also exploit spatially separated foraging grounds and, like wandering albatross, differential habitat exploitation leads to fundamental differences in distance covered, spatial pattern and predictability of resources exploited, imposing different foraging strategies on each sex (Gonzalez-Solis and Croxall, 2005). However, differential habitat exploitation in northern giant petrel has resulted in sex differences in diet. Whilst scavenging on coastal penguin and seal carcasses is the preferred foraging strategy of both sexes, they also consume burrowing petrels, fish and cephalopods (Gonzalez-Solis *et al.*, 2000; Hunter and Brooke, 1992). Satellite tracking and direct observation of breeding birds has revealed that males primarily forage coastally, scavenging carrion on beaches, but females have a more pelagic distribution and consume larger proportions of fish and cephalopods (Gonzalez-Solis, 2004; Gonzalez-Solis and Croxall, 2005; Gonzalez-Solis *et al.*, 2000, 2002; Hunter and Brooke, 1992). As with wandering albatross, whilst female foraging effort (flight speed, distance covered, duration of foraging trips) is greater, foraging efficiency (proportionate daily mass gain whilst foraging) is significantly greater for males (Gonzalez-Solis *et al.*, 2000).

Like the northern giant petrel, male southern giant petrels, *Macronectes giganteus*, also forage closer to the coast than females (Gonzalez-Solis and Croxall, 2005). However, separation in diet is less marked than in the northern giant petrel (Hunter and Brooke, 1992), its sister species which is more sexually size dimorphic. Spatial separation of the sexes also occurs in Buller's albatrosses (*Diomedea b. bulleri*) and in Magellanic (*Spheniscus magellanicus*) and Adélie penguins (*Pygoscelis adeliae*). Satellite tracking revealed that, whilst distances covered during foraging trips are similar between male and female Buller's albatrosses, females foraged further from breeding colonies and in different sectors to males (Stahl and Sagar, 2000). Stable isotope analysis of Magellanic penguin males revealed that they consume fish and squid, foraging further inshore and taking significantly more anchovies than other prey species (Forero *et al.*, 2002). Female Adélie penguins also ranged greater distances than males, undertaking longer foraging trips and, like northern giant petrels and magellanic penguins, exhibited sex differences in diet: Females consumed larger quantities of krill, whereas males fed more extensively on fish (Clarke *et al.*, 1998). However, Volkman *et al.* (1980) attributed this heterogeneity in diet to a highly synchronous breeding cycle

(the male takes the first 2-week incubation shift) and short-term differences in food availability rather than differential habitat exploitation.

Despite the aforementioned studies, it is not always male seabirds that stay closer to the breeding colony. Male brown boobies (*Sula leucogaster*) undertake significantly longer foraging trips than females, a behavioural pattern which may be explained by reversed sexual size dimorphism in this species (the females are larger than the males) (Lewis *et al.*, 2005). However, South Georgian shags, *Phalacrocorax georgianus*, exhibit male-biased size dimorphism and yet males spend more time flying, diving and on the sea than females, which spend more time at the nest (Wanless *et al.*, 1995). Indeed, contrasting strategies are even seen in closely related species. Black-browed (*Thalassarche melanophrys*) and grey-headed (*T. chrysostoma*) albatross exhibit male-biased size dimorphism and in both species the sexes exploit largely mutually exclusive core foraging ranges. However, in black-browed albatross, the female travels further from breeding colonies than males, but in grey-headed albatross males travel further than females (Phillips *et al.*, 2004). The pattern of sexual segregation may also vary geographically. For example, whilst Lewis *et al.* (2005) found male brown boobies foraged further off-shore than females in the Central Pacific Ocean, Gilardi (1992) found the opposite pattern in the eastern Pacific Ocean.

Another form of spatial sexual separation seen in seabirds is segregation of foraging location by water depth, a pattern which is seen in king cormorants (*Phalacrocorax albiventer*), blue-eyed Crozet shags (*Phalacrocorax melanogenis*) and blue-footed boobies (*Sula nebouxii*). In both king cormorants and blue-eyed Crozet shags, where the body size of males exceeds that of females, the male dives deeper than females (Cook *et al.*, 2007; Kato *et al.*, 2000). Similarly, in the blue-footed booby, which exhibits reversed sexual size dimorphism, it is the larger female that dives significantly deeper than the male (Zavalaga *et al.*, 2007). However, sexual size dimorphism cannot be the only explanation for sex-specific diving behaviour in seabirds as the monomorphic northern gannet, *Morus bassanus*, also exhibits sex differences in diving behaviour whilst foraging. Female gannets are more selective and undertake longer, deeper dives and spend more time on the surface (Lewis *et al.*, 2002). Sex differences in dive depth do not always translate into sex differences in diet or provisioning as compensation in terms of increased dive frequency (female king cormorant: Kato *et al.*, 2000) or increased time allocated to diving (female blue-eyed Crozet shags: Cook *et al.*, 2007) may occur. However, there is evidence to suggest that the deeper diving, larger sex, whilst consuming the same prey species, consumes larger individuals (Cook *et al.*, 2007; Zavalaga *et al.*, 2007).

Spatial sexual segregation may be temporal in some species. Blue-eyed shags (*Phalacrocorax atriceps*), South Georgian shags (*P. georgianus*), Crozet shags and king cormorants, all exhibit diurnal temporal separation of foraging with females foraging in the morning and males foraging in the

afternoon (Bernstein and Maxson, 1984; Cook *et al.*, 2007; Kato *et al.*, 2000; Wanless *et al.*, 1995). At the larger temporal scale, male wandering albatross, *Diomedea exulans*, arrives at the South Georgia breeding colony 2 weeks earlier than females (Tickell, 1986, cited in Xavier and Croxall, 2005).

As exemplified by the above-mentioned studies, much of what is known about seabird sexual segregation is generally restricted to observations made during the breeding season. This is because seabirds must return to a breeding colony to nest. However, with advances in miniaturisation of data-logging and satellite transmitter technology, our knowledge of seabird life history is expanding beyond terrestrial/maritime observations made during breeding to the foraging ecology of non-breeding birds. In addition, the availability of small, long-life batteries in devices has enabled studies to extend well into the overwintering period.

Evidence suggests that wandering albatross also segregate sexually between breeding attempts. Weimerskirch and Wilson (2000) demonstrated spatial separation of the sexes during the non-breeding period, with individuals restricting movements to preferred sectors to which they probably return year after year. Females tracked from the Crozet Islands in the southern Indian Ocean used tropical and subtropical waters south of Madagascar, whereas males occupied sub-Antarctic and Antarctic waters just north of the pack ice. In contrast, the activity and pelagic movements of northern giant petrels were more similar between the sexes outside breeding seasons, although there was evidence to suggest that the greater use of coastal habitats by males persists throughout the year (Xavier and Croxall, 2005).

Sexual segregation of overwintering birds is also characteristic of wading species. For example, oystercatchers, *Haemalopus ostralegus*, exhibit sexual segregation in foraging niche as males chiefly prey upon near surface, mudflat species such as cockles and mussels whereas females consume more deep-living prey (Durell *et al.*, 1993; Swennen *et al.*, 1983). In contrast, overwintering western sandpiper, *Calidris mauri*, exhibits spatial segregation at a much coarser spatial scale: females tend to winter south of males (Mathot *et al.*, 2007).

In summary, spatial segregation of the sexes is widespread in marine birds. In breeding populations, the smaller sex will generally forage further offshore. Spatial separation of the foraging niche of the sexes may lead to sex differences in diet, whether in prey species or prey size. Sex differences in foraging efficiency may also result, although apparently at the cost of resource predictability. Sexual segregation of foraging niche appears largely attributable to sexual size dimorphism, with the smaller sex species foraging further offshore. Similarly, as is the case with marine mammals, the larger sex is generally able to forage at greater depths. However, there are exceptions. Sex differences are seen in the diving behaviour of monomorphic species and in some species the larger sex will undertake longer foraging

excursions, opposite patterns are seen in closely related species and geographical variation also occurs. Therefore, sexual size dimorphism is unlikely to be the only explanation for segregation in marine birds.

### 3.3. Sexual segregation in marine reptiles

The diversity of present-day marine reptiles is low, being limited to only three groups: sea snakes, marine turtles and the marine iguana. Yet, representatives of all three groups segregate sexually. All reptiles are air breathers and thus must periodically return to the water's surface. Whilst this aids the study of these animals, it does not limit marine reptile distribution to coastal waters: Marine turtles migrate across oceans (Hays *et al.*, 2004) and exhibit shifts in behaviour at the ocean-basin scale (Hays *et al.*, 2006). Many marine reptiles must return to land to breed, offering an opportunity for the attachment of tracking devices. However, the need to return to land is not absolute. Whilst some species rely on the marine environment only for food (e.g., marine iguanas), the wholly marine Hydrophiinae (a subgroup of the sea snakes) spend their entire lives in the sea where they give birth to live young.

Within marine reptile breeding populations, sex differences in habitat use appear widespread. For example, the turtle-headed sea snake, *Emydocephalus annulatus*, exhibits male–female differences in habitat occupancy. This species consumes the eggs of damselfish and blennies which nest in coral rubble substrates and the habitat use of juvenile and adult females, *E. annulatus*, which spend most of their time foraging, closely matches the distribution of the nests of these fish (Shine *et al.*, 2003). However, breeding males do not feed and shift their behaviour towards mate searching: They actively court any adult female they encounter, swim more rapidly and are found across a broader range of habitat types (Shine *et al.*, 2003).

Turtles, probably the best studied of the marine reptiles, also exhibit sex differences in behaviour during the breeding season. Green turtles (*Chelonia mydas*) on mating grounds at Ascension Island in the mid-Atlantic Ocean display sex differences in activity patterns. With the aid of satellite-tracking technology, Hays *et al.* (2001) have demonstrated that the dive duration of male green turtles (typically <15 min) is much shorter than that of females during the internesting period, reflecting greater levels of activity. A similar pattern has been observed in loggerhead turtles (*Caretta caretta*) in the Mediterranean (Schofield *et al.*, 2006). Spatial sexual segregation of green turtles on breeding grounds off Australia has also been documented. Booth and Peters (1972) made underwater observations of a section of lagoon occupied only by resting females. Unmated males patrolled the area but did not attempt to mate with females within the lagoon. As soon as a female left the lagoon, she was immediately courted by the circling males. Mating pairs entered the lagoon, often followed by an escort of up to five males, but, whilst the mating pair were open to 'attack' by a member of the escort, these

unattached males ignored other unmated females within the sheltered area. Similarly, the identification of an area of male predominance within the green turtle breeding areas of Oman has been suggested to represent a designated mating ground (Ross, 1984).

At the end of the breeding season, both male and female green turtles migrate away from nesting grounds to distant foraging grounds. There is a sex difference in the timing of this migration: Male green turtles leave the nesting grounds much earlier than females (Godley *et al.*, 2002), but there is currently no evidence of sexual segregation at any other time in the life cycle of marine turtles (G. Hays personal communication).

In contrast, sexual segregation outside the breeding season has been documented in both marine snakes and the marine iguana. The Galapagos marine iguana, *Amblyrhynchus cristatus*, which feeds exclusively on marine algae, exhibits sex differences in foraging location. Whilst most individuals obtained their algal diet from foraging in intertidal areas which were only accessible for a short time each day at low tide, large males were able to feed independently of the tidal cycle by diving to forage in subtidal areas (Wikelski and Trillmich, 1994). High grazer density in intertidal areas and a gradient of increasing availability of food with distance down the shore enabled male subtidal foragers to consume more macrophytic algae per unit effort than intertidal foragers, thereby increasing intake rates (Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994). Intertidal foragers compensated for lower intake rates by foraging at every opportunity (every day, whereas subtidal foragers fed every second day) and by increasing bite rate (Wikelski and Trillmich, 1994; Fig. 2.3).

Sex differences are also present in the diving behaviour of the yellow-lipped sea krait, *Laticauda columbrina*. This species exhibits substantial sex



**Figure 2.3** Only large male Galapagos marine iguanas, *Amblyrhynchus cristatus*, dive to forage subtidally. Photo courtesy of M. Evans, with permission.

differences in body size, with males being about one-third the bulk of females (Pernetta, 1977). Female-biased size dimorphism is common in snakes due to the necessity for females to carry numerous large eggs and which, at least in part, may enable females of several species to forage deeper (Shine and Wall, 2005). However, as this species also exhibits dietary niche specialisation of the sexes (males consume smaller, reef-flat species such as morays, whilst females consume larger species such as conger eels associated with the waters adjacent to the reef: Pernetta, 1977; Shetty and Shine, 2002), Pernetta (1977) suggested that female-biased dimorphism based on reproductive strategy has been reinforced by enhanced survival of larger and larger females that can exploit previously unused food resources. However, it is likely that significant sexual dimorphism in head morphology plays a significant role (Shine and Wall, 2005). Female yellow-lipped sea kraits have longer, wider heads than males of same length, and have disproportionately larger jaws, characteristics which increase the upper size limit of prey that can be consumed (Shetty and Shine, 2002). Sex differences were also observed in stomach fullness: Females generally consumed only one prey item per foraging trip (compared to multiple items in males), and contained prey more frequently than males (Pernetta, 1977; Shetty and Shine, 2002).

Taken together these studies show that sexual segregation is seen in all three groups of present-day marine reptile. Sex differences in behaviour are particularly apparent within breeding populations. Whilst males are actively searching for mates, females appear to range less, matching their distribution to that of their prey or aggregating with other females. However, sexual segregation of foraging niche is also seen outside the breeding season. Once again, this appears to be largely attributable to sexual size dimorphism, with the larger sex diving deeper to consume larger prey.

### 3.4. Sexual segregation in marine fish

With over 15,000 known species, marine fish are the most diverse group of marine vertebrates. Fish are considered wholly aquatic since completion of their lifecycle does not rely on the terrestrial environment and, unlike all species discussed thus far, they are not air breathers. As a result, our understanding of the behavioural ecology of this group of marine vertebrates, relative to their abundance and diversity, is particularly limited. Relatively more is known about the behavioural ecology of freshwater fishes. Indeed, the Trinidadian guppy, *Poecilia reticulata*, is one of the only aquatic vertebrates for which hypotheses about sexual segregation have been investigated (see: Croft *et al.*, 2004, 2006). This part of this chapter examines sexual segregation in both marine teleosts (bony fishes) and marine elasmobranchs (sharks and rays). Relatively more is known about sexual segregation in elasmobranchs, perhaps due to the ability to determine elasmobranch gender based on external morphology alone; male

elasmobranchs possess external paired intromittent organs called claspers, which are used by the male to transfer sperm into the female cloaca.

### 3.4.1. Sexual segregation in teleost fish

One of the best documented sex differences in behaviour among marine teleost fish is sex-specific foraging behaviour. For example, male dolphinfish, *Coryphaena hippurus*, consume proportionately more active, fast swimming species such as flyingfish and squid than do females (Oxenford and Hunte, 1999). Similarly, female clingfish, *Diademichthys lineatus*, eat shrimp eggs and bivalves more frequently than adult males (Magurran and Garcia, 2000) whilst female dab, *Limanda limanda* feed on significantly more ophiurids (brittlestars) than males (Temming and Hammer, 1994). However, sex differences in the foraging behaviour are not limited to dietary preferences in this latter species. Females dab had significantly more food in their stomachs than males of the same size, and there were differences in the diurnal feeding rhythm between males and females, with females feeding in the morning and males in the afternoon (Temming and Hammer, 1994). Sex differences have also been documented in the time allocated to feeding behaviour. For example, male sandperch, *Parapercis polyophtalma*, spent much less time foraging and more on territorial and social activities than females. Male and female sandperch foraged in the same habitats and consumed similar prey items, but female bite rates were 3 times greater, resulting in a mean weight of food per stomach that was 2.4 times greater than that in males (Sano, 1993). Similarly, the bite rate of the female sharknose cleaning goby, *Elacatinus evelynae*, also exceeds that of males as a result of spending 5 times longer cleaning (Whiteman and Côté, 2002). However, feeding rate does not appear to be fixed and, in the case of the sharknose cleaning goby, can be influenced by the presence of the opposite sex: female cleaning rate was significantly lower when males were present, whereas males cleaned for longer and took more bites when females were present (Whiteman and Côté, 2002).

Sex differences are also apparent in the spatial distribution of some teleost species. For example, in American eel, *Anguilla rostrata*, the sexes differ in habitat choice and geographic distribution. Male eels are primarily found in south-eastern U.S. estuaries, where they are close to the spawning areas of the Sargasso Sea, whereas females are more widely distributed both within rivers and along the eastern American coastline (Magurran and Garcia, 2000). In Atlantic salmon, *Salmo salar*, males undertake their seaward migration earlier than females (Jonsson *et al.*, 1990). Sex differences in occupancy of spawning grounds occur in Atlantic cod, *Gadus morhua*. Males remain on spawning grounds whilst females move in and out of these male-dominated spawning aggregations when ready to release an egg batch (Robichaud and Rose, 2003).



Clearly, for the majority of marine teleost species virtually nothing is known about sexual segregation, that is, whether it is present in the first place and if it is, what are the patterns and why may they occur? As mentioned previously, this has much to do with the difficulties of sexing teleosts where no external clues as to sex are present. Despite this, it appears that males and females within a teleost species do differ in many regards, not least in their foraging behaviour, so it may be expected that sexual segregation by habitat, for example, may indeed be quite common in this taxa.

### 3.4.2. Sexual segregation in elasmobranch fish

There are about 900 extant species of elasmobranch, among which sexual segregation is considered to be a general characteristic (Springer, 1967). In a recent review of sexual segregation among sharks, Sims (2005) noted evidence for sexual segregation in 38 out of the 400 or so extant shark species. Whilst it would appear that a behaviour exhibited by 10% of all available shark species does not constitute a general behaviour across all elasmobranchs, this small proportion reflects how little we currently know about the general biology of the majority of species. Elasmobranchs are difficult to observe due to the relative inaccessibility of the marine environment. However, of the species which have been studied in sufficient detail, sexual segregation is a general characteristic. Despite its widespread nature, sex differences in shark and ray behaviour have not been investigated until relatively recently.

The first evidence for sexual segregation in elasmobranch populations came from fisheries observations which recorded unequal sex ratios in trawl catches. An 'excess' of female thornback ray, *Raja clavata*, was reported in catches whilst males were thought to outnumber females in the starry ray, *Amblyraja radiata* (Day, 1884). On investigating Scottish landings of Rajiformes, Fulton (1890, 1903) also noted a bias towards females in thornback ray (65.7% female), and, additionally in the sandy ray, *Leucoraja circularis* (61.7%), and partially in the common skate, *Dipturus batis* (51.3%). However, unlike the observations of Day (1884), female starry ray were more frequent than males (54.7%) (Fulton, 1890, 1903). Indeed, the only elasmobranch species investigated for which Fulton did not report a female-biased sex ratio was the shagreen ray (*L. fullonica*); the sex ratio was equal based on eight individuals examined (Fulton, 1903). Unequal sex ratios were also reported in landings of Canadian Rajiformes. Females dominated landings of little skate (*Leucoraja erinacea*) by 55%, winter skate (*L. ocellata*) by 61%, thorny skate (*A. radiata*) by 60% and barndoor skate (*Dipturus laevis*) by 65% (Craigie, 1927).

Unequal sex ratios have also been reported for the dogfishes. Ford (1921) noted male dominance in landings of smoothhound, *Mustelus vulgaris*, in the western English Channel inshore fisheries off Plymouth, United Kingdom,



whilst autumn landings of spurdog, *Squalus acanthias*, were female dominated (up to 92%). Similarly, females dominated Canadian spurdog landings (68% female) (Craigie, 1927). Deviation from a 1:1 sex ratio was also observed in the Pacific dogfish, *Squalus suckleyi*, with the direction of the bias varying between locations and possibly also between seasons (Craigie, 1927).

Despite widespread reporting of biased sex ratios in elasmobranch landings and the different direction of this bias apparent between geographical locations, Ford (1921) and Steven (1933) were the only researchers to investigate whether these inequalities reflected a bias in the operational sex ratio or differential behaviour of the sexes. Segregation by age is thought to be a universal feature of shark populations (Springer, 1967) and it is thought that size-assorted schools of active shark species may be maintained by the different swimming speeds that can be sustained by different-sized individuals (Wardle *et al.*, 1996). By examining the catches of individual vessels, Ford (1921) and Steven (1933) were able to identify that, where catches were composed of immature individuals, the sexes occurred in approximately equal proportions, indicating no deviation from a 1:1 sex ratio at birth. However, biased sex ratios did occur in catches of mature specimens.

Steven (1933) recorded a pattern in the landings of thornback ray within the fishing season (January–March), as determined from availability of good size fish on the fishing grounds. Females predominated in inshore areas throughout the majority of the season, but declined towards the end of March when male numbers began to increase, which was suggested to indicate male migration into inshore areas (Steven, 1933). Ford's (1921) Plymouth investigations also revealed sex-specific seasonal migrations into inshore areas. Several thousand specimens of lesser spotted dogfish (*Scyliorhinus canicula*) were examined at Plymouth and showed that males dominated catches during winter (65% of numbers caught), whereas females marginally predominated in summer (58%).

Ford (1921) and Steven (1933) were in broad agreement that sexual segregation of adult fish, and the consequential sampling of unisexual aggregations, provided the most satisfactory explanation for sex-biased landings. Therefore, it appeared there was sexual segregation present in the species studied as a consequence of sex differences in behaviour. These changes over time were interpreted as being the result of same sex individuals clustering more often in preferred habitat rather than in other available habitats. This form of segregation has been termed 'geographical' sexual segregation (Backus *et al.*, 1956).

Over the next 40 years, numerous studies similarly documented unequal sex ratios in fishery and fishery-independent catches of sharks. Geographical segregation was shown to be present in oceanic whitetip sharks (*Carcharhinus longimanus*) in the Gulf of Mexico (Backus *et al.*, 1956) and in school

sharks (*Galeorhinus galeus*) off southern Australia (Olsen, 1954). As illustrated by Ford and Steven (Ford, 1921; Steven, 1933) in thornbacks and lesser spotted dogfish, geographical segregation in elasmobranchs is often temporal in nature: for example, male cownose rays, *Rhinoptera bonasus*, dominate in Chesapeake Bay from June to early July and gravid females from late July through to mid-September (Smith and Merriner, 1987). Temporal geographic segregation is often characterised by seasonal movements of mature females into shallow water. Indeed, landings of *G. galeus* off California showed that not only did catch composition vary by area with respect to the ratio of sexes present, but also with depth, with females occurring in shallower water than males (Ripley, 1946). This probably accounts for the fact that gravid females of some shark species undertake long-distance migrations to sheltered nursery grounds to give birth away from adult sharks (Feldheim *et al.*, 2002). In these locations, females do not feed and do not stay in the area. Indeed, a further explanation for age segregation in sharks may be to reduce the risk of cannibalism and depredation of juveniles and sub-adults by mature individuals (Ebert, 2002; Morrissey and Gruber, 1993; Snelson *et al.*, 1984). The migration of gravid females to designated inshore pupping grounds has been documented in oceanic white-tip shark (Backus *et al.*, 1956), leopard sharks (*Triakis semifasciata*: Ebert and Ebert, 2005), Caribbean sharpnose sharks (*Rhizoprionodon porosus*: Mattos *et al.*, 2001) and spurdog (*Squalus acanthias*: Hickling, 1930).

Spurdog have attracted particular attention. This pelagic-demersal species forms large schools, which are targeted by commercial fishers (Compagno, 1984). Ford (1921) collected data on the number of spurdog landed at Plymouth, England, and found that 92% of those captured in November were mature females. Over the following year, records showed that the sex ratio of landings varied widely, with four categories of schools evident: large females that were mostly gravid, exclusively mature males, immature females and immature males and females in equal number. Ford (1921) concluded that inequality in sex composition of the schools was largely due to the tendency of individual, *S. acanthias*, to school with others of similar size and sex. This type of sexual segregation was termed 'behavioural' (Backus *et al.*, 1956).

However, sexual segregation is by no means restricted to mature individuals. Klimley (1987) noted that female scalloped hammerhead sharks, *Sphyrna lewini*, moved away from inshore nursery areas at a younger age than males. This early offshore migration was followed by an apparent increased consumption of pelagic prey and greater predatory success, as inferred from larger stomach content masses in females than in males of the same size. Similarly, dietary differences between the sexes are not only seen in juveniles: Sex differences in the diet blue sharks, *Prionace glauca*, have been interpreted to result from sex-specific preferences in foraging locations (McCord and Campana, 2003).

Temperature may also influence the habitat selection of the sexes. Grey reef sharks, *Carcharhinus amblyrhynchos*, form female-only aggregations in the shallow lagoons of Johnston Atoll in the Central Pacific Ocean. The water temperatures in the lagoons were 1–2 °C warmer than in the open ocean and segregation was maximal at the warmest time of the day (Economakis and Lobel, 1998). Sexual segregation in white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia, may also be related to temperature. Males were more prevalent during winter, spring and summer, with a peak in sightings during September when water temperatures were lowest (males observed within the temperature range 14.3–17.8 °C), whereas females predominated during autumn when water temperatures were highest (females present within the temperature range 15.7–18.1 °C) (Robbins, 2007). The selection of shallower habitats by female nurse, *Ginglymostoma cirratum*; tiger, *Galeocerdo cuvier* and blue sharks (Carrier *et al.*, 1994; Heithaus *et al.*, 2006; Litvinov, 2006) may also be related to sex-specific temperature preferences.

By the end of the 1960s, there was a burgeoning literature of observations of sexual segregation in sharks (Bullis, 1967; Springer, 1967). Further studies in the 1970s and 1980s expanded the number of species for which sexual segregation was observed or suspected (e.g., *Carcharias taurus*: Gilmore *et al.*, 1983, *Sphyrna lewini*: Klimley, 1985, *Carcharhinus amblyrhynchos*: McKibben and Nelson, 1986, *Sphyrna tiburo*: Myrberg and Gruber, 1974, *Prionace glauca*: Pratt, 1979; Stevens, 1976). Despite this, by 1987, the causes of sexual segregation had not been formally investigated in any species, although differences in swimming capabilities, dietary preferences, absence of aggression between similar-sized sharks, or migration of gravid females to nursery grounds were all forwarded as possible explanations (Klimley, 1987; Springer, 1967).

In summary for fish, within marine teleost fish, sexual segregation has been observed in foraging behaviour as well as the spatial distribution of breeding populations. However, these observations are limited to only a few species, primarily due to an inability to identify the sex of the majority of teleost fish based on external morphology. In contrast, sexual segregation is considered a general characteristic of elasmobranch populations. Several hypotheses have been forwarded to account for sexual segregation in this group of marine vertebrates. 'Geographical sexual segregation' is thought to result from sex differences in habitat preferences, for example, when females migrate to designated inshore nursery areas for oviposition/parturition. 'Behavioural sexual segregation' also occurs. Unisexual schools are thought to form in schooling species as a result of differences in the swimming capabilities of the sexes, although an absence of aggression between individuals of a similar size may also be important. Yet, despite the generality of sexual segregation among elasmobranches, the underlying causes of sexual segregation remain to be rigorously tested in any species.

## 4. MECHANISMS UNDERLYING SEXUAL SEGREGATION: HYPOTHESES

Whilst sexual segregation is a widespread phenomenon among animals, the underlying causes remain poorly understood. Much attention has been devoted to understanding sexual segregation in group-living ungulates, particularly among species within Ruminata. These investigations have inspired several explanatory hypotheses, summarised below, with assumptions and predictions summarised in [Table 2.1](#). Sexually segregating ungulates typically exhibit sexual dimorphism with respect to body size (i.e., there is a significant difference between the sizes of mature males and females), with male-biased size dimorphism being the prevalent form. Therefore, the ecological implications of sexual size dimorphism feature heavily in hypotheses attempting to account for sexual segregation. As such, this may complicate the interpretation of predictions from hypotheses when investigating species which exhibit female-biased sexual size dimorphism, or are monomorphic with respect to body size. In addition, as these conceptual models have been developed from research which primarily focuses on endothermic vertebrates, the assumptions and prediction of the hypotheses necessarily relate to specific features of these organisms. Interpreting sexual segregation in ectotherms within the same framework proves difficult, particularly as not all of the sexual segregation hypotheses are mutually exclusive. As a result, the assumptions and predictions of some of the hypotheses have been re-framed where necessary to apply more closely to specific features of ectotherm life history and ecology. It is our view that incorporation of ectotherms within the existing (mammal-focused) theoretical framework will help by translating and broadening the application of the existing hypotheses.

### 4.1. Predation-risk hypothesis (reproductive strategy hypothesis)

The predation-risk hypothesis focuses on sex differences in the way individuals strive to maximise their lifetime reproductive success. It is assumed that females and/or their offspring are more at risk to predation than males. These sex differences in predation risk occur due to sexual dimorphism in body size, or because gestation and/or parental care (supervision of small, slow-moving, predator naïve offspring) impede predator evasion. Therefore, female habitat choice is primarily driven by a necessity to reduce predation risk, maximising offspring security, even at the cost of sub-optimal foraging conditions. On the other hand, male habitat choice is driven by resource availability. Males strive to maximise future mating opportunities and thus must be able to compete successfully for mates. Therefore, males

**Table 2.1** Summary of assumptions and key predictions of the hypothesis forwarded to account for sexual segregation

Hypothesis	Assumptions	Predictions	Case studies
Predation-risk hypothesis	Female reproductive success is determined by offspring survival	Females select habitats that enhance offspring survival	Leopard sharks (Ebert and Ebert, 2005) Spotted dolphins (Bernard and Hohn, 1989) Elephant seals (Le Boeuf <i>et al.</i> , 2000)
	Male reproductive success is influenced by size and/or condition	Males exploit areas where resources are abundant	
	Offspring (and the smaller sex) are more vulnerable to predation	Provisioning parents and offspring occupy 'safer' habitats	
Forage selection hypothesis	The larger sex has greater absolute metabolic requirements, but more efficient digestion	The larger sex exploits areas where resources are abundant, the smaller sex exploits areas with high-quality resources	Grey seals (Austin <i>et al.</i> , 2006) Common dolphins (Young and Cockcroft, 1994) Northern giant petrels (Gonzalez-Solis, 2004)
	Reproductive females must satisfy the nutritional demands of gestation and lactation	Reproductive females segregate from both males and non-reproducing females	
	Sex-specific morphological adaptations influence foraging efficiency	More efficient foragers competitively exclude other individuals from preferred resources	

(continued)

Table 2.1 (continued)

Hypothesis	Assumptions	Predictions	Case studies
Activity budget hypothesis	Large differences in activity budgets, resulting from sexual dimorphism in body size and/or reproductive investment make synchrony of behaviour costly in group-living species and leads to divergent habitat requirements in solitary species	In group-living species, animals with similar activity budgets will form groups in solitary species, size- or reproductive mode-specific habitat use is exhibited	South Georgian shags (Wanless <i>et al.</i> , 1995) Marine iguanas (Wikelski and Trillmich, 1994) Wandering albatross (Phillips <i>et al.</i> , 2004)
Thermal niche–fecundity hypothesis	Ambient temperature influences fecundity and sex differences exist in the temperatures at which fecundity is maximised; for example, optimal temperatures for sperm and egg production differ	The sexes select different thermal habitats in an effort to maximise reproductive success	Cod (Robichaud and Rose, 2003) Grey reef shark (Economakis and Lobel, 1998)
Social factors hypothesis	Social affinity (intra-sexual cooperation or information transfer), social aversion (avoidance of aggression) or a combination of both determine social groupings	Groups comprise individuals of varying ages (experience) or group size decreases with age. In many cases, group members are related. The ‘aggressor’ is aggressive and dominant to the ‘avoider’	Sperm whales (Lyrholm <i>et al.</i> , 1999) Nurse sharks (Carrier <i>et al.</i> , 1994) Bottlenose dolphins (Connor <i>et al.</i> , 1992)

exploit areas with abundant, high-quality forage and engage in behavioural patterns to maximise body condition in preparation for mating, even when these behaviours increase risks of predation.

The predation-risk hypothesis is also applicable to situations where males experience higher predation rates as a result of female-biased sexual dimorphism. For example, male harbour porpoise (*Phocaena phocaena*) are found in more protected waters than the larger females which inhabit riskier habitats where they are subject to attack from white sharks and killer whales, but where they can satisfy their huge nutritional needs resulting from simultaneous pregnancy and lactation (Michaud, 2005).

As the predation-risk hypothesis focuses on reproductive strategy, we have extended the definition of the hypothesis to include situations where female habitat selection is influenced by the habitat requirements of its offspring. For example, it has been hypothesised that habitat selection in female sperm whales may be constrained by the thermal requirements of the calf, resulting in a restriction to low latitudes (Gaskin, 1973; Lyrholm *et al.*, 1999; Whitehead and Weilgart, 2000).

The adoption of a more risk-averse strategy by females may explain sex differences in the diet of dolphinfish (*Coryphaena hippurus*). A greater proportion of active, fast swimming prey species in male diets suggests intersexual differences in schooling behaviour, with males spending more time away from flotsam (Oxenford and Hunte, 1999). Sex differences in diet may also result from females, altering their behaviour to reduce predation risk to their offspring. For example, lactating spotted dolphins remain close to their calf at the surface rather than exploiting squid at depth (Bernard and Hohn, 1989). Predation risk is also thought to influence the distribution of beluga whales, *Delphinapterus leucas*. Summer aggregations of female belugas in coastal waters are thought to result from the approach of killer whales which leads to crowding close to shore (Michaud, 2005). Similarly, the selection of shallow, nearshore waters by maternal humpback whales (*Megaptera novaeangliae*) in the tropics and bottlenose dolphins of Australia has been suggested to minimise the possibility of predation by sharks and/or killer whales (Clapham, 2000; Mann *et al.*, 2000; Smultea, 1994). In contrast, it is predicted that foraging in inshore areas renders male elephant seals (*Mirounga angustirostris*) more at risk to predation by sharks and killer whales than females foraging on more patchy, pelagic prey in open water. Nevertheless, it is suggested that greater mass gain in males, indicating that they forage in more productive habitats, presumably makes this risk worthwhile (Le Boeuf *et al.*, 2000). Rather than segregating spatially to reduce predation, some species may group socially to benefit from a dilution effect. Dusky dolphins, for example, form nursery groups during surface-active feeding bouts (Michaud, 2005).

The predation-risk hypothesis also provides the most parsimonious explanation for sex differences in the spatial distribution of pinnipeds during

the breeding season, where female distribution is constrained by the necessity to provision dependent young. However, the predation-risk hypothesis may also be applicable to species which do not exhibit parental care. In several species of shark, for example, gravid females migrate to designated pupping areas, which are often sheltered, inshore areas where predation rates are low, where they give birth to live young. This behavioural pattern is seen in oceanic white-tips (*Carcharhinus longimanus*: Backus *et al.*, 1956) leopard shark (*Trikas semifasciata*: Ebert and Ebert, 2005) and lemon shark (*Negaprion brevirostris*: Feldheim *et al.*, 2002). Similarly, it is likely that seasonal changes in haul-out site used in common seals (*Phoca vitulina*) result from the females need for safe pupping and lactation sites (Thompson, 1989).

Where both parents undertake parental care of the offspring, it may be the male whose habitat use is more influenced by offspring provisioning than that of the female. This appears to be the case for brown boobies (*Sula leucogaster*) and Adélie penguins (*Pygoscelis adeliae*). Male brown boobies remain close to the colony to maintain territory and prevent or acquire extra-pair copulations (Gilardi, 1992). Similarly, male Adélie penguins are more aggressive than females and thus are more efficient at protecting the nest from skua and human predators (Clarke *et al.*, 1998). One consequence of this role reversal is segregation of foraging location. Male dominate in close-at-hand foraging sites whilst females go further afield, presumably to reduce intraspecific competition (Catry *et al.*, 2005; Clarke *et al.*, 1998).

#### 4.2. Forage selection hypothesis (sexual dimorphism—body-size hypothesis) incorporating the scramble competition and incisor breadth hypotheses

The forage selection hypothesis focuses on sex differences in nutritional requirements. It is assumed that sex-related differences in body size confer significant differences in nutritional requirements. As gut capacity is a constant proportion of body mass, large-bodied animals are able to retain food longer and digest more efficiently (Gross, 1998). Therefore, whilst large-bodied animals have greater overall metabolic requirements they can meet their metabolic requirements by consuming a lower quality diet than small-bodied animals. It is proposed that the larger-bodied sex selects habitats where intake rates are high, if necessary at the expense of dietary quality, whereas small-bodied individuals must compensate for their digestive inferiority and so are constrained to sites where they can obtain a high-quality diet. However, there is some controversy surrounding a prediction of this hypothesis, and it is that males actively seek out habitats with abundant, low-quality forage.

The scramble competition and incisor breadth hypotheses provide a possible mechanism for this observation. It is argued that, where competition for forage is high, males are competitively excluded by smaller females.



The bite size of ungulate grazers, at least, is a function of the width of the incisor teeth and forage height, and, as larger-bodied males have narrower incisor breadth in relation to body size, under heavy grazing pressure where forage height is low, they are less efficient competitors for forage than smaller-bodied females (Illius and Gordon, 1987). Thus, suitability of a patch may differ between the sexes and, as resource value decreases with increasing competition, the ideal free distribution predicts that individuals should distribute themselves such that all individuals receive equal fitness gains (Goss-Custard and Sutherland, 1997; Parker, 1978). In addition, males demonstrate greater mobility and an absence of parental responsibilities and thus are more inclined to avoid competition (Main, 1998). Similarly, as energetic requirements are also affected by reproductive condition, competition from lactating females may force the exclusion of other females and males from high-quality habitats as the lactating females strive to satisfy their additional metabolic requirements.

Whilst we have incorporated the sexual dimorphism—body-size hypothesis within the forage selection hypothesis, the existence of sexual dimorphism in body size alone is not sufficient to justify the selection of this hypothesis to explain sexual segregation. Indeed, sexual dimorphism in body size also featured heavily in the assumptions of the predation-risk hypothesis. Similarly, there is considerable overlap between the forage selection hypothesis and the activity budget hypothesis (see Section 4.3). For example, sex differences in dietary niche may be explained by differential habitat selection based on attributes such as diving ability and flight efficiency, which are influenced by body size, rather than by size-specific nutritional requirements. Where this is the case, we have suggested that the activity budget hypothesis may provide a more parsimonious explanation for sexual segregation than forage selection.

There exists much evidence of sex-specific forage selection in marine vertebrates. However, in relatively few instances, can these differences be explained by sexual dimorphism alone, in concordance with the forage selection hypothesis. This is due to one prediction of the forage selection hypothesis which appears rare in marine vertebrate populations, and this is the competitive exclusion of the larger sex from high-quality habitats by greater foraging efficiency in the smaller sex. It has been argued above that the incisor breadth hypothesis provides a mechanism for this form of competition to operate. However, this argument may not be relevant in the marine environment. For example, sex differences in the diet of magellanic penguins (*Spheniscus magellanicus*) and blue-eyed Crozet shags (*Phalacrocorax melanogenis*) have been attributed to larger male size and consequential larger bills, enabling the capture of a higher proportion of fish, and larger fish, than females resulting in more efficient foraging (Cook *et al.*, 2007; Forero *et al.*, 2002). Indeed, competitive exclusion of the smaller sex by the larger sex may be more commonplace among marine vertebrates. However, one apparent

exception is the grey seal (*Halichoerus grypus*), where it has been suggested that males may consume prey of lower energetic value and so must feed more (Austin *et al.*, 2006).

In contrast, the prediction that female diet should differ based on reproductive status is well supported in the marine vertebrate literature. The diet of lactating females differs from that of other females in both common (*Delphinus delphis*) and spotted dolphins (*Stenella attenuata*), where it has been suggested that the diet of lactating females reflects their divergent nutritional requirements, for example, consuming food such as flyingfish which are high in protein, calcium and phosphorous; and squid which have a high water content (Bernard and Hohn, 1989; Young and Cockcroft, 1994). Sex-specific nutritional requirements, for example, the need to restore calcium levels, have also been forwarded to explain sexual segregation in female wandering albatross (*Diomedea exulans*: Phillips *et al.*, 2004; Xavier and Croxall, 2005) and the sexually monomorphic northern gannet (*Morus bassanus*: Lewis *et al.*, 2002).

Similarly, differences in the seasonal pattern of reproductive investment of the sexes may also lead to sexual segregation. Grey seals (*H. grypus*) mate shortly after parturition. Females must therefore recover condition earlier in the year than males to support the developing embryo and thus spend more time diving and exhibit greater selectivity (Austin *et al.*, 2006; Beck *et al.*, 2003a,b; Breed *et al.*, 2006). The need for females to recover condition quickly may also influence the moulting behaviour of the sexes, further contributing to the spatial separation of the sexes. Male common seals (*Phoca vitulina*) haul out every day during moult (where high skin temperature increases the speed of moult), whereas females spend more time at sea after lactation, enabling them to feed intensively at the cost of slower moult (Thompson *et al.*, 1989).

Sex-specific morphological adaptations which lead to sex differences in foraging efficiency and thus sex differences in foraging location may be predicted under the forage selection hypothesis. Northern giant petrels (*Macronectes halli*), oystercatchers (*Haematopus ostralegus*) and western sandpipers (*Calidris mauri*) for example, all exhibit sex differences in bill morphology which contributes to divergent dietary niches of the sexes. Male northern giant petrels have disproportionately larger bills than females (Gonzalez-Solis and Croxall, 2005), which may result in increased foraging efficiency of males over females and thus competitive exclusion of females from mutually preferred resources (Gonzalez-Solis, 2004). In oystercatchers, females generally have pointed bill tips whereas male bills are blunt, resulting in dietary specialisation of the sexes and, as a consequence, sexual segregation of foraging locations; females forage for worms and clams on mudflats, whilst males feed at mussel beds (Durell *et al.*, 1993; Swennen *et al.*, 1983). Oystercatchers foraging in mudflats have difficulty in maintaining adequate intake rates at low tide resulting in lower body condition and survival;

therefore, tend to forage longer and supplement their diet by foraging in fields (Durell *et al.*, 1993). Longer-billed western sandpipers are able to extract prey that are buried more deeply in the sediment and, by investigating the vertical distribution of invertebrates, Mathot *et al.* (2007) demonstrated that latitudinal sexual segregation of this species (longer-billed females winter south of males) reflected the abundance of surface prey, which declined in abundance with decreasing latitude.

Similarly, sexual dimorphism in head morphology of the yellow-lipped sea krait (*Laticauda columbrina*) may contribute to dietary niche specialisation of the sexes. Female sea kraits have longer, wider heads than males of the same length, enabling them to consume larger eels than males relative to their head size and body length, whilst the smaller heads of males may enable them to reach further into crevices to obtain small eels (Pernetta, 1977; Shetty and Shine, 2002). It has also been suggested that the larger snout seen in female clingfish (*Diademichthys lineatus*) contributes to the sex differences in diet seen in this species (Magurran and Garcia, 2000). Likewise, female dab have heavier stomachs and intestines (empty weight) than males which may increase both passage rates and assimilation efficiency in this, the faster growing sex (Temming and Hammer, 1994).

#### 4.3. Activity budget hypothesis (body-size dimorphism hypothesis)

The activity budget hypothesis, developed simultaneously by Conradt (1998a) and Ruckstuhl (1998) for ungulate species, focuses on sex differences in activity budgets. It is proposed that species which exhibit sexual dimorphism in body size also exhibit sex differences in energetic requirements, digestive efficiencies and possibly also movement rates, resulting in high fission rates in mixed-sex groups and thus the formation of single-sex groups. These sex-related differences in activity budgets make synchrony of behaviour costly, resulting in high fission rates in mixed-sex groups and thus the formation of single-sex groups. To test this hypothesis, Conradt (1998a) developed an index of activity synchronisation (see Box 2.2) and was able to demonstrate that red deer (*Cervus elaphus*) in mixed-sex groups were significantly less synchronised in their activity than deer in single-sex groups. However, the factors which render the segregation coefficient largely inappropriate for quantifying the degree of sexual segregation in marine vertebrates (namely the difficulty in determining which individuals constitute a group/population and the sex of all individuals within a group) are also applicable to the synchronisation coefficient.

The activity budget hypotheses can be extended to species in which the reproductive investment of the sexes is not equal; for example, in most mammals this is the case due to the increased energetic demands of lactation. Alternatively, in solitary animals, sex differences in activity budgets may

**Box 2.2** The synchronisation coefficient (after [Conradt, 1998a](#))

Conradt's synchronisation coefficient (SynC) determines the degree of synchronisation in single-sex groups (or single-sex parts of mixed-sex groups) of an animal population using the following formula:

$$\text{SynC} = 1 - \sum_{h=08.00}^{20.00} \left( \frac{N_h (N_h - 1)}{N A_h R_h} \sum_{i=1}^{k_h} \frac{a_{h,i} r_{h,i}}{n_{h,i} - 1} \right) \quad (2.2)$$

where  $h$  is hour of the day,  $N$  is total number of animals observed,  $N_h$  is total number of animals observed in  $h$ th hour of the day,  $A_h$  is total number of active animals observed in the  $h$ th hour of the day,  $R_h$  is total number of resting animals observed in the  $h$ th hour of the day,  $n_{h,i}$  is number of animals observed in the  $h$ th hour of the day in  $i$ th group,  $a_{h,i}$  is number of active animals observed in  $h$ th hour of the day in  $i$ th group, and  $k_h$  is number of groups observed in  $h$ th hour of the day.

The resulting synchronisation coefficient or index of synchronisation ranges from 0 (no synchronisation in activity within groups) to 1 (complete synchrony of activity within groups).

The degree of synchronisation between males and females in mixed-sex groups can be measured using the following formula:

$$\text{SynC}_{(\text{male-female})} = 1 - \sum_{h=08.00}^{20.00} \left( \frac{N_h N_h^2}{N A_h R_h} \sum_{i=1}^{k_h} \frac{x_{a,h,i} \gamma_{r,h,i} + x_{r,h,i} \gamma_{a,h,i}}{2x_{h,i} \gamma_{h,i}} \right) \quad (2.3)$$

where  $x_{a,h,i}$  is number of active males observed in  $h$ th hour of the day in  $i$ th group,  $x_{r,h,i}$  is number of resting males observed in  $h$ th hour of the day in  $i$ th group,  $x_{h,i}$  is number of males observed in  $h$ th hour of the day in  $i$ th group ( $x_{h,i} = x_{a,h,i} + x_{r,h,i}$ ),  $\gamma_{a,h,i}$  is number of active females observed in  $h$ th hour of the day in  $i$ th group,  $\gamma_{r,h,i}$  is number of resting females observed in  $h$ th hour of the day in  $i$ th group,  $\gamma_{h,i}$  is number of males observed in  $h$ th hour of the day in  $i$ th group ( $\gamma_{h,i} = \gamma_{a,h,i} + \gamma_{r,h,i}$ ).

result in sex-specific habitat use. As sex-related differences in activity budgets will increase with divergence in the body size of the sexes, so should the tendency to form sex-segregated groups. This is because, whilst

the larger sex will have higher absolute energy requirements, an allometric relationship between metabolic rate and body size results in the smaller sex having a higher metabolic rate and higher energy requirement per unit of body mass. Therefore, monomorphic species are not expected to form single-sex groups unless reproducing females need to compensate for the higher energy demands of reproduction.

The activity budget hypothesis may explain size-related scaling of foraging trip duration and range in common seals (*Phoca vitulina*). [Thompson et al. \(1998\)](#) have suggested that high levels of intraspecific competition for prey in inshore areas, results in larger males travelling as far from the central resting place as possible within energy and time limits. However, as female foraging duration and range were short for their body size, the increased costs of reproduction in females (and possibly also an increased cost of transport in pregnant females) likely also influences the activity budgets of the sexes in this species. Sex-specific swimming capabilities have also been forwarded to explain sexual segregation in transport of sharks ([Smith and Merriner, 1987](#); [Springer, 1967](#)).

Body-size dimorphism is also known to influence diving ability in marine vertebrates. In air breathers, smaller individuals have a smaller functional oxygen store ([Wanless et al., 1995](#)) and thus sexual size dimorphism constrains diving capability physiologically. For example, in the blue-footed booby (*Sula nebouxii*), females are larger so a positive relationship between body size and dive depth means females dive significantly deeper and longer than males, suggesting that separation of vertical feeding niche based upon sex is mediated by sexual size dimorphism in this species ([Zavalaga et al., 2007](#)). Sexual body-size dimorphism and the consequential effects on diving capability have also been forwarded as an explanation for sexual segregation in killer whales (*Orcinus orca*: [Michaud, 2005](#)), New Zealand fur seals (*Arctocephalus forsteri*: [Page et al., 2005](#)) and South Georgian shags (*Phalacrocorax georgianus*: [Wanless et al., 1995](#)). However, the smaller sex may compensate for shallower dive depths by undertaking longer foraging excursions and/or increasing dive rate. Indeed, this has been observed in brown (*Sula leucogaster*) and red-footed boobies (*S. sula*) where the increase in dive rate of the smaller males is scaled to the degree of sexual dimorphism ([Lewis et al., 2005](#)). Sex differences in the temporal pattern of diving behaviour may also be related to body size. It has been suggested, for example, that male blue-eyed Crozet shags (*Phalacrocorax melanogenis*) and female northern gannets (*Morus bassanus*) forage at depth in the afternoon when the penetration of sunlight is maximal ([Cook et al., 2007](#); [Lewis et al., 2002](#)). Thus, sexual body-size dimorphism and the consequential differences in activity budgets can lead to sex differences in foraging behaviour as well as foraging location ([Fig. 2.4](#)).

In ectothermic marine reptiles, diving capabilities are likely to be constrained by temperature rather than by an individual's functional oxygen



**Figure 2.4** In blue-footed boobies, *Sula nebouxii*, females (right) are larger than males (left) and consequently undertake significantly deeper foraging dives and remain underwater for longer. Photo courtesy of M. Evans, with permission.

store. In marine iguanas for example, due to mass-related changes in cooling and heating rates, only large males are able to forage subtidally, where food availability and consequential intake rates are increased (Wikelski and Trillmich, 1994). By painting some individuals white and thereby manipulating rewarming rates, Wikelski and Trillmich (1994) were able to demonstrate that large males adopted a strategy of ‘forage while warm and warm up when getting inefficient at grazing’.

In marine birds, body-size dimorphism influences flight efficiency. Indeed, the mediation of flight performance through dimorphism in body mass has been highlighted as an important determinant of at-sea distribution of wandering albatross since larger males need winds to fly (Phillips *et al.*, 2004). This may, therefore, lead to niche divergence. Increased flight efficiency in the smaller sex, combined with high levels of intraspecific competition and dominance of the larger sex close to breeding sites, has also been highlighted as a possible mechanism underlying sex differences in foraging location and an increased foraging range in the smaller sex in both giant petrels (Gonzalez-Solis and Croxall, 2005) and boobies (Lewis *et al.*, 2005). Female flight efficiency relative to that of males is further increased in northern giant petrels through trait exaggeration. Isometric analysis has revealed that not only do males have longer bills than expected, but females have longer wings than expected (Gonzalez-Solis, 2004).

The energetic constraints of offspring provisioning may influence activity pattern of humpback whales (*Megaptera novaeangliae*) and explain latitudinal segregation in this species. It may be advantageous for pregnant or lactating females not to migrate to tropical breeding grounds due to energetic costs of reproduction (Brown *et al.*, 1995). In addition, the necessity for maternal females to select habitats based on the activity budgets of their

offspring has been suggested to explain sexual segregation of female hump-back whales with a calf into shallow, nearshore waters to avoid turbulent offshore or deep-sea conditions (Clapham, 2000; Smultea, 1994).

#### 4.4. Thermal niche–fecundity hypothesis

The thermal niche–fecundity hypothesis, like the predation–risk hypothesis, focuses on intra-specific differences in the way the sexes strive to maximise their lifetime reproductive success. This hypothesis, however, assumes fecundity is temperature dependent and that sex differences occur in the temperature at which fecundity is maximised. Therefore, it is predicted that the sexes occupy different thermal habitats in an effort to maximise reproductive output.

The thermal niche–fecundity hypothesis emerged with the onset of the study of sexual segregation in ectotherms (Sims, 2005). For ectotherms, body temperature is largely determined by ambient temperature and, as body temperature influences many aspects of thermal biology including activity, metabolism, and growth, habitat selection plays a key role in thermoregulation. Behavioural thermoregulation enables ectotherms to select appropriate body temperatures for specific activities (Shine and Wall, 2005), hence differences in thermal optima have the potential to generate sex differences in habitat use. Body temperature is known to influence rates of egg development in many invertebrates and fish, for example, a 1 °C drop in temperature during vitellogenesis can delay spawning of Atlantic cod, *Gadus morhua*, by up to 10 days (Kjesbu, 1994). Similarly, body temperature may also influence rates of sperm production in males, and low temperatures are known to inhibit sperm formation in male sticklebacks (Wootton, 1976). Therefore, thermal habitat selection may play a key role in determining individual fecundity, and each individual should, theoretically, select habitats at their appropriate optimal temperature in an attempt to maximise reproductive success.

The thermal niche–fecundity hypothesis may explain sexual segregation in Atlantic cod, which have been shown to exhibit sex differences in residency times on spawning grounds (Robichaud and Rose, 2003). Robichaud and Rose (2003) showed that male cod remained resident, whereas females moved in and out of these male-dominated spawning aggregations. They proposed females moved into warmer waters to ‘incubate’ developing eggs before subsequently returning to aggregation sites for spawning.

The thermal-niche hypothesis has also been proposed to explain sexual segregation in grey reef (*Carcharhinus amblyrhynchos*) and white sharks (*Carcharodon carcharias*). Female grey reef sharks have been observed to aggregate in the shallow lagoons of Johnston Atoll in the Central Pacific Ocean where water temperatures are 1–2 °C warmer than in the open ocean.



As sampled sharks contained embryos in the early stages of development, Economakis and Lobel (1998) hypothesised that pregnant female sharks were aggregating in shallow warm waters to raise their body temperature thereby increasing rate of embryonic development. A similar aggregation of female white sharks at the Neptune Islands, South Australia during the warmest months of the year has been suggested to represent female preference for warm water habitats where developmental growth rates of their young are increased (Robbins, 2007).

#### 4.5. Social factors hypothesis (social preference and social avoidance hypotheses)

Under the social factors hypothesis, social mechanisms drive sexual segregation. This hypothesis is generally interpreted in terms of social preferences. The formation of same-sex groups may enable reproductively naïve individuals to locate suitable breeding sites and potential breeding partners. Similarly, social affinities between males may reflect the need for males to develop fighting skills, establish dominance relationships and evaluate potential rivals (Main *et al.*, 1996). An alternative hypothesis is that of social avoidance, inter-sexual aggression, such as aggressiveness of females during parturition, or the avoidance of sparring males may drive sexual segregation. Inter-sexual social avoidance may also arise where there is a conflict of interests between individuals of the two sexes (Parker, 2006). Social conflict usually develops from asymmetry between the reproductive strategies of the sexes: typically, female lifetime fecundity is a function of age and condition, whereas that of males is determined by the number of offspring they sire (Magurran and Garcia, 2000). As a consequence, optimum rates of mating frequency also differ between the sexes and male harassment of females may result (Parker, 2006).

The social factors hypothesis has received increasing support in recent years as investigations have begun on sexual segregation in species other than ungulates. Indeed, the social affinity hypothesis has received little support within the terrestrial ungulate literature (Main *et al.*, 1996), but on several occasions has been forwarded to explain sexual segregation in marine mammals. Michaud (2005) suggested that, in cetacean societies, the benefits of being a member of a stable group, such as communal care of calves and cultural transmission of learned information, outweigh the costs associated with group living. Cooperative care of offspring has been suggested to be a primary function of female units in sperm whales (Lyrholm *et al.*, 1999; Whitehead and Weilgart, 2000; Whitehead *et al.*, 1991). Similarly, it has also been suggested that female sperm whales may benefit from coordinated foraging formations and combined memory for distribution of temporally variable food sources (Whitehead and Weilgart, 2000; Whitehead *et al.*, 1991). As sperm whales form matrilineally related female



units, it is thought that kin selection may have played a role in their evolution (Lyrholm *et al.*, 1999). In this context, the social affinity hypothesis could also explain the grouping behaviour of females with differing reproductive development.

In some species, a combination of social affinity and social aversion may explain sexual segregation. It is suggested that cooperative behaviour of males (social affinity) and male avoidance (social aversion) could account for sexual segregation in bottlenose dolphins. A high proportion of strandings of bottlenose dolphin calves show signs of attack from conspecifics (Dunn *et al.*, 2002; Patterson *et al.*, 1998). Males of this species appear to cooperate in pairs and triplets to sequester and control the movements of females (Connor *et al.*, 1992). These male 'alliances' preferentially coerce females in mating condition (Connor *et al.*, 1992; Scott *et al.*, 2005), which, together with direct observation of an aggressive interaction between an adult bottlenose dolphin and a dead bottlenose calf (Patterson *et al.*, 1998) has been taken to suggest infanticide occurs in this species. This is supported by the fact that the inter-birth period is long in this species but that females become sexually receptive following death of dependent offspring (Dunn *et al.*, 2002).

Social affinity and aversion may also explain sex differences in the behaviour of green turtles (*Chelonia mydas*). It is thought that males maintain relatively high activity levels in an attempt to locate and mate with as many females as possible to maximise reproductive output (Hays *et al.*, 2001). However, energetic limitations constrain both how long a male will stay at the breeding grounds and how much he will be able to partake in reproductive activities before compromising chances of survivorship. This may account for observed sex differences in the timing of migration (Godley *et al.*, 2002). In contrast, females aggregate in an area away from males. The utilisation of a female-only reserve, together with the documentation of behaviours which appear to avoid copulation and the storage of sperm (females can lay all their eggs after just one mating), are thought to represent female social avoidance of mating males (Booth and Peters, 1972). Analogous behaviours are also seen in loggerhead turtles (*Caretta caretta*). Males are always 'on the prowl' whilst females often just seek to be solitary to let their eggs develop prior to laying (Schofield *et al.*, 2006).

Male mate searching behaviour also explains male–female differences in habitat occupancy in the turtle-headed sea snake, *Emydocephalus annulatus*. Whilst the distribution of adult females closely matches that of their reef prey, males do not feed during breeding, but swim more rapidly, are found across a broader range of habitat types, including sandy substrates where black females may stand out more, and actively court any adult female they encounter (Shine *et al.*, 2003). Similarly, female sandperch, *Paraperchis polyophthalma*, allocate most of their time to foraging and resting, whereas males spend more time engaging in social activities and actively patrol the borders of their territories (Sano, 1993).

The social avoidance of males by females presumably to avoid unsolicited mating attempts and potential injuries arising from such unwanted activity may explain sexual segregation in female humpback whales (*Megaptera novaeangliae*), Galapagos (*Zalophus wollebaeki*) and South American sea lions (*Otaria flavescens*) and nurse sharks (*Ginglymostoma cirratum*). It has been suggested that maternal female humpback whales may use shallower water to reduce interactions with conspecifics. The temporal pattern of segregation by maternal humpbacks coincides with periods of increased courting and aggression by adult males, activities that cows may wish to avoid to reduce harassment and injury to calves (Clapham, 2000; Smultea, 1994). Cow-calf use of shallow habitat may discourage courting males, which may select deep water to avoid collisions with the sea floor or coral (Smultea, 1994). Similarly, female Galapagos and southern sea lions with pups aggregate within the territories of dominant males to avoid harassment from other males, which has been shown to influence pup survival and growth (Connor, 2002; Wolf *et al.*, 2005). Female nurse sharks, like green turtles, inhabit female-only areas, exhibit behaviours which appear to avoid copulation and are capable of storing sperm. Therefore, it is thought that sexual segregation in this species represents female social avoidance of mating males: They may wish to control the frequency of mating attempts or alternatively, to control access by particular males (Carrier *et al.*, 1994; Fig. 2.5).

## 5. SEXUAL SEGREGATION IN CATSHARK: A CASE STUDY

In this chapter, we have (1) described the principal findings of previous research which finds evidence of sexual segregation in marine mammals, birds, reptiles and fish, (2) reviewed the hypotheses which have been proposed to explain sexual segregation and (3) have attempted to use this existing framework to account for the cases of sexual segregation we have described. This latter task has proved particularly difficult. An author will often suggest a possible mechanism which may underlie the sex-specific behaviours they describe, but, more often than not, this explanation will feature predictions of several of the hypotheses proposed to account for sexual segregation in animals. Confounding factors such as sex differences in body size and offspring provisioning may cloud the distinction between the predictions of the hypotheses and may lead one to focus on proximate rather than ultimate causes of segregation. For example, species which are sexually dimorphic with respect to body size may exploit sex-specific foraging locations and prey types, but as a result of sex differences in flight efficiency (activity budget hypothesis) rather than forage selection (forage selection hypothesis). In addition, there is often a lack of information on various aspects of the behaviour of the species in question, making critical



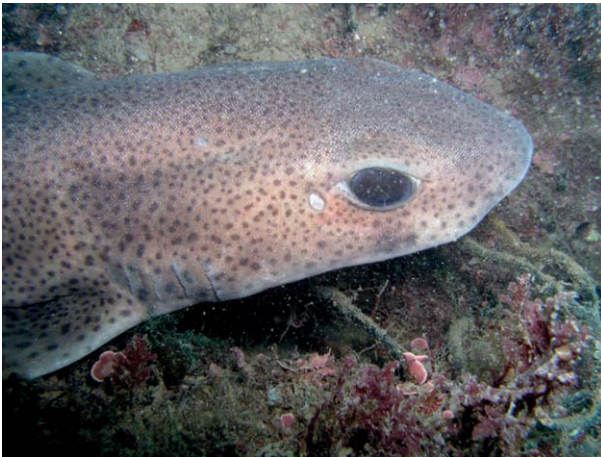
**Figure 2.5** Female Galápagos sea lions, *Zalophus wollebaeki*, aggregate within the territories of dominant males, avoiding harassment from other males and thus enhancing survival of their pups (shown above). Photo courtesy of M. Evans, with permission.

evaluation of the hypotheses impossible. What is needed is the systematic behavioural study of individual marine vertebrate species such that numerous proposed hypotheses for the determinants of sexual segregation can be formally examined to discount particular potential explanations.

Here we present a case study of recent research on a common marine vertebrate which exhibits sexual segregation, the small spotted catshark, *Scyliorhinus canicula*. This species is monomorphic with respect to body size and does not exhibit any parental care. A lack of sexual dimorphism, high relative abundance and a largely coastal distribution, coupled with a small adult size enabling laboratory experiments, combine to identify *S. canicula* as a good model species with which to investigate the underlying causes of sex differences in behaviour and sexual segregation. However, whilst there exists an abundance of information on the physiology, feeding ecology and reproductive cycle of this species (Rodríguez-Cabello *et al.*, 1998), comparatively little was known about its natural, free-ranging behaviour until relatively recently.

Greer Walker *et al.* (1980) were the first to track this catshark species acoustically, but only short-term tracks (<1 day) of male movements

were achieved. Moreover, these short trackings only demonstrated that, post-tagging, dogfish simply swam in the direction of the prevailing current. This study clearly is not able to elucidate natural patterns in behaviour. Small spotted catshark movements were investigated by [Rodriguez-Cabello \*et al.\* \(1998\)](#) using mark-recapture, concluding that this species did not travel long distances. [Sims \*et al.\* \(2001\)](#) were the first to investigate the behaviour of individual male and female small spotted catsharks in any detail. Through the application of acoustic telemetry, they showed male and female *S. canicula* exhibited alternative behavioural strategies. In the study location in southwest Ireland (Lough Hyne, a tidal sea lough), males were observed to be crepuscularly and nocturnally active, moving from deep (12–24 m) to shallower (<4 m) water to feed at dusk and during the night. In contrast, females refuged in shallow water (0.5–1.5 m) rock crevices and caves during daytime and were nocturnally active in deeper water only once every 2 or 3 days. The home ranges of the sexes also appeared spatially separated ([Sims \*et al.\*, 2001](#)). More recently, [Sims \*et al.\* \(2006a\)](#) demonstrated the existence of diel vertical migration (DVM) in this bottom-living species. Through the use of short- and long-term acoustic and archival telemetry, they were able to show that male catshark undertook nocturnal along-bottom movements up submarine slopes from deeper, colder areas occupied during the day into warmer, shallow, prey-rich habitats at night. The results suggested that, whilst males forage in warm water, they prefer to rest and digest in cooler water. Energetic modelling of this ‘hunt warm–rest cool’ strategy indicated male daily energy costs were reduced by just over 4%, implying that male *S. canicula* uses DVM as an energy conservation strategy that increases bioenergetic efficiency ([Sims \*et al.\*, 2006a](#); [Fig. 2.6](#)).



**Figure 2.6** During daylight hours, female small spotted catshark (*S. canicula*) refuge rock crevices in shallow water habitats, whereas males exhibit saltatory behaviour in comparatively deeper water.

Overall, sexual segregation is a general feature of shark populations yet remains to be investigated in the majority of species. In a review of sex differences in habitat selection and reproductive strategies of sharks, Sims (2005) used *S. canicula* as a model species with which to investigate the sexual segregation hypotheses. The forage selection hypothesis was discounted for this species as it did not exhibit sex differences in dietary niche. The predation-risk hypothesis was not likely since small spotted catshark are subject to low levels of seasonal predation in the sea lough study site and yet females refuge throughout the year. The activity budget hypothesis was not investigated explicitly, however, both the thermal niche–fecundity and social factors hypotheses were highlighted as possible mechanisms for segregation in this species.

As ectotherms, thermal habitat selection plays a key role in determining catshark energy budgets. Females generally select warmer waters than males. In a tidal sea lough, daytime refuging in shallow water exposes female catshark to temperatures exceeding 18 °C during August and September, whereas temperature exposure of males, which remain at depth during the day and only enter the shallows as they cool at night, peaks at 15.7 °C (Sims, 2003). Although increased rates of embryonic development in females have been suggested to be associated with the selection of warmer habitats, direct evidence is lacking. Indeed, there may possibly be an inhibitory effect. Male small spotted catshark, in contrast, actively select cooler water temperatures even at the expense of short-term feeding opportunities (Sims *et al.*, 2006a). However, the selection by males of cooler water on the whole may be related to optimum temperatures for sperm production (Kime and Hews, 1982).

Elasmobranch courtship and mating involves a prolonged series of complex behaviours. Single females may be pursued by multiple males, with injuries arising from both aggressive courtship and mating. During copulation itself in *S. canicula*, extreme contortion is involved as the male coils his body tightly around the pelvic region of the female (Dodd, 1983). Hence, courtship and mating can be prolonged, not only because of multiple males all vying for the female but because copulation itself requires the maintenance of body contact and postural control. However, female *S. canicula* (along with many other elasmobranch species) are known to store sperm, which suggests that copulation need not precede every ovulation in this species. To maintain scope for fecundity and growth, female catshark may therefore seek to limit energetically demanding (and injurious) mating activity. Unisexual refuging behaviour in this species may function to reduce levels of male sexual harassment to individual females and facilitate female choice. Nevertheless, despite the fact that several hypotheses for sexual segregation have been partially examined in this species, dedicated studies are needed to test these hypotheses fully (Sims, 2005).

The only other marine vertebrates in which a similar analysis has been attempted are the grey seal (Breed *et al.*, 2006), the wandering albatross (Xavier and Croxall, 2005) and the giant petrels (Gonzalez-Solis and Croxall, 2005; see previous sections). However, critical analysis of the underlying causes of sexual segregation in all these species is confounded by the fact that they all exhibit sexual body-size dimorphism. Behavioural experiments are particularly informative when testing competing hypotheses explaining sexual segregation (Catry *et al.*, 2005). However, controlled laboratory manipulations are not feasible in large, wide-ranging marine vertebrates such as seals and albatross. Thus, there is much need for hypothesis-led research which uses an integrative approach of field-based tracking and complementary laboratory studies to evaluate the potential of the sexual segregation hypotheses in a monomorphic species.

## 6. CONSERVATION IMPLICATIONS OF SEXUAL SEGREGATION

Sex differences in behaviour are widespread among marine vertebrates. Where these differences between the sexes are sufficiently diverse, spatial or temporal segregation may result. Understanding sex-based differences in the spatio-temporal dynamics of animal populations is of fundamental importance for their successful management. This is particularly so for *k*-selected species, such as marine mammals and large marine birds, reptiles and fish, which typically exhibit slow growth, late maturation and low fecundity.

One potential implication of sexual segregation is differential exploitation of the sexes of target animals by humans. Commercial whaling catches of humpback whales near winter-breeding colonies were highly skewed towards males (Brown *et al.*, 1995), yet sex ratio at birth is 1:1 (Clapham, 2000). This sex bias is now known to result from sex differences in migration patterns: around 50% of Antarctic females remain in high-latitude feeding areas throughout winter, whilst the majority of the population migrates to breeding areas in low-latitudes in winter (Brown *et al.*, 1995). The observed sex bias may be exacerbated by evidence of sexual segregation within migrating individuals. Males appear on breeding grounds earlier and have longer residence times than females (Stevick *et al.*, 2003). However, male-biased exploitation is likely to have less impact on humpback whale populations than female-biased exploitation. This is primarily due to the fact that male mating success is variable: Some males will father many offspring, whilst others may not father any. In contrast, the majority of females will either be pregnant or provisioning offspring for much, if not all of their



reproductive years. As a result, a decrease in the size of the female population will result in a decrease in the fecundity of the population.

The broad-scale effects of differential exploitation of the sexes by fisheries on sexually segregated shark and ray populations remains, however, so poorly studied that any implications have yet to be clearly identified. But there is anecdotal evidence that suggests human exploitation of sexually segregated sharks may lead to dramatic population declines. The existence of sexual segregation in the demersal–pelagic shark, spurdog (*Squalus acanthias*), with mature females aggregating to form large unisexual schools, probably resulted in sex-biased exploitation. Schools of mature females were found to dominate landings in southwest England during the early part of the 20th century. This was probably a major factor responsible for the collapse of the spurdog fishery in the English Channel when between 1928 and 1931, landings declined from 2710.3 tons to 802.4 tons (Steven, 1933). Similarly, basking shark (*Cetorhinus maximus*) catches from harpoon fisheries off West Ireland and northwest Scotland were principally large females, and which was thought to have contributed to an apparent population collapse (Anderson, 1990; McNally, 1976). Although sexual segregation is beginning to be mapped spatially at the large scale for high value sharks, for example, shortfin mako shark, *Isurus oxyrinchus* (Mucientes *et al.*, in press), there is no requirement by fishing vessels to document the sexes of sharks and rays captured. Therefore, the role of fisheries in exacerbating declines in elasmobranch populations due to spatial targeting of particular areas, where one sex may predominate over another, is at present masked by a lack of data.

Female-biased mortality may also result from indirect harvesting. Wandering albatross are frequently killed when they attempt to scavenge baited hooks deployed by long-line fishing vessels (Nel *et al.*, 2002). In 1991, it was estimated that the number of albatross killed annually on Japanese longlines in the southern oceans could exceed 44,000 (Brothers, 1991). The wandering albatross breeding population at Bird Island, South Georgia, declined at a rate of 1% per annum over the 30-year period between 1961 and 1991 (Croxall *et al.*, 1990). However, annual declines of up to 6% have been reported for other populations (Weimerskirch and Jouventin, 1987). High rates of incidental capture by longliners recorded by Brothers (1991) substantiate claims that these declines are due to fishing activity. In addition, sex differences in foraging zones (females forage further offshore where pelagic tuna longliners operate) are evident. Consequently, sex-specific susceptibility rates result in females having a lower rate of survival than males (Croxall *et al.*, 1990). Similarly, giant petrels also experience female-biased mortality as a result of interactions with fisheries. Light measurements recorded for geolocation purposes have revealed that this species associates with nocturnal fisheries which use lights to 'jig' for squid.



Because of sex differences in foraging locations, only females are associated with these fisheries during breeding (Gonzalez-Solis and Croxall, 2005).

Interactions between wandering albatross and marine fisheries also influence chick survival. The at-sea distribution of adult males overlaps with that of the Patagonian toothfish (*Dissostichus eleginoides*) fishery. The probability of incidental capture in this demersal fishery is low, but males scavenge fishery debris (such as discarded fish heads) which they then bring back and feed to their chicks (Nel *et al.*, 2002). Longline hooks are often consumed with the cut-off heads, and thus are also fed to the chicks, which may result in chick fatality.

Like whales and sharks, albatross are extreme  $k$ -selected species. Fisheries observations reveal that most birds seen following longliners are current breeders (Croxall *et al.*, 1999) and, as albatross are highly monogamous, sex-biased mortality will decrease the fecundity of the population, not only through individual mortality but also by decreasing the number of potential breeding pairs. For this reason, even male-biased mortality may adversely affect population fecundity.

Indirect interactions with fisheries may also influence survival, with species and/or sexes which forage on commercially exploited species suffering most. For example, the survival of Hawaiian monk seal, *Monachus schauinslandi*, populations is endangered as a result of a population decline attributed to starvation of juveniles, which largely feed on commercially exploited fish species (Goodman-Lowe, 1998). Similarly, a decline in seal populations would likely have an adverse affect on northern giant petrel, *Macronectes halli*, populations. Time of egg hatching corresponds with that of pupping in the local seal populations, with each bird species matching a different seal species (Hunter and Brooke, 1992), indicating a high level of reliance on this food source. If seal populations decline, large, heavy males may not be able to feed offshore, resulting in male-biased mortality.

Sex-specific diets may in addition lead to differential exposure to environmental pollutants. Carrion-scavenging male giant petrels forage on the South Georgian coast, which is relatively pristine. In contrast, females forage on the Patagonian shelf, which is polluted by river transport discharges, offshore oil operations and high shipping activity. As a result, females have higher levels of metal contamination in their blood than males (Gonzalez-Solis and Croxall, 2005). Similarly, as females feed at higher trophic levels (Antarctic food webs are comprised of fewer trophic levels than those north of the Antarctic polar front, i.e., in Patagonian waters), their feathers have a higher mercury content than those of males (Becker *et al.*, 2002, cited in Gonzalez-Solis *et al.*, 2002).

Another implication of sexual segregation concerns the use of designated cetacean calving and elasmobranch pupping sites, which are frequently situated in shallow, nearshore areas. Whilst the protection of humpback whale calving areas has been recommended under management plans, little

information on the qualities that define such sites has been gathered (Smultea, 1994). However, the management of these areas may be further complicated if different reproductive stages and events occur under different jurisdictions and the sexes are not equally distributed throughout the species' range. For example, southwest Atlantic sand tiger sharks mate within Argentinian waters and yet are found in Brazilian waters whilst pregnant (Lucifora *et al.*, 2002). Management strategies involving more than one country are difficult to coordinate and implement, especially if the interests of the countries concerned differ. In addition, little attention has focused on the effects of human use of the coastal zone and its implications on population viability, despite the likely importance of these sites for juveniles (Smultea, 1994).

Finally, climate change also has the potential to impact sexually segregating marine vertebrate populations. Not only will increased sea temperatures have the potential to influence animal distributions (e.g., through range expansion: McMahon and Hays, 2006), but the sex ratio of entire populations may be influenced. Sexual differentiation of a number of turtle species is affected by the incubation temperatures of the eggs, and a few tenths of a degree can alter the sex ratio of the hatchlings (Mrosovsky, 1995; Mrosovsky and Yntema, 1980). Current climate warming scenarios predict a continuation in the current warming trend and, as higher temperatures bias the sex ratio in favour of females, there exists potential for increasingly feminised marine turtle populations. Whilst there has been suggestion that turtle populations may be able to adapt to climate warming by adjusting pivotal temperature (the temperature at which the sex determination switches from male to female), or by altering nesting spatially (e.g., by nesting under shade) or temporally (i.e., earlier) (Hawkes *et al.*, 2007), there is currently little evidence to support such adaptation. Indeed, feminisation represents a real threat to marine turtle populations: Males currently constitute less than 10% of the Florida loggerhead population (Hawkes *et al.*, 2007). Warmer incubation temperatures may also affect organismal traits that are likely to be related to lifetime reproductive success, and the nature of this effect could differ between the sexes (Shine, 1999). Colder incubation temperatures produce shorter, fatter but more active and faster moving hatchlings (Shine and Harlow, 1993). In addition, should temperatures increase to lethally high levels, hatchling production itself could be adversely affected. With a temperature increase in as little as 3 °C, many loggerhead turtle nests in southern Florida would begin to experience incubation temperatures above lethal limits (Hawkes *et al.*, 2007; Fig. 2.7).

But what affect will these factors have on sexual segregation in marine turtles? The distance males need to move to locate females is a function of male density (Hays *et al.*, 2001). Therefore, an increasing proportion of females will mean males will find it easier to find mates, male harassment



**Figure 2.7** Florida's Loggerhead turtle (*Caretta caretta*) population is becoming increasingly feminised as a result of climate change. Incubation temperatures influence hatching sex determination with warmer temperatures favouring females.

of females for mating opportunities will decrease, and therefore sexual segregation will also decrease. Similarly, as males will not have to search as hard or compete for mates, they will be able to remain on breeding grounds for longer, which may also reduce temporal segregation of the sexes. However, if the proportion of females increases to 100%, the population will become extinct.

## 7. A SYNTHESIS AND FUTURE DIRECTIONS FOR RESEARCH

This chapter has examined sexual segregation in marine vertebrates (mammals, birds, reptiles and fish) and found the incidence of this phenomenon widespread within all groups. Marine vertebrates exhibit sex differences in habitat selection over varying spatial (local to latitudinal) and temporal

(diurnal to annual) scales and in two dimensions (horizontal and vertical). Sex-specific dietary specialisation, in terms of forage size, quantity, quality was widespread, as was sex differences in activity rates and mating strategies. In some instances, adaptive evolution has led to exaggerated traits, increasing the divergence between the habits of the sexes, whereas in other species segregation appears more plastic and will only occur under certain conditions. In addition, sexual segregation appears to be based not only on differences between the sexes and also on the reproductive status of individuals.

Current hypotheses forwarded to account for sexual segregation were also reviewed: the predation risk, forage selection, activity budget, thermal niche–fecundity and social factors hypotheses. Whilst these hypotheses have arisen primarily from the literature concerned with terrestrial ungulate behaviour, with relatively little adaptation to account for specific life–history differences, it has been possible to apply these hypotheses to marine vertebrate case studies across a broad range of both endothermic and ectothermic species. With the exception of the thermal niche–fecundity hypothesis, evidence was found supporting each hypothesis within most marine vertebrate groups.

A common theme throughout the sexual segregation literature is the search for a unifying hypothesis. In a review of studies of sexual segregation in ungulates, [Main \*et al.\* \(1996\)](#) found most evidence supported the predation–risk hypothesis. A similar review by [Ruckstuhl and Neuhaus \(2002\)](#) concluded that sex differences in activity budgets were the most likely driving force behind sexual segregation. The findings of [Ruckstuhl and Neuhaus \(2002\)](#) were subsequently refuted by [Bowyer \(2004\)](#) who, in a review of sexual segregation in ruminants, stated that, as the activity budget hypothesis cannot explain spatial separation and differential habitat or forage use, the forage selection and predation–risk hypotheses were the only hypotheses necessary to explain sexual segregation in ruminants.

Clearly, this raises the question of how likely is it that the underlying causes for sexual segregation are similar across species? Is there a unifying principle? In several species, more than one hypothesis has been developed to account for sexual segregation within a species. For example, sex-specific foraging locations in wandering albatross (*Diomedea exulans*) are influenced by activity budgets since smaller birds are more efficient flyers, but possibly also by sex differences in nutrient requirements such as a need for females to replenish calcium levels after egg-laying ([Phillips \*et al.\*, 2004](#); [Xavier and Croxall, 2005](#)). [Smultea \(1994\)](#) also suggested multiple causes for sexual segregation in humpback whales (*Megaptera novaeangliae*): Maternal females may select nearshore waters to avoid predators, or more turbulent offshore conditions, or, alternately, to avoid sexual harassment from males. Furthermore, humpback whales appear to segregate for different reasons at different spatial scales. It has been proposed that an energy conservation strategy may explain why reproducing females do not migrate to breeding

grounds with conspecifics, consistent with the activity budget hypothesis, whereas, as detailed above, predation risk or social aversion may explain sexual segregation by depth (Smultea, 1994). Thus, given that several hypotheses have been developed to account for sexual segregation both between and within a species, it seems more likely that several important factors may contribute.

The social factors hypothesis has received little support to date and thus has been largely overlooked by recent studies (e.g., Ruckstuhl and Neuhaus, 2002). Sexual segregation hypotheses are generally assumed to explain either social or habitat segregation and indices have been developed to quantify the degree of social and habitat segregation in animal populations (Conradt, 1998b). These indices have been suggested to provide a useful first step to identify likely hypotheses (Conradt, 2005). However, classifications rely on the assumption that solitary animals are not social and therefore cannot segregate for social reasons (Conradt, 1998b; Neuhaus and Ruckstuhl, 2004a). This chapter suggests that solitary animals may exhibit habitat segregation for social reasons. Therefore, wide appraisal of the literature indicates that these indices should not be used to exclude hypotheses when investigating sexual segregation in animals which do not live in groups.

The causes of sexual segregation appear complex and in some species seem equivocal. Yet, despite this, several researchers on ungulates assert that, whilst several ecological variables may be influential, there exists a common underlying cause for sexual segregation across species (Main, 1998). Ruckstuhl and Neuhaus contend that the activity budget hypothesis is that proximate cause that sex differences in activity budgets are most likely driving sexual segregation and that sex differences in predation risk and forage selection are additive factors (Neuhaus and Ruckstuhl, 2004b; Ruckstuhl and Neuhaus, 2002).

However, the activity budget hypothesis has received some criticism. Mooring and Rominger (2004) suggest that '*perhaps the most serious problem with the activity budget hypothesis is that activity budgets are inherently flexible and are not fundamental attributes of animals (such as body size, predation risk and reproductive strategies)*'. Indeed, this would appear to be the case, with individuals adjusting their activity budgets to coordinate with the activity patterns of conspecifics. For example, sub-adult male bighorn sheep, *Ovis canadensis*, have been shown to switch between nursery and male bachelor groups and to alter their activity budget accordingly (Ruckstuhl, 1998, 1999). Thus, it would appear that activity synchrony is not a passive process, and, as such, is likely to incur a cost to the synchronising individual (Conradt, 1998a).

Whether a unifying theory is feasible, probable or detectable, depends to a large extent on all competing hypotheses being tested. As a first step, any confounding factors should be eliminated, or at least minimised where possible to avoid bias. The degree of sexual size dimorphism a species exhibits is known to influence sex differences in behaviour and will

therefore also impact sexual segregation. For example, in a meta-analysis of data extracted from the literature on 40 species of large herbivores, [Mysterud \(2000\)](#) noted that the frequency of ecological segregation was higher among more dimorphic species as a result of diverging nutritional needs. Similarly, sex differences in the trip duration and diving behaviour of sexually size-dimorphic brown booby, *Sula leucogaster* (females 38% bigger) and red-footed booby, *S. sula* (females 15% bigger) were scaled to the degree of size-dimorphism between the sexes ([Lewis et al., 2005](#)). Significant differences in  $^{15}\text{N}$  enrichment were not found in species with lower levels of sexual dimorphism; therefore, body-size dimorphism may lead to sex differences in trophic position—males have a higher position and are bigger ([Lesage et al., 2001](#)). However, sexual segregation does occur in monomorphic species (for a review of sexual segregation in monomorphic ungulates see: [Ruckstuhl and Neuhaus, 2002](#)). For example, the monomorphic northern gannet, *Morus bassanus*, exhibits sex differences in foraging behaviour; females are more selective, exhibit longer, deeper dives and spend more time on the surface ([Lewis et al., 2002](#)). Therefore, as body-size differences may affect factors such as predation risk, nutritional requirements and activity budgets, the search for a ubiquitous underlying cause for sexual segregation may be best employed by studying species that are not sexually dimorphic. If the differences in body-size effects are removed, it seems logical to assume that the effects of other variables on sexual segregation can be evaluated more objectively. To this end, future research in this area should have a greater focus on the systematic study of sexually size monomorphic species.

A handful of marine vertebrate researchers have, in retrospect, attempted to explain sexual segregation in their study species within the sexual segregation framework. However, the hypotheses proposed have not been rigorously tested. Such investigations are difficult to conduct due to the large size of study animals and the general inability for performing 'natural-experimental' manipulations at the appropriate scales. However, within marine vertebrates, the catsharks (of which there are about 100 species) may provide a useful model group with which to investigate the underlying causes of sexual segregation. Importantly, many are monomorphic with respect to body size, they do not exhibit parental care, and they are relatively abundant with a small adult size amenable to manipulations in laboratory aquaria. The latter characteristic emphasises what it perhaps most sorely needed to make progress in this field—the systematic test of hypotheses with the aid of behavioural manipulations. Without doubt, future research should employ a multi-faceted approach, incorporating field observation and manipulative experiments under controlled conditions to attempt to elucidate proximate and ultimate explanations of sexual segregation in species.

Understanding the underlying causes of sexual segregation is important for conservation reasons due to the need to understand space used by individuals to help with their conservation, but also because of the potential

for differential human exploitation of the sexes, for example, through spatially focused fisheries. To effectively manage animal populations, careful and thorough evaluation of distribution, habitat requirements and potential threats to populations are needed (Catry *et al.*, 2005). This information, especially where the sexes are concerned, is frequently lacking. Widespread sex-specific habitat and/or forage selection in marine vertebrates advocates separate treatment of the sexes in population models and management plans. However, in the case of marine fisheries for large pelagic fish such as sharks, there is currently no requirement for vessels to record the sexes of captured individuals. Given the widespread decline in many marine vertebrates worldwide, there is a clear and prescient need to understand in greater detail the spatial and temporal dynamics of sexes within populations. The careful study of the behavioural strategies underpinning observed distributions including sexual segregation are a means to approach effectively particular conservation problems. Nevertheless, marine vertebrates range widely within the marine environment and often span national jurisdictions, where different regulations may apply, and which makes effective population management extremely difficult. The studies reviewed in this chapter are the first step towards a greater understanding of spatial population dynamics, a field which we think when mature has the potential to contribute significantly not only to behavioural ecology and evolution, but to management strategies and conservations priorities also.

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