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Movements of Marine Fish and Decapod Crustaceans: Process, Theory and Application

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Many marine species have a multi-phase ontogeny, with each phase usually associated with a spatially and temporally discrete set of movements. For many fish and decapod crustaceans that live inshore, a tri-phasic life cycle is widespread, involving: (1) the movement of planktonic eggs and larvae to nursery areas; (2) a range of routine shelter and foraging movements that maintain a home range; and (3) spawning migrations away from the home range to close the life cycle. Additional complexity is found in migrations that are not for the purpose of spawning and movements that result in a relocation of the home range of an individual that cannot be defined as an ontogenetic shift. Tracking and tagging studies confirm that life cycle movements occur across a wide range of spatial and temporal scales. This dynamic multi-scale complexity presents a significant problem in selecting appropriate scales for studying highly mobile marine animals. We address this problem by first comprehensively reviewing the movement patterns of fish and decapod crustaceans that use inshore areas and present a synthesis of life cycle strategies, together with five categories of movement. We then examine the scale-related limitations of traditional approaches to studies of animal–environment relationships. We demonstrate that studies of marine animals have rarely been undertaken at scales appropriate to the way animals use their environment and argue that future studies must incorporate animal movement into the design of sampling strategies. A major limitation of many studies is that they have focused on: (1) a single scale for animals that respond to their environment at multiple scales or (2) a single habitat type for animals that use multiple habitat types.

We develop a hierarchical conceptual framework that deals with the problem of scale and environmental heterogeneity and we offer a new definition of ‘habitat’ from an organism-based perspective. To demonstrate that the conceptual framework can be applied, we explore the range of tools that are currently available for both measuring animal movement patterns and for mapping and quantifying marine environments at multiple scales. The application of a hierarchical approach, together with the coordinated integration of spatial technologies offers an unprecedented opportunity for researchers to tackle a range of animal–environment questions for highly mobile marine animals. Without scale-explicit information on animal movements many marine conservation and resource management strategies are less likely to achieve their primary objectives.

1. INTRODUCTION

Understanding animal movement patterns in time and space is fundamental to the study of animal ecology and to the design of effective conservation and resource management strategies. Animal movement is an important ecological process that determines the spatial, demographic and genetic structure of

populations (McCauley, 1995; Hanski and Gilpin, 1997; Wiens, 2000) and links levels within trophic and nutrient hierarchies through the transport of material (including biomass) (e.g. Deegan, 1993; Kneib, 1997b; Marguillier *et al.*, 1997; Laffaille *et al.*, 1998). Movement paths of individuals and populations reflect both ecological and evolutionary responses to environmental heterogeneity (Southwood, 1977; Levin *et al.*, 1984; Cohen and Levin, 1991). For some species, movements between habitat types, such as coral reefs and adjacent seagrasses and mangroves are thought to be critical to the maintenance of populations in an area (Parrish, 1989; Eggleston *et al.*, 1998; Acosta, 1999; Nagelkerken *et al.*, 2001). Highly mobile species, such as many fish and decapod crustaceans, exhibit complex and sometimes predictable movement patterns (e.g. home range activity and movements associated with ontogenetic shifts, spawning migrations and planktonic eggs and larvae). These patterns cover temporal scales ranging from a few minutes to many years and spatial scales from several centimetres to trans-oceanic movements spanning hundreds of kilometres (Quinn and Brodeur, 1991). The complex nature of movements, however, presents both a conceptual and operational problem in selecting appropriate scales in ecological studies (Wiens, 1976; Addicott *et al.*, 1987; Wiens and Milne, 1989; Kotliar and Wiens, 1990; Levin, 1992).

Despite the growing realisation that inferences about ecological phenomena are scale-dependent, ecological scale has rarely been incorporated explicitly into conceptual models or experimental design (Meentemeyer, 1989; Milne, 1991; Levin, 1992; Gardner, 1998). Instead, scales of observation are often selected for their methodological convenience, rather than for their ecological suitability (Meentemeyer, 1989; Haslett, 1990; Petersen and Hastings, 2001). As a result, many studies are undertaken at scales very different from those that are most relevant to the ecological phenomena under study and in many instances, the scales are markedly finer than the routine daily movements of an animal. Unfortunately, this practice constrains and in some cases confounds meaningful inference in ecology. The key question is: How do we identify the appropriate temporal and spatial scales at which to study animal–environment relationships?

The problem of scale selection is by no means a new problem in ecology (reviewed by Schneider, 2001). In terrestrial ecology, it is now widely acknowledged that animals respond to environmental heterogeneity at different scales and in different ways. The variability in response, is in part, a consequence of the way animals move through their environment (Johnson *et al.*, 1992). For instance, highly mobile animals are likely to respond to spatial and temporal heterogeneity at broader scales than sessile animals. Although some marine studies have addressed issues of scale, particularly for foraging studies of broad-ranging marine vertebrates (e.g. Russell *et al.*, 1992; Boyd, 1996), scale selection has often been overlooked in studies of marine fish and decapod crustaceans. Consideration of animal movement patterns, however, may provide a focal point

for the development of a suitable approach to scaling a functionally meaningful environment (Addicott *et al.*, 1987; Wiens and Milne, 1989).

Our overall objective is to develop a scale-explicit conceptual and operational framework that can be applied in the study of animal ecology. The paper is divided into four broad sections. First, we examine a range of life-history strategies and movement patterns of fish and decapod crustaceans that use shallow-water inshore areas, for some or all of their life cycle. Our goal here is to focus explicitly on the scales of movement and to show that: (a) different activity during the life cycle can occupy very different domains in time and space and (b) the scales of animal movement differ widely between species and even between individuals of the same species.

Second, we present a critique of the traditional approach to studies of animal-environment relationships by identifying a number of scale-related limitations. We argue that animal movement has crucial implications for the design of sampling strategies. We focus on examples from studies of free-ranging animals and do not include enclosed experimental studies (e.g. mesocosms), although some of the same scale-related limitations apply (see Petersen and Hastings, 2001). Third, we develop a hierarchical conceptual framework that explicitly incorporates animal movement in scale selection. To facilitate this, a shift in perspective is necessary, away from the traditional anthropocentric view of the 'habitat', with its arbitrary and convenient scales of observation, towards an 'organism-based perspective'. To set the context for this approach we examine the development and application of concepts related to animal-environment relationships including the concept of habitat. Fourth, we present and evaluate a variety of existing techniques that can be integrated through Geographical Information Systems to track animal trajectories and map the environment at multiple spatial scales. These 'tracking and mapping' techniques acquire spatially explicit data that are appropriate for the application of the conceptual framework.

Finally, we discuss the importance of understanding movement patterns to the advancement of our ecological knowledge of marine animals and for improving marine conservation and resource management strategies. We argue that by not considering animal movements, basic ecological studies will have no meaningful spatial and temporal context. Furthermore, without information on animal trajectories throughout their life cycle, many marine resource strategies are less likely to achieve their primary objectives.

2. LIFE CYCLE MOVEMENT PATTERNS IN TIME AND SPACE

Marine fish and decapod crustaceans exhibit a wide range of movements, often covering distances and time scales of several orders of magnitude within a single life cycle. The life cycle movements can be categorised into five broad

types: (1) Movement of eggs and larvae; (2) Home range movement (including tidal and diel movements); (3) Ontogenetic shift; (4) Relocation of home range and (5) Migrations: non-spawning and spawning. Generally, routine movements occupy the smallest domains in time and space and rare movements often occur over greater distances (Meentemeyer, 1989). For instance, home range movements such as foraging activity usually occur at finer spatio-temporal scales than do migrations for spawning. Eggs and larvae can be spatially displaced over large distances owing to hydrographic processes, although throughout most of their life cycle marine fish and decapod crustaceans exhibit active movement (such as swimming, buoyancy control or walking). Movements within a life cycle often occur with predictable sequence and duration, for instance, within daily, tidal, lunar or seasonal cycles.

2.1. Life cycles

Many marine species have evolved a multi-phase ontogeny, in which each phase of life is characterised by changes in morphology, physiology and behaviour (Thorson, 1950; Balon, 1984; Hines, 1986; Fuiman, 1997). These life cycle changes are usually associated with temporally and spatially discrete phases of movement and resource use (Harden-Jones, 1968; Roughgarden *et al.*, 1988; Wootton, 1990; Eckman, 1996). In the life histories of fish and decapod crustaceans, a wide variety of strategies and tactics has evolved, often exhibiting high phenotypic plasticity in response to complex abiotic and biotic patterns and processes, including human activity (Johannes, 1978; Morgan and Christy, 1994; Rochet, 2000). The strategies determine and constrain the pattern and purpose of movements in both time and space (e.g. offshore spawning migrations and the subsequent use of inshore nursery areas). Such movements and resource use patterns have been observed and documented for many years and have probably always been an important process for human coastal populations. Over 2000 years ago Aristotle (approx. 340–350 BC) documented the seasonal inshore–offshore movements of several fish species, the locations and scheduling of their spawning and use of nursery areas. Furthermore, he detailed a wide range of reproductive strategies for cartilaginous and teleost fishes. He wrote “Fishes deposit their eggs close in to shore...for the water close in to shore is warm and is better supplied with food than the outer sea and serves as a protection to the spawn against the voracity of the larger fish. The chalcis, however, spawns in deep water in dense shoals” and “the mullet goes up from the sea to marshes and rivers; the eels, on the contrary, make their way down from the marshes and rivers to the sea” (*Historia Animalium* VI, translated by D’Arcy Wentworth Thompson). More recently, extensive studies of estuarine fish have resulted in the recognition of a number of life cycle categories (Day *et al.*, 1981; Potter *et al.*, 1990). For instance, Whitfield (1999) proposed and described seven life cycle categories

for fish using coastal areas of South Africa and Dall *et al.* (1990) described four strategies for penaeid prawns.

Many individuals of anadromous and catadromous species such as salmon (*Oncorhynchus* spp.) and eel (*Anguilla* spp.) may undertake offshore–inshore migrations over hundreds of kilometres (spanning several years), with each individual releasing several thousand eggs at spawning (Healey and Groot, 1987; McCleave and Kleckner, 1987). Amphidromous species regularly migrate between the sea and fresh water but not directly for breeding, as in anadromous and catadromous species. Other animals appear to have a critical dependence on shallow inshore areas (primarily in the early-life stages) and are thought to benefit in terms of rapid growth and enhanced predator avoidance (Boesch and Turner, 1984; Rozas and Odum, 1988; Sogard, 1992; Gibson, 1994; Perkins-Visser *et al.*, 1996; Rooker and Holt, 1997). In contrast, some animals use inshore areas only occasionally, this often occurring when conditions fluctuate in their favour (termed ‘stragglers’ by Potter *et al.*, 1990 and Whitfield, 1999). Potter *et al.* (1990) estimated at least 70 % of species recorded in estuaries of south-western Australia and temperate southern Africa were ‘marine stragglers’. Furthermore, some life cycles will directly link terrestrial and aquatic environments, such as through the spawning activities of semi-terrestrial crabs, which have evolved to live on land but spawn in the sea, thus ensuring the broad-scale distribution of their progeny. In the Caribbean, the grapsid crab (*Sesarma angustipes*) can live in coastal marine, terrestrial and freshwater environments but the larval stages all retain a critical dependence on sea water (Anger *et al.*, 1990). In contrast to the ‘broadcast spawners’, some site-attached animals such as the damselfish (*Acanthochromis polyacanthus*) are non-migratory and have a non-dispersive larval stage. They exhibit intensive biparental care of a small clutch of several hundred relatively large eggs (Kavanagh, 2000), which enhances survival and ensures retention of juveniles to areas of high quality resources.

In inshore coastal areas, a tri-phasic life-history strategy seems to be the most widespread for many highly mobile species of fish and decapod crustaceans (Fairweather, 1991; Whitfield, 1999). Deegan (1993) stated “estuarine fish faunas around the world are dominated in numbers and biomass by species which move into the estuary as larvae, accumulate biomass, and then move offshore after attaining a large proportion of their adult size”. There are several features common to animals with tri-phasic life cycles (Figure 1). Typically, three key phases of ontogeny, movement and resource use occur: (1) the planktonic movement of eggs and larvae; (2) juvenile use of shallow water areas; and (3) an increase in the home range related to both animal body size and ontogenetic shifts in resource use. Some animals undertake a movement offshore that coincides with the onset of maturity and for some individuals and populations a distinct seasonal migration may also occur. For example, populations of pipefish (*Syngnathus fuscus*) that spawn inshore make extensive offshore seasonal

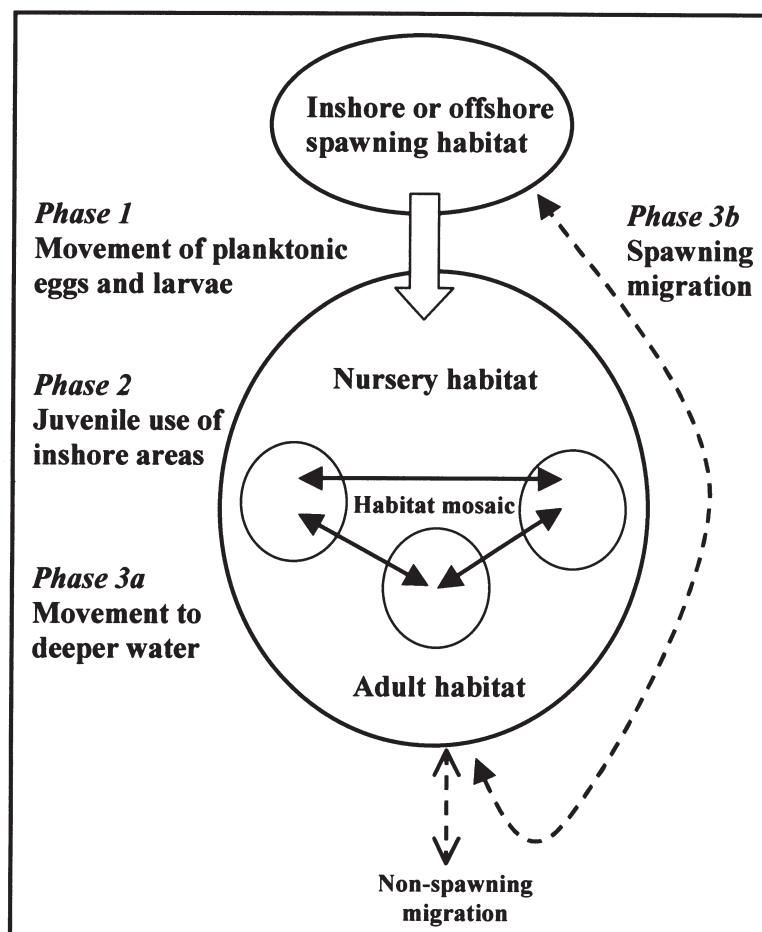


Figure 1 Generalised model of a tri-phasic life cycle showing discrete phases of development and movement. Plasticity in tactics will occur in response to environmental fluctuations and the duration at any developmental phase will vary between species, individuals and geographic location.

migrations to make temporary use of warmer waters (Lazzari and Able, 1990). Life cycle closure may also necessitate a spawning migration to deep offshore waters (Dall *et al.*, 1990; Hill, 1994) or to inshore waters where tidal currents will distribute progeny (Campbell, 1990; Campbell and Able, 1998).

Based on the general tri-phasic life cycle model presented in Figure 1, at least two important features relating to scale and resource use are apparent. First, the life cycle can potentially extend over a range of spatial and temporal scales, with the maximum time and movement defined by the life-history characteristics of

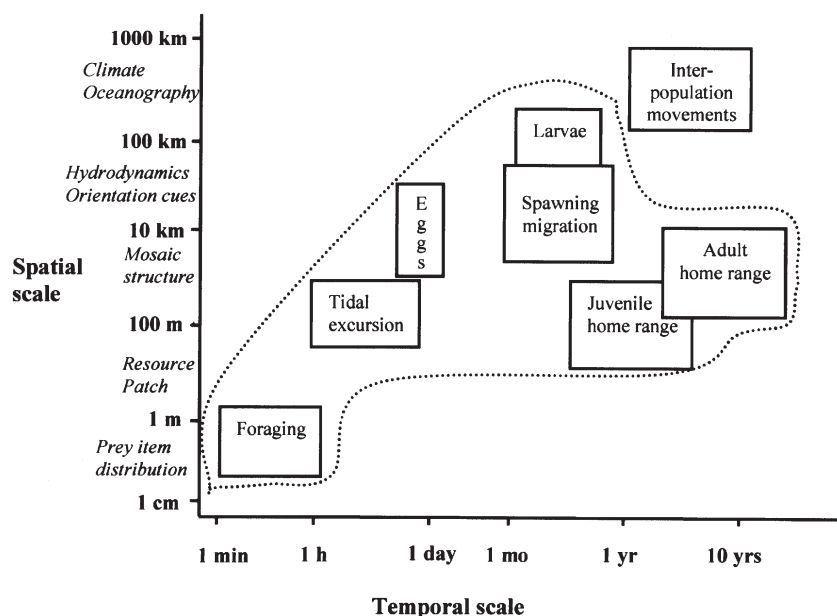


Figure 2 Estimates of space use in time for the life phases of an individual *Acanthopagrus australis* (Sparidae) from Moreton Bay, south-east Queensland, Australia. Scale domains have been estimated using information from tagging studies (Pollock, 1982; Pollock *et al.*, 1983). The *x*-axis displays the temporal scope (maximum relative to minimum duration of a life phase and movement pattern). The *y*-axis displays the spatial scope (maximum relative to minimum extent of space use). The environmental patterns and processes that interact to maintain populations in Moreton Bay are aligned on the spatial scale. Scope diagrams such as this can be useful in matching scales between research programs and natural phenomena (Schneider, 1994) and are a useful tool in the scaling procedure undertaken while planning a study. Broken line: scale domain for the whole life cycle.

the species. Second, an animal often requires different resources at different life stages and therefore, the composition and spatial arrangement of those resources will be critical for achieving life cycle closure. For example, yellowfin bream (*Acanthopagrus australis*) is a tri-phasic and estuarine-dependent fish, endemic to eastern Australia (Figure 2). The following is specific to the life cycle of this species in Moreton Bay, southeast Queensland.

- Phase 1: Female yellowfin bream produce between 300 000 and 3 million eggs in a single spawning that takes place at entrances to the bay. Several weeks later on a full moon, planktonic larvae move inshore at night to settle in seagrasses.
- Phase 2: Post-settlement juveniles use multiple inshore habitat types (e.g. seagrasses and mangroves) through regular tidal excursions from shallow subtidal to upper intertidal areas, which function as 'nurseries'.

Phase 3: Sub-adults and adults make more use of deeper water than young juveniles through a broader home range. In early spring, some mature adults undertake a spawning migration to specific sites near surf bars at the oceanic entrances to the bay.

2.2. Movements of eggs and larvae

Movement and retention of eggs and larvae of many fish and decapod crustaceans is generally thought to occur through a combination of hydrodynamic processes (e.g. tidal flows, surface and subsurface currents and circulation) and active larval behaviour through horizontal and vertical movements (e.g. swimming, buoyancy control) (for fish see Boehlert and Mundy, 1988; Sponaugle and Cowen, 1997; Leis and Carson-Ewart, 1997; 1998; Forward *et al.*, 1999; Epifanio and Garvine, 2001 and for crustaceans see Phillips, 1981; Sulkin, 1990; Young, 1995; Forward *et al.*, 1997; Epifanio and Garvine, 2001). Interaction with water motion occurs at a range of scales, from near-substratum flow, which may influence the settlement process (centimetres-metres) (Butman, 1987; Breitburg *et al.*, 1995) to Langmuir circulation and Ekman transport, tidal currents, internal waves, fronts, eddies and upwelling (100s metres–100s kilometres) (Phillips, 1981; Kingsford, *et al.*, 1991; Shanks, 1995; Werner *et al.*, 1997). Even broader-scale (100s kilometres–1000s kilometres) oceanic circulation patterns (e.g. equatorial gyres) are known to influence the distribution of those species with an extensive planktonic duration (Scheltema, 1986) (Figure 3).

Many of these broad-scale physical hydrodynamics are cyclical and animals have evolved behavioural interactions such as the scheduling of spawning to coincide with lunar phases, seasonal winds and tidal currents (Norcross and Shaw, 1984; Morgan and Christy, 1994; Botsford *et al.*, 2001), or to place the juvenile ‘growing season’ in the warmer, more productive months of the year (Conover, 1992). For example, in Chesapeake Bay, USA, hatching of blue crab larvae (*Callinectes sapidus*) mainly coincides with night-time ebb tides, which distribute progeny offshore in spring and summer when planktonic food resources for larvae are most abundant (Hines *et al.*, 1995). Clearly, this spatio-temporal scheduling of life histories is critical to the maintenance of populations.

For many tri-phasic species, the scales at which eggs and larvae interact with the environment are largely constrained by the distance required for them to reach nursery areas and their duration as a passive, rather than an active component of the plankton. The egg stage is usually just a few days long and has no ability to control its movement, so that individuals can be carried long distances before they begin to influence their movement actively. However, the time spent as eggs and planktonic larvae varies considerably between species. For example, in a variety of fish associated with coral reefs, the planktonic duration can last from a few

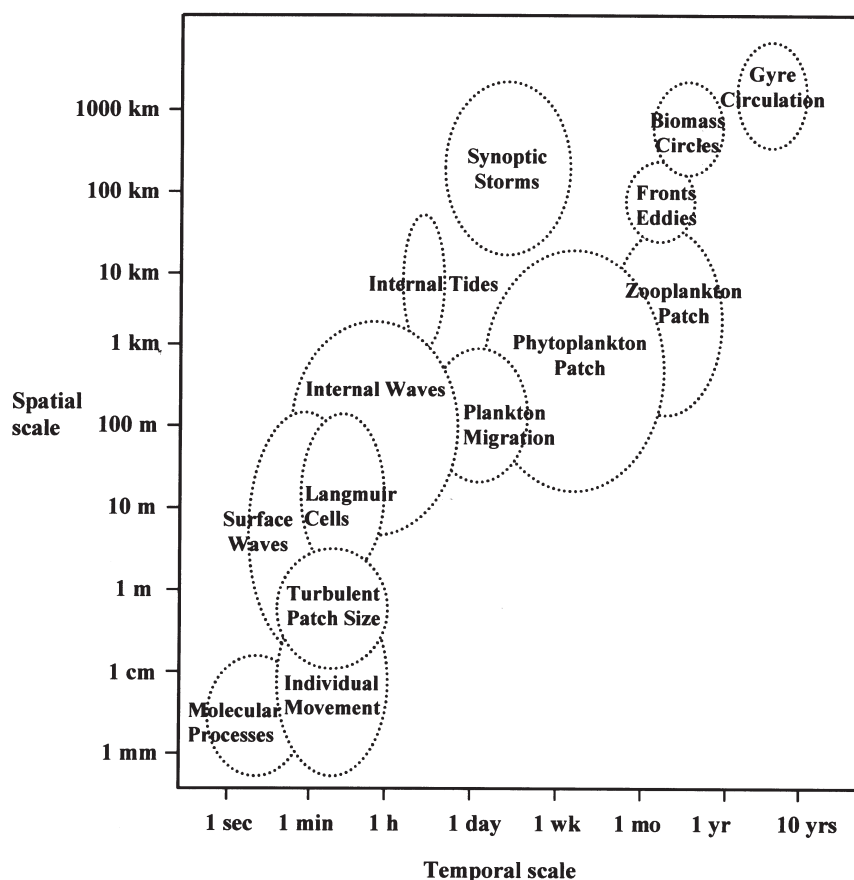


Figure 3 Time-space diagram showing some of the important temporal and spatial scales for physical and biological patterns and processes that are relevant to the movement of planktonic animals in marine ecosystems (adapted from Dickey, 1990).

days to more than three months (Victor, 1991; Lindeman *et al.*, 2000). Victor (1986) recorded planktonic larval duration (PLDs) for 100 species of wrasse (Labridae) and found that PLDs varied widely between and within species, from 17 to 103 days. Some species may have an even more extensive planktonic phase, with active behaviour exhibited only late in the larval phase. For example, after hatching on the edge of the continental shelf off Western Australia, phyllosoma larvae of the western rock lobster (*Panulirus cygnus*) spend almost a year offshore and are driven great distances by wind-induced water movements into the southeastern Indian Ocean. Some larvae have been found more than 1000 km offshore although little is known of their subsequent survival. During this time, the larvae undergo significant development and return shoreward using diurnal

vertical migrations to interact with seasonal geostrophic inflows. Metamorphosis to a free-swimming phase occurs at the continental shelf-break and closer to shore, the Leeuwin Current assists in their transport to coastal reefs of Western Australia, where they settle (Phillips, 1981; Phillips and Pearce, 1997). In addition to the western rock lobster, species such as the Atlantic menhaden, *Brevoortia tyrannus* (Quinlan *et al.*, 1999) and the blue crab, *Callinectes sapidus* (Olmi and Orth, 1995) offer some fascinatingly complex examples of the multi-scale interaction between physical oceanographic features, animal behaviour and life-history evolution.

Hydrological connectivity is a key determinant of population distributions of herring (*Clupea harengus*) in the North Sea (Figure 4). Herring larvae move to more southerly nursery areas facilitated by oceanic inflow and wind-driven currents, and juveniles and adults use the Norwegian Current to move north to spawning grounds (Harden-Jones, 1968; Steele, 1991). This requires an individual animal to travel at least 3500 km (straight-line distance) in order to close the life cycle. Symonds and Rogers (1995) postulated that the population distributions of adult and juvenile sole (*Solea solea*) in the Irish Sea and Bristol Channel, UK, are determined by the spatial relationship between the spawning and nursery areas and suitable hydrographic conditions, which link the two. Studies on fish associated with coral reefs have suggested that in some regions converging currents and eddies facilitate larval retention to areas beneficial to both larval and post-settlement growth and survival (Jones *et al.*, 1999; Swearer *et al.*, 1999). However, the importance of water motion in determining distribution varies between species and geographic location (Gaylord and Gaines, 2000).

2.3. Home range movements

Most animals do not roam randomly. Instead, they exhibit site-fidelity and establish areas where they undertake routine activities such as feeding, resting and defending (Elton, 1927; Burt, 1943; Stamps, 1995; Powell, 2000). Much of the understanding of home range use has come from terrestrial studies, which provide great insight into the way animals respond to their environment. Few studies have attempted to study home range movement patterns of marine animals. For instance, Hooge *et al.* (1999) reviewed the scientific literature from the BIOSIS bibliographic database (1994–1999), revealing that of 374 articles investigating movement in fish and crabs, only 48 had examined home range patterns. The majority of these studies have examined the movements of fish in shallow inshore areas that are typically highly structured, such as rocky shores, kelp forests, coral reefs and seagrass beds. The interaction between animals and benthic structure in these heterogeneous environments influences home range size, shape and use patterns. For example, in the southern Caribbean Sea,

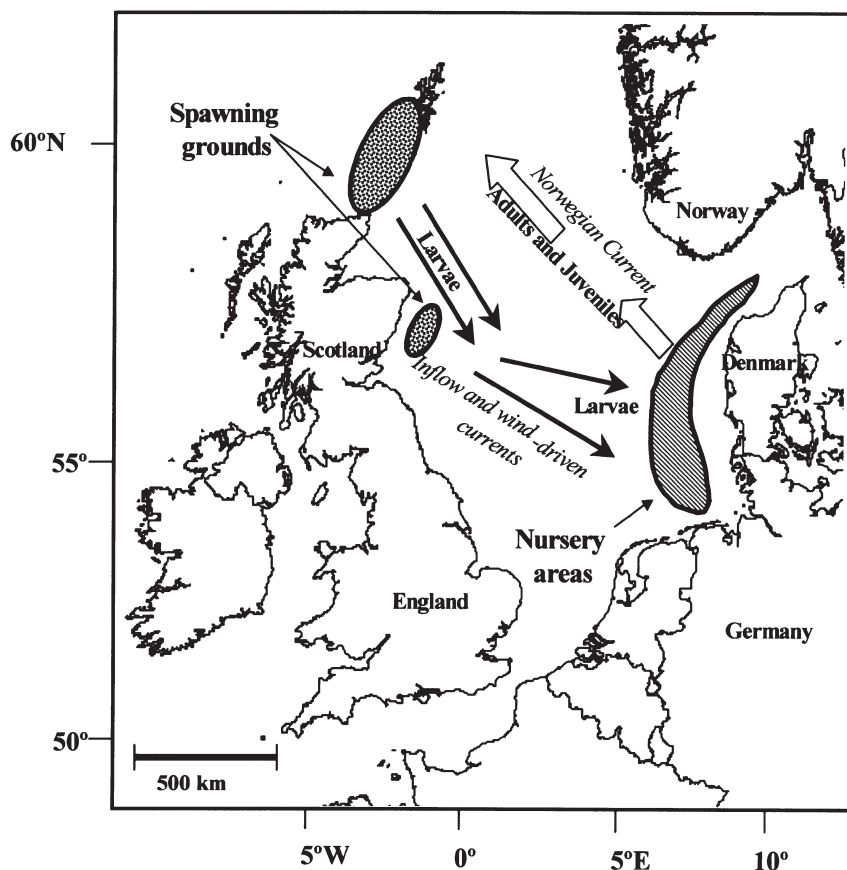


Figure 4 Schematic presentation of the movements within the herring (*Clupea harengus*) life cycle in the North Sea. The larvae move south to nursery areas with wind-driven currents, and juveniles and adults move north to spawning grounds with the Norwegian Current. Movement patterns adapted from Steele (1991). Coastline adapted from a map of the world produced by Environmental Systems Research Institute (ESRI) Inc.

Nemtsov (1997) experimentally manipulated benthic structure by planting artificial seagrasses in close proximity to the territory of green razorfish (*Xyrichtys splendens*). The results showed that individual females increased their home range territory substantially in order to include patches of the artificial seagrasses. Studies by Zeller (1997) on the activity patterns of coral trout (*Plectropomus leopardus*) living in the Great Barrier Reef, Australia, showed that home range contours generally followed the shape of a patch reef. Furthermore, individuals had a preference for a small number of locations within a larger home range area. Similarly, Reese (1989) observed that foraging butterflyfish had highly predictable paths within their home range where they routinely visit,

inspect and feed on certain coral heads. For some animals, a core area within the home range can be identified and within this core area, an individual may move between specific sites for feeding and resting on a daily basis. The home range, therefore, may consist of one or more activity spaces joined by relatively narrow and highly directional movement paths. Covering more than one habitat type with routine, daily movements is thought to be advantageous for many species since this creates an opportunity to use different resources in different patches (Kozakiewicz, 1995).

Some ecological properties of an organism are a function of body size (McNab, 1963; Calder, 1983; Holling, 1992). For land mammals (McNab, 1963; Reiss, 1988; McLoughlin and Ferguson, 2000) and freshwater fish (Minns, 1995) studies have found that home range scaled allometrically with body size. Many authors have found a similar relationship for some marine fish (Sale, 1978; Fitch and Shapiro, 1990; Kramer and Chapman, 1999; Overholtzer and Motta, 1999; Meyer *et al.*, 2000; Shepherd and Clarkson, 2001) but not for others (Zeller, 1997). For example, Kramer and Chapman (1999) regressed body size (23–502 cm) and home range length (0.4–4.6 km) for 29 species of fish using coral reefs, to reveal that body size is strongly correlated with home range length ($r^2 = 0.73$). In contrast, Morrissey and Gruber (1993) reviewed 74 published studies that examined the home range sizes of a broader range of fish and did not find any correlation. The likelihood of finding a positive correlation may depend on the selection of species for the analysis. For instance, many of the fish included by Kramer and Chapman (1999) were relatively small species (almost all ≤ 30 cm fork length) and known to be highly territorial, with larger species more able to defend larger home ranges. Further generality requires that analyses include both temperate and tropical species as well as species from a broader range of distinct functional groups. To our knowledge no attempt has been made to examine such scaling relationships for decapod crustaceans, in part due to the dearth of studies that have estimated their home range size.

Some examples of studies that have estimated home range size for marine fish and crabs with various body sizes are provided in Table 1. The minimum home range size was <1 m² for damselfish (body size 2.5–5.5 cm) ranging to a maximum of 93 km² for adult lemon sharks (body size 1.5–2.3 m). These data are presented to demonstrate that home range size varies widely between species and between individuals of different sizes and ages. It is important to realise, however, that home range size estimation is also influenced by the methods of data collection and analysis, thereby confounding most comparative analyses.

For marine animals, variability in home range use can be more complex than a simple scaling relationship with body size. For example, ultrasonic telemetry of the cunner (*Tautoglabrus adspersus*) in Newfoundland revealed seasonal differences in home range and even differences between the times of day, with broader space-use patterns in the afternoon than in the morning (Bradbury *et al.*,

Table 1 Home range sizes for marine animals of different species, life stage and body size. The examples are listed in descending order of home range size, which generally increases with body size. However, correlation between body size and home range size is confounded by differences in home range shape, space-time use patterns, sampling strategy and measurement technique.

Species	Home range (km ²)	Life stage/ body length (cm)	Measurement time (frequency and duration)	Technique	Source
<i>Dascyllus aruanus</i> Damselfish (Australia)	< 0.001	Juvenile/ Adult 2.5–5.5	Daily for 12 weeks	Mark and resight	Sale (1971)
<i>Scarus</i> spp. Parrotfish (Florida)	0.018–0.036	Juvenile 4–10	1 hour per fish	Visual sighting using SCUBA	Overholtzer and Motta (1999)
<i>Tautoglabrus</i> <i>adspersus</i> Wrasse (Canada)	0.3–2.3	Adult 19.4–25	2–32 days per fish	External ultrasonic	Bradbury <i>et al.</i> (1995)
<i>Maia squinado</i> Spider crab (NW Spain)	0.5–3.7 horizontal distance	Juvenile/ Adult 9–17.1	19.8–141.8 days 0.4–11 d intervals	External ultrasonic	González- Gurriarán and Freire (1994)
<i>Negaprion</i> <i>brevirostris</i> Lemon shark (Caribbean)	Juvenile 0.23–1.26 Adult 9–93	Juvenile 46.8– 100.6 Adult 150–230	<10 h continuous day/night	External and internal ultrasonic	Morrissey and Gruber (1993); Gruber <i>et al.</i> (1988)
<i>Mulloides</i> <i>flavolineatus</i> Goatfish (Hawaii)	Day 1.2–3.2 Night 5.2–11.6	Adult 28.4–31.8	24–48 h continuous 2–16 days	Internal ultrasonic	Holland <i>et al.</i> (1993)
<i>Plectropomus</i> <i>leopardus</i> Grouper (Australia)	Fringing reef 10.4 Patch reef 18.7	Adult 37.6–67.5	3–4 records per day	Internal ultrasonic	Zeller (1997)
<i>Parupeneus</i> <i>porphyreus</i> Goatfish (Hawaii)	14.97– 35.16	Juvenile/ Adult 20.5–25.7	42–92 h continuous 3–14 days	Internal and external ultrasonic	Meyer <i>et al.</i> (2000)
<i>Kyphosus sectatrix</i> Chub (Caribbean)	14.97– 52.54	Adult 26–45	5–51 days	Internal ultrasonic	Eristhee and Oxenford (2001)

1995). In the same region, Clark and Green (1990) tracked Atlantic cod (*Gadus morhua*), revealing broader home ranges during summer. These summer home ranges had distinct diel movements from deep to shallow water and nocturnal feeding activity. In contrast, autumn home ranges were smaller and confined to shallow waters (<20 m), with daytime feeding and resting at night. Differences in home range use between males and females have also been found in some species (Bradbury *et al.*, 1995). For several shark species, males and females have been found to segregate into single sex aggregations and this behaviour is an important factor in the structuring of populations in time and space (Klimley, 1987; Sims *et al.*, 2001).

For terrestrial animals, McLoughlin and Ferguson (2000) suggested that a hierarchical pattern of ecological and physiological factors including body size, seasonal food availability, predation and even climate change might determine home range size. It is not clear exactly which factors control home range use for marine animals, but it is likely to be a result of a combination of life-history characteristics, body size, resource requirements, composition and spatial arrangement of resources, as well as inter- and intra specific-interactions. Consequently, home range size, shape and temporal-use patterns vary widely among animals. This variation makes attempts at boundary delineation difficult (Powell, 2000). For marine fish, Kramer and Chapman (1999) hypothesised that a more 'generalist' species (i.e. able to use multiple patches or habitat types) will have a larger home range than a more 'specialist' species. They also proposed the development of an index, based on easily measured morphological, physiological and behavioural traits. The index would provide estimates of mobility and therefore scale, without the direct measurement of movement patterns. For instance, traits associated with low mobility would include relatively small body size, non-schooling behaviour, critical dependence on a particular resource and morphological features associated with a more site-attached mode of locomotion (i.e. non-continuous swimming) (Kramer and Chapman, 1999). However, the calculation and verification of such an index would require extensive data collection on movement patterns using techniques such as those listed in Table 1.

Daily tidal fluctuations in water level and changes in light intensity also significantly influence home range movements. These movement patterns are particularly important considerations in the selection of spatial and temporal scales for studies of animals using inshore areas and therefore warrant further study.

2.3.1. Tidal excursions

In tidally dominated waters many fish and crustaceans move with the ebb and flow of the tide on routine excursions between intertidal and subtidal areas. For these animals, the neighbourhood or home range extent will be determined by

interacting factors related to the cost-benefit of an excursion, including life-cycle strategy, body size, shore profile, tidal range and amplitude (water depth change), predation pressure, food availability and the composition and spatial arrangement of resources (e.g. patchy and continuous vegetated areas). In most areas, the overall patterns of distribution are continually changing as individual species move into and out of shallow water at a variety of time scales. For temperate fish, Kuipers (1973), van der Veer and Bergman (1986), Kneib (1987), and Rangeley and Kramer (1995) have recorded higher densities in shallow subtidal waters at low tide than at high tide in both the subtidal and intertidal. This suggests a large influx of fish moving inshore and dispersing over intertidal areas with the flooding tide. Wirjoatmodjo and Pitcher (1984) in Northern Ireland and Szedlmayer and Able (1993) in New Jersey, USA, tracked flounder using ultrasonic telemetry. The authors demonstrated that these fish follow the tide and that frequency, direction, distance, speed and duration of movement were all significantly linked to tidal dynamics.

Many penaeid prawns also have strong tidally-based patterns of behaviour and can be sensitive to small changes in pressure owing to changes in water level (Dall *et al.*, 1990; Kneib and Wagner, 1994; Kneib, 2000). For instance, in Kuwait, Bishop and Khan (1991) observed that in the absence of aquatic vegetation, juvenile penaeid prawns (*Metapenaeus affinis*) moved with the edge of the advancing and receding tide. In Moreton Bay, Queensland, some species of toadfish (Tetraodontidae) will use the very edge of the advancing water, moving in and out of the intertidal in only a few centimetres of water (pers. obs). This movement pattern would maintain an animal's position in the shallowest water, thereby gaining refuge from aquatic predators and limiting energy expenditure. Regular tidal excursions may benefit growth in some species (Weisberg and Lotrich, 1982; Peterson and Turner, 1994; Irlandi and Crawford, 1997). Studies have shown a tidal periodicity in feeding, as evidenced by fuller guts on ebbing tides than on flooding tides (for fish see Kuipers, 1973; Rountree and Able, 1992; and for crustaceans see Ryer, 1987).

Another example of tidally synchronous movements was observed for fish assemblages using an inner reef flat in Madagascar (Vivien, 1973). Two distinct species assemblages were recognised, a numerically dominant "permanent stock" composed mainly of smaller omnivorous fish, whose feeding behaviour appeared unaltered by the tides and a "temporary stock", composed mainly of larger carnivores and herbivores that moved with the flooding tide to feed in shallower water. This study showed that fish response to fluctuating water levels was highly variable, even within a relatively small area (Figure 5). On a flooding tide, some fish moved more than a kilometre from open water to the inner reef flat to feed, whilst others moved a few hundred metres from reef to seagrasses or remained within a particular zone and instead moved vertically into the water column. Although home ranges were not estimated, of importance here is that Vivien (1973) recognised the significance of tidal excursions to the

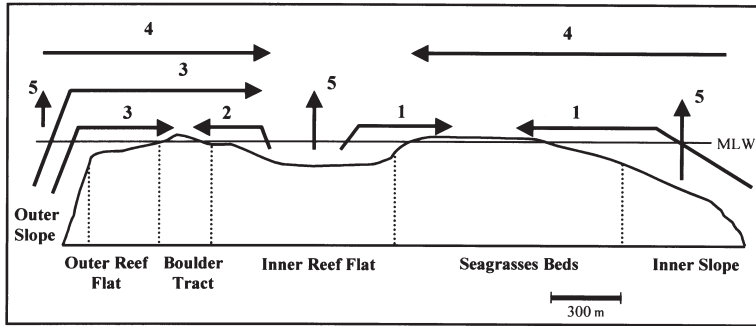


Figure 5 Tidal movements for assemblages of fish on the fringing reef of Tulear, Madagascar. Fish are grouped according to the type of movement between distinct reef zones that were observed during a rising tide. **1** and **2**: movement from the inner reef flat to feed in seagrasses and on the rubble bank; **3**: movement from the outer slopes to feed in shallower water in the inner reef; **4**: movement of pelagic fish from deeper waters to feed on the inner reef; **5**: movement up into water column. Modified from Williams (1991). Originally from Vivien (1973) and redrawn and translated from the French by Williams (1991).

dynamics of assemblage structure. This type of basic movement data is rare, with few studies explicitly stating the scales of movement and even fewer estimating species-specific scales of movement for multi-species assemblages.

From studies in Georgia, USA, Kneib and Wagner (1994) demonstrated that for fish and decapod crustaceans using saltmarshes, a life-history specific relationship with tidal marsh utilisation existed, where distance travelled by resident species was less than that travelled by transient species. Kneib (1997b) proposed that resident species moved in with the tidal front earlier in the tidal cycle than transient species and were the last to leave with the receding tide. However, it is likely that the details of this pattern vary between species and functional groups and from region to region. In some inshore areas of Moreton Bay, Queensland, large-bodied transient species such as mullet (*Mugil cephalus*) are capable of early entry with the flooding tide and of leaving surprisingly late on the ebb. The timing of 'turn-around' of an animal and movement back to subtidal waters will vary and for some, will be related to the need to avoid stranding. Cues for scheduling may include pressure, temperature, direction of water flow and oxygen concentration, as well as biological features such as body size, morphology and physiology. For instance, some crabs and fish have evolved pressure sensors such as specialised hair cells and swim bladders that respond to slight changes (nanometre scale) in hydrostatic pressure enabling them to synchronise their behaviour to tidal cycles (Fraser and Macdonald, 1994; Fraser and Shelmerdine, 2002). Enright (1970) argued that environmental cues alone would not be reliable enough to facilitate a timely turn-around, and in his 'ebb tide theory' proposed that an internal rhythm was necessary to ensure survival.

Not all animals move inshore with a rising tide (Gibson *et al.*, 1996) and an inshore assemblage may be composed of animals with varying dependencies on periodically available intertidal resources. Janssen and Kuipers (1980) sampled common shrimp (*Crangon crangon*) in the Wadden Sea, Netherlands, at a range of water depths and found that only 5% of the population made extensive tidal excursions. Although almost all animals found in the intertidal are there as a result of tidal excursions at some stage, some species (and life stages) may be adapted to remain in intertidal areas whether inundated or not, through burial or an ability to survive in residual bodies of water (Gibson, 1982). Many small-bodied animals use residual water trapped in topographically complex areas such as rock pools, pits excavated by feeding stingrays, ponds, creeks, waterlogged areas or human induced modifications to substratum such as baitdug pits, drainage channels and even trampled mud (Gibson, 1982; Kneib, 1997a,b; pers. obs.). It is not clear whether these animals actively select pools or are stranded, or indeed whether they experience enhanced growth and survival. Shallow pools appear to be poor quality since they are exposed to predation from shore birds and some fish and crustaceans and have higher abiotic variability than water in the moving tidal front. For example, on sandflats, mangroves and seagrasses in Moreton Bay, Queensland, high densities of early juveniles (<20 mm TL) of transient schooling species including whiting (*Sillago* spp.), crescent perch (*Terapon jarbua*), mullet (*Mugil cephalus*) and small decapod crustaceans were often observed in stingray pits. In the summer months, these pits frequently experienced low salinity (after heavy rainfall) and attained relatively high temperatures (37°C) (unpub. data). However, early life stages of some species are known to have broad tolerance ranges and the animals in most pits appeared to survive at least until the next flood tide. Experiments by Kneib (1987) suggest that juvenile killifish (*Fundulus heteroclitus*) are adapted to remain in residual water to avoid predation by adults in subtidal waters.

2.3.2. *Diel movements*

In numerous extractive sampling studies and visual censuses, differences in space-use patterns between day and night have been reported as evidence of diel movements (extractive sampling, e.g. Robblee and Zieman, 1984; Sogard *et al.*, 1989; Vance and Staples, 1992; Rountree and Able, 1993, 1997; and visual census, e.g. Rooker and Dennis, 1991; Nagelkerken *et al.*, 2000a). Evidence of diel movements has also been found for some species through observations of a behavioural response to light in laboratory conditions (e.g. Vance, 1992; Borg *et al.*, 1997). Telemetric studies have also shown that many fish move cyclically between the day and night sections of a home range. For instance, using ultrasonic telemetry Holland *et al.* (1996) revealed that blue trevally (*Caranx melampygus*) in Hawaii exhibited predictable movements between spatially

distinct daytime and night-time areas. For some species, the daily 'migrations' are movements from daytime refuges to nocturnal foraging grounds, although for other species the schedule is the opposite. Meyer *et al.* (2000) tracked five goatfish (*Parupeneus porphyreus*) using acoustic transmitters and revealed a distinct diel pattern of movement. The largest individual (257 mm) was tracked continuously for 48 hours travelling distances of up to 500 m from daytime resting areas to night-time foraging areas, where it ranged over as much as 10 000 m² for up to nine hours. Klimley (1993) tracked individual scalloped hammerhead sharks (*Sphyrna lewini*) in the Gulf of California to reveal that individuals undertook highly directional movements (along the same paths) between nocturnal feeding areas and daytime schooling areas.

Using simultaneous ultrasonic telemetry of 28 juvenile cod (*Gadus morhua*) off Newfoundland, Cote *et al.* (1998) observed that some individuals travelled several hundred metres to shallow inshore areas at night and spent daylight hours in deeper water (Figure 6). The nocturnal feeding regime is exemplified by juvenile grunts (*Haemulon flavolineatum*) in the Caribbean Sea, which move along highly predictable pathways from daytime refuge in aggregations over coral reefs to individual foraging behaviour in adjacent patches of sand, seagrasses and macroalgae at night (Helfman *et al.*, 1982; Nagelkerken *et al.*, 2000a). In Hawaii, Holland *et al.* (1993) tracked goatfish (*Mulloides flavolineatus*) and found that they used a consistent route between fixed schooling locations during the day and individual feeding grounds during the night. Brown surgeonfish (*Acanthurus nigrofuscus*) in the northern Red Sea also follow distinct pathways inshore every morning, from nocturnal shelter to daytime feeding sites, with distances ranging from 10 m to over 1 km (Mazeroll and Montgomery, 1998). These authors observed an emergence of *A. nigrofuscus* just before sunrise, with aggregations forming before departure, which they suggest is the use of an internal clock rather than a response to light. In contrast, Zeller (1997) reported high site fidelity throughout day and night for rockcod (*Plectropomus leopardus*) in the Great Barrier Reef, Australia. A diel cycle of emergence and movement is also common in burrowing decapod crustaceans (Vance and Staples, 1992), with most species burrowing during the day and emerging at night (Vance, 1992). Some species of penaeid prawns show peaks in activity following a 'bimodal crepuscular pattern', with a peak after dusk and before dawn (Dall *et al.* 1990).

2.4. Ontogenetic shifts

Ontogenetic changes in morphology and physiology allow life stages to respond individually to the different selection pressures they experience in their environment (Ebenman, 1992). Effective exploitation of widely differing resources often requires different movement patterns within the life of an individual. The most commonly reported ontogenetic changes in movement patterns are

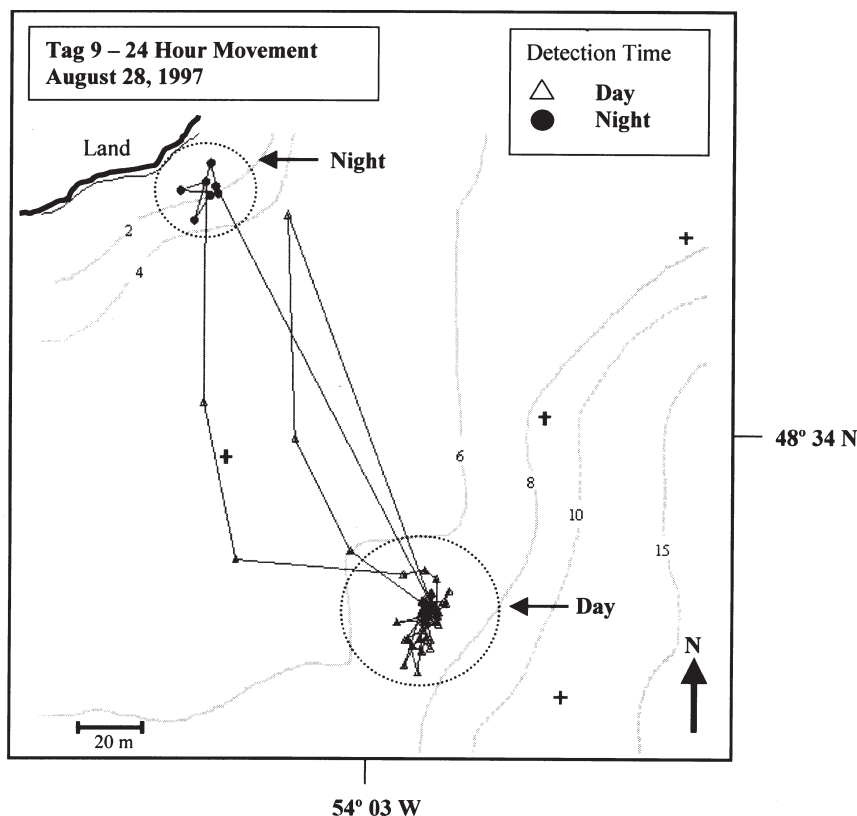


Figure 6 Temporal trace of an individual Atlantic cod (*Gadus morhua*) for a 24-hour period in the summer (Aug. 28th, 1997) off Newfoundland (Cote *et al.*, 1998). The data indicate a pattern of relatively limited movements in deeper water during the day followed by distinct linear movements to shallower inshore water at dusk. Numbers along contours indicate depth in metres. Reproduced with permission of David Cote, Parks Canada, Newfoundland, Canada.

associated with refuge function, predation pressure, physiological requirements and diet, all of which are usually associated with increasing body size (Werner and Gilliam, 1984; Dahlgren and Eggleston, 2000). For many species, significant shifts in space-use patterns are reported to occur within the first few weeks and months after settlement, when movement patterns are often represented by a strong size-depth relationship (Ruiz *et al.*, 1993; Gibson *et al.*, 1996, 2002). For example, after settlement, plaice (*Pleuronectes platessa*) in the North Sea concentrate in shallow waters (<1 m deep) and show a positive relationship between body length and water depth (Gibson *et al.*, 2002). Macpherson and Duarte (1991) observed a significant positive size-depth relationship for most of 75 coastal demersal fish from the Mediterranean and southeast Atlantic. In the same region, Macpherson (1998) observed that juveniles of three species of sparid fish exhibited initial high site

fidelity to shallow water areas and, after several months, a subsequent size-dependent movement to deeper water. Harmelin-Vivien (1989) and Chabanet and Letourneur (1995) observed a differential distribution of size-class cohorts for many fish species around coral reefs. In North Carolina, USA, size-selective offshore movement of brown shrimp (*Penaeus aztecus*) from inshore nurseries has been surmised from catch data showing changes in the length frequency distributions (Wicker *et al.*, 1988). Furthermore, extensive studies of nekton using saltmarshes in Georgia, USA, by Kneib (1997b, 2000) resulted in the development of a conceptual model that represented size depth patterns of utilisation for a range of life-cycle strategies (e.g. resident and transient species) (Figure 7).

Few studies have actually tracked animals for long enough periods to capture directly ontogenetic shifts in space-use and almost all evidence that supports movement is largely indirect, based on spatio-temporal changes in the distribution and abundance of animals (Beck *et al.*, 2001). However, some direct evidence has been provided through telemetric and tagging studies. For example, using ultrasonic telemetry, Hines *et al.* (1995) showed an ontogenetic change in movement pattern of juvenile blue crabs (*Callinectes sapidus*) in Chesapeake Bay. After settlement to seagrasses, the crabs moved between 50–250 km into shallower, brackish water sub-estuaries in order to evade predators, feed and grow. After one

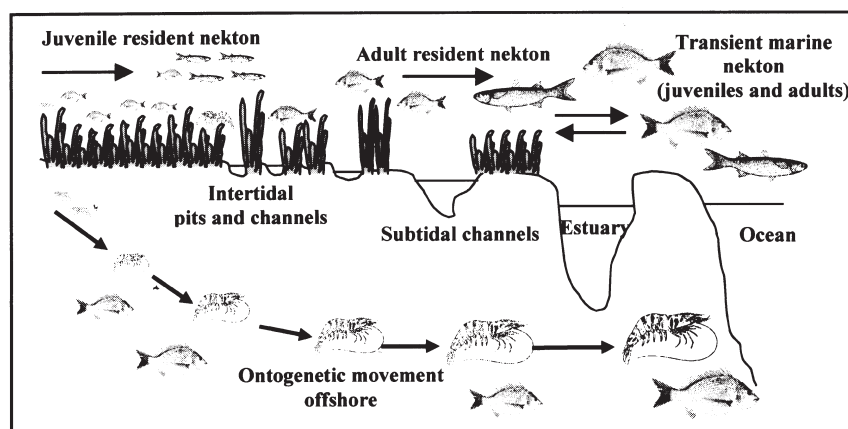


Figure 7 A model of spatial patterns in nekton use of intertidal saltmarsh and adjacent estuarine waters by different life stages of resident and transient species. This is redrawn from Kneib's conceptual model of a trophic relay concept (Kneib, 2000) that represents the inshore-offshore transport of production. The youngest individuals of both resident and transient species use the vegetated intertidal for food and refuge, with some species even remaining on the marsh surface at low tide. As they outgrow refugia, the home range broadens to include deeper water. In subtidal areas at low tide adult resident species become prey for larger juveniles of transient species. This trophic interaction forms another link in the 'trophic relay' (*sensu* Kneib, 2000) that transports intertidal productivity offshore. Animals depicted are intended to be schematic.

year, the crabs moved further into deeper water. In the Tamar Estuary in England, extensive mark-recapture studies for newly-arrived juvenile Dover sole (*Solea solea*) suggest an initial up-estuary movement as far as 22.7 km from the estuary mouth, followed by a later down-estuary movement forced by a seasonal decrease in salinity (Coggan and Dando, 1988).

Some ontogenetic shifts are related to size-specific changes in food types. The most typical changes are from planktonic to benthic feeding, which may also be accompanied by a change in movement patterns. McCormick and Makey (1997) observed a shift in diet and home range size in the goatfish (*Parupeneus multifasciatus*) at Lizard Island, Australia. These animals exhibited a shift from plankton feeding in the water column to the broader roaming movements that are associated with benthic foraging. Furthermore, after settlement McCormick and Makey (1997) observed a rapid increase in home range size from a strongly site-attached home range of 3 m² at four days post-settlement to a mean home range of 60 m² at seven days and 245 m² at two months. In some cases, dietary shifts are attributed to the morphological changes in feeding apparatus. Stoner and Livingston (1984) detailed how the estuarine pinfish (*Lagodon rhomboides*) shifted from zooplanktivore to epibenthic invertivore to omnivore, finally becoming herbivorous. Although, no concomitant change to movement patterns was reported.

The functional attributes of the environment of an animal can either change or diminish with a progressively larger body size. Eggleston (1995) found Nassau grouper (*Epinephelus striatus*) in the Bahamas settle and remain in and around macroalgal clumps for 3–5 months before outgrowing their shelter and moving out to patch reefs. Lipcius *et al.* (1998) found similar shifts in Caribbean spiny lobster (*Panulirus argus*), describing a movement away from areas with ample food but limited shelter, to a high quality refuge in coral reefs. Acosta (1999) also examined the distribution of spiny lobster in the Caribbean Sea and concluded that a range of interlinked habitat types was necessary to meet the changing resource requirements that occurred throughout the complex life cycle. In fact, many fish and decapod crustaceans, shift through a ‘critical chain’ of habitat types whilst using heterogeneous inshore areas (Acosta and Butler, 1997; Nagelkerken *et al.*, 2000b; Nagelkerken and van der Velde, 2002).

Clearly, the composition and spatial arrangement of component habitat types (including their proximities to one another) across a range of scales, is important in meeting the requirements of ontogenetic change. However, it is important to note that some animals show no evidence of ontogenetic shift and juveniles are found in the same areas and using the same resources as adults (Harmelin-Vivien, 1989; Green, 1996).

2.5. Relocations of home range

Relocation of a home range is a change in the location of the home range that is not recognised as an ontogenetic shift or a migration. The factors that initiate

relocation are unlike those that initiate an ontogenetic shift, as they are not necessarily related to life-cycle changes during the morphological and physiological development of an animal. Furthermore, the relocation movement process is unlike a migratory trajectory since it relies largely on routine sensory responses during searching behaviour and will likely be multi-directional. Kramer and Chapman (1999) described relocating behaviour as a highly adaptive response to the changing environment when the net benefits of moving are greater than the net benefits of not moving. Most fish and decapod crustaceans have a highly-tuned sensory ability and great mobility throughout most of the life cycle, which provide an enhanced ability to relocate in response to unfavourable conditions (Sogard, 1994). Several processes can create situations where animals may seek an alternative home range location. For instance, planktonic stages arriving in areas with sub-optimal conditions for growth and survival may settle and redistribute or on not receiving the necessary cues, will delay transition to the benthos and keep moving. However, it is debatable whether a home range would have been established at this early stage. Nevertheless, this type of movement is an important consideration and rarely reported.

Bell and Westoby (1986a, b, c) proposed a "settle-and-stay" hypothesis to explain distribution patterns of animals in seagrasses in New South Wales, Australia. Their model proposed that competent larvae settle into the first seagrass bed they encounter (regardless of quality), then redistribute to suitable microsites within that bed. This model implies site-attachment and largely underestimates the mobility of many marine animals. Several studies suggest that a settle-and-move behaviour is more common for fish. For example, large numbers of fish (of a variety of age classes) moved even over broad expanses of sand to utilize small patches of artificial seagrass (Sogard, 1989) and concrete patch reefs (Walsh, 1985). In addition, Frederick (1997) observed fish that had recently settled on coral reefs move as far as 100 m over open sand. Robertson (1988) has argued that relocation between patches by highly mobile animals is a common phenomena and a major source of the variability reported in studies of fish associated with coral reefs. Furthermore, tagging studies of adults of exploited species have revealed that some animals will move several hundred kilometres, for example, from one bay or estuary to another (Pollock, 1982). The reasons for these types of relocation are usually not known and little information is available on the frequency of such broad-scale inter-population movements.

More well known are examples of relocations resulting from deleterious change to the environment. For instance, a severe storm may increase or decrease availability of shelter and food resources or a pollution event may change water and substratum quality, which may initiate a movement to seek a more suitable location. After severe storms, Stouder (1987) found changes in the distribution of temperate reef fish off Santa Barbara, California, USA. The study area was composed of a complex mosaic of substratum types, which exhibited spatially variable susceptibilities to the storms, thus resulting in patchiness.

In response, some resident fish shifted their home range to include less disturbed patches and some non-resident fish abandoned the reef entirely. Direct human activity such as physical manipulations to the benthos from dredging can also result in some resident animals abandoning or temporarily avoiding an area and opportunistic species moving in to use the disturbed area (Jennings and Kaiser, 1998). Lenihan *et al.* (2001) found that eutrophication, density stratification and oyster dredging combined to deplete dissolved oxygen in bottom waters in the Neuse River estuary, North Carolina, USA. In response, some fishes (termed 'refugees' by Lenihan *et al.*, 2001) abandoned the area and moved to nearby oyster reefs in well-oxygenated waters, where they accumulated in high densities, which resulted in a rapid depletion of prey populations. Changes in animal density and assemblage composition, therefore, can also result in changes to the availability of resources and the dynamics of competition, which may evoke a relocation response. Density-dependent relocations in response to localised increases in fish numbers and biomass have been observed as net movements away from some marine reserves and are thought to result in a phenomenon known as the 'spillover' effect (Russ and Alcala, 1996).

It is not always clear when movement of an animal is a response to suboptimal environmental conditions or to an ontogenetic shift. For example, Lirman (1994) found that juvenile damselfish (*Stegastes planifrons*) living around coral reefs in Honduras avoided the dominant adults of the same species by moving to less favourable areas of the reef to hold territories, before moving back to the main reef as sub-adults to increase their chances of finding a mate. Lirman (1994) described these movements and resource use patterns as ontogenetic shifts. However, if the juveniles are displaced by conspecifics or other species (as observed here) it may be appropriate to consider these movements as home range relocations, rather than ontogenetic shifts. Alternatively, changing body size and the onset of sexual maturity may drive some of the space-use patterns observed for damselfish and warrant the description of an ontogenetic shift. The changes that result in a relocation of a home range are numerous and diverse and cannot be adequately covered here. Further examples can be found in Sogard (1994) and Kramer and Chapman (1999).

2.6. Migrations: non-spawning and spawning

Many marine animals exhibit highly directed and often broad-scale migrations, which are usually quite different from those movements within a home range. Migratory movements can be associated with both changing external environmental conditions (e.g. associated with seasonal variations in temperature, rainfall, productivity and hydrodynamic features) and internal conditions, such as reproductive maturity. Migrations are characterised by the temporary suppression of responses to normal environmental stimuli (e.g. food resources)

and high directionality, with animals often following well-defined routes that usually extend beyond the home range (Dingle, 1995). For example, Herrnkind and McLean (1971) investigated movement patterns of the spiny lobster (*Panulirus argus*) in the Caribbean Sea. In an extraordinary synchronised mass migration, the lobsters were observed walking in single file over 10 km, with deviations generally less than 10°. In the scientific literature, migration is often used to describe diel movements and tidal excursions, however, we consider these to be routine movements within the home range. The definition of migratory behaviour as a highly directional movement may also be applied to the movement of some planktonic larvae and post-larvae. However, for present purposes we confine the term to describe animal movements to spawning areas outside their home range and for seasonal movements to alternative home ranges that cannot be defined as relocations. Furthermore, migrations are usually return journeys, although this depends on the life-history characteristics of the animal.

2.6.1. Non-spawning migration

A non-spawning migration is a highly directional movement to a temporary alternative home range, typically associated with seasonal changes in abiotic environmental factors, such as temperature or salinity changes. For example, by examining the spatial and temporal distribution of the northern pipefish (*Syngnathus fuscus*) in the North-Western Atlantic Ocean, Lazzari and Able (1990) found that the pipefish undertook an extensive seasonal inshore–offshore migration. During winter, the fish moved to warmer continental shelf waters, an estimated 20 km offshore and from spring through to late autumn returned to estuaries. The authors reported that winter inshore temperatures were as much as 10°C colder than offshore waters. This seasonal use of warmer waters is exhibited by many other fish and decapod crustaceans in temperate latitudes. Another example of this type of migration is shown by the Atlantic silverside (*Menidia menidia*). Conover and Murawski (1982) reported a mass offshore winter migration to warmer inner continental shelf waters. At other times of the year they are found in salt marshes, estuaries and embayments in the western Atlantic Ocean and are known to spawn on daytime high tides in saltmarshes (Middaugh and Takita, 1983). Blue crabs (*Callinectes sapidus*) in Chesapeake Bay, USA, and spider crabs (*Maia squinado*) in northwest Spain have also been observed to move in response to seasonal cycles in temperature and food availability (Hines *et al.*, 1995).

Some species, however, undertake seasonal migrations that are strategically placed en route to spawning areas (for fish see, Pihl and Ulmestrand, 1993; Koutsikopoulos *et al.*, 1995; and for crustaceans, Hines *et al.*, 1995). For instance, multiple recapture data from tagged ovigerous lobsters (*Homarus americanus*), off eastern Canada showed a range of movements, from a few kilometres to 322 km (although most were less than 30 km). Many lobsters moved to deeper

water during winter, returning inshore in summer for egg hatching (Campbell, 1986, 1990). This seasonal shallow to deep migration takes place to meet the physiological requirements (i.e. higher temperature) of molting, mating and egg extrusion (Campbell, 1986). Blue crabs are also known to exhibit an over-wintering or hibernation phase in deeper water, which is thought to be associated with an ontogenetic transition from juvenile to sexually mature adults (Hines *et al.*, 1995). Although they may have other functions, these seasonal movements may be better categorised as pre-spawning migrations, rather than seasonal migrations.

2.6.2. Spawning migration

Some individuals may remain within a well-defined area for most of their routine activities and may even mate and spawn within the home range (Robertson, 1983; Fitch and Shapiro, 1990; Shpigel and Fishelson, 1991). Others may move to discrete spawning areas (Shapiro, 1987; Aguilar-Perera and Aguilar-Dávila, 1996), which are usually at specific locations and in specific seasons or phases within lunar and tidal oscillations. The distance of a spawning migration is largely constrained by the frequency of spawning and the size and locomotory ability of the animal (Roff, 1988). In Chesapeake Bay, USA, inseminated female blue crabs migrated 150–200 kilometres down-estuary to deep water in the mouth of the bay to over-winter and to brood their eggs during the following spring and summer. Males, on the other hand, over-winter in the main estuary and do not migrate (Schaffner and Diaz, 1988). In Queensland, Australia, mud crabs (*Scylla serrata*) spend most of their lives in mangrove-lined inshore areas, although ovigerous females have been caught as far as 95 km offshore (mean 30 km), before the onset of the monsoon wet season (October–November) (Hill, 1994). The intolerance of larvae to low salinity (*S. serrata* zoea cannot tolerate salinities below 20), combined with a strategy for broader scale distribution of progeny, necessitates this extensive offshore spawning and is common to most species of portunid crab (Norse, 1977; Hill, 1994).

From observations of fish assemblages using mosaics of habitat types in Palau, Micronesia, Johannes (1978) reported that individual fish move a range of distances from their normal home range to their spawning site (Figure 8). The majority of species in the Palau study moved seaward of their home range and spawned on the outer reef slope. However, high within-species and between-species variation is evident. In the Caribbean Sea, for instance, some bluehead wrasse (*Thalassoma bifasciatum*) will travel more than 1.5 km along specific pathways to join large (>10 000 fish) mating aggregations (Warner, 1995), whilst others spawn within the home range (Fitch and Shapiro, 1990). At specific times of the year, some groupers will migrate large distances to form aggregations that can last from days to weeks. For example, Bolden (2000) tagged 11 adult Nassau grouper (*Epinephelus striatus*) with visual markers and

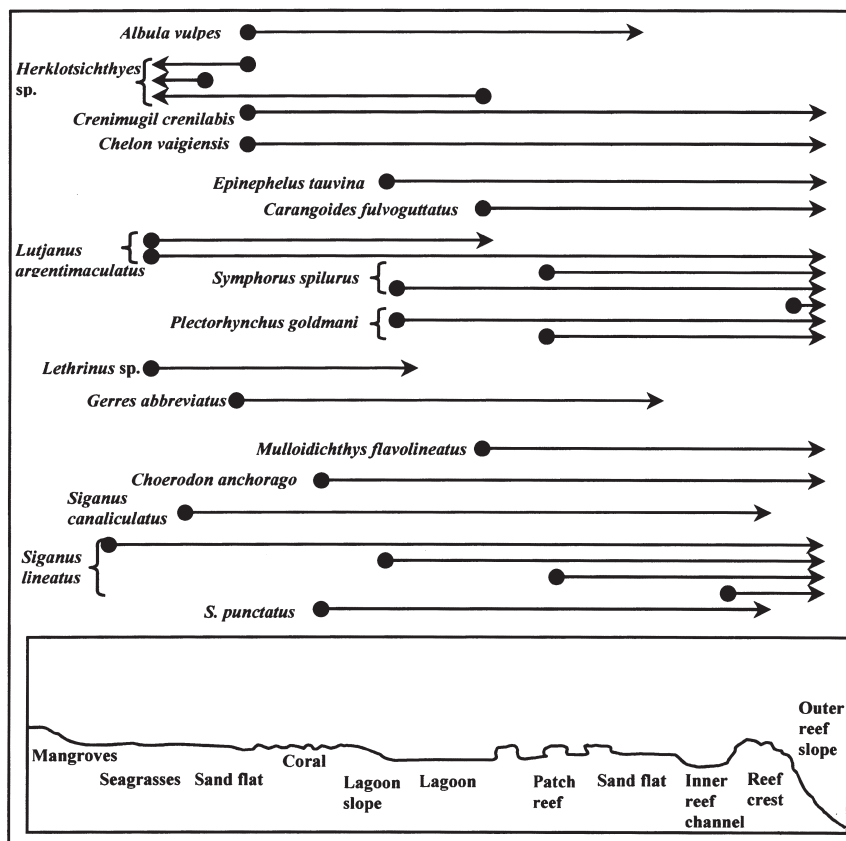


Figure 8 Spawning migrations of fish in Palau, Micronesia, from data collected through underwater observations by Johannes (1978). Arrows show the movement from usual habitat (•) to spawning sites (→). Actual distances travelled were not provided by Johannes (1978). Almost all species undertake a seaward spawning migration, with more than half of all species moving to the outer reef to spawn.

ultrasonic transmitters and tracked them for three weeks, reporting one grouper travelling 220 km to a spawning aggregation. In the Red Sea, Mazeroll and Montgomery (1998) tagged and observed brown surgeonfish (*Acanthurus nigrofusus*) and found that they exhibited simultaneous evening spawning migrations to either one of two mass spawning sites up to 1 km away. Individuals were then observed returning in long lines along specific pathways to nocturnal shelter. Mazeroll and Montgomery (1998) suggested that fish used landmarks on the reef for navigation and proposed that individuals learn routes to spawning sites before active reproduction begins. Socially transmitted learning of routes has also been found in other marine fish (Helfman and Schultz, 1984).

The factors determining the scheduling of spawning can be complex and usually relate to one or more cues over a range of temporal scales. These can include the stage of the tide, time of day, lunar period and season. In Japan, Yabuta (1997) observed the Indo-Pacific butterflyfish (*Chaetodon trifasciatus*) spawning in the vicinity of offshore tidal currents at dusk at either a full or new moon. Monogamous pairs travelled to specific spawning sites, established a small temporary territory in which to spawn and rest for the night, and then returned to their normal home range the next day.

3. CRITIQUE OF TRADITIONAL APPROACHES IN MARINE ANIMAL ECOLOGY

The above sections provide a wide range of specific examples of animal movements, some of which demonstrate that individuals and species operate over a range of scales in time and space. It is clear, however, that although movement patterns are diverse, they can be usefully categorised according to life cycle strategies and the type of activity or behaviour associated with a particular movement. We now discuss both the theoretical and applied aspects of incorporating animal movements in ecological studies, which have crucial implications for scale selection and the design of sampling strategies. This section reviews and critically examines some of the traditional approaches to field studies of marine animal–environment relationships in relation to scale selection. The examples used here reflect the primary focal area of one of the authors (SJP), which is the utilisation of shallow water inshore areas by marine nekton.

The fundamental questions in any study of animal–environment relationships are: At what scale(s) to measure? How to measure? What to measure? Conventionally, nekton in shallow inshore areas have been sampled using a range of techniques, including both active and passive fishing gears such as trawls, seine nets, drop traps etc. (Rozas and Minello, 1997; Millar and Fryer, 1999) and remote sensing techniques, such as underwater visual census (Samoilys and Carlos, 2000). In attempts to link animals to their environment, relationships have been examined by quantifying variables, including sediment grain size, leaf length or percentage live coral cover using benthic cores, quadrats and transect lines. However, rarely have these studies been undertaken at the scales most appropriate to the way that animals use and respond to their environment. This mismatch has occurred because many studies have not explicitly considered the spatio-temporal patterns of animal movement. Instead many studies have collected data at finer scales than even the home range of the target animals. In addition, environmental data have been collected as point samples without spatial and temporal coordinates and without a spatial context with regard to the surrounding environment. As a result, any correlation with the environment can only represent a relatively small spatio-temporal

segment of the animal–environment relationship. Furthermore, few authors have reported the specific scales at which their observations are made or have considered the existence of a scale bias in their methodology. This has serious implications for attempts to undertake comparisons among different studies, particularly between studies of species with distinctly different life histories (Addicott *et al.*, 1987).

The key limitations of traditional approaches to the study of animal–environment relationships are related to:

1. The assumption that animals respond to their environment at a single temporal and spatial scale.
2. The focus on a single ‘habitat type’ for animals that use a mosaic of habitat types.
3. Mismatching scales in the design of sampling strategies.

3.1. Single scale

We now know that animals are influenced by patterns and processes occurring at a range of scales of space, time and organisational complexity (Haury *et al.*, 1978; Hatcher *et al.*, 1987; Steele, 1988, 1989; Barry and Dayton, 1991; Holling, 1992; Levin, 1992; Marquet *et al.*, 1993). Furthermore, marine animals are likely to respond to and be constrained by the composition and spatial arrangement of resources in a hierarchical way, as has been suggested for many terrestrial animals (Senft *et al.*, 1987; Schaefer and Messier, 1995; McAlpine *et al.*, 1999; Rolstad *et al.*, 2000). A single scale approach cannot incorporate important patterns and processes at scales above and below the focal scale and therefore this approach is limited in ecology. In addition, working at one scale is particularly inappropriate for studies of multi-species assemblages since species vary in their response to the environment due to functional differences related to dietary requirements, habitat specialisation, and body size (Pearson, 1993; Lee *et al.*, 2002).

3.2. Single habitat type

Until recently, many studies have focused their research questions on single ‘habitat types’ or ‘biotopes’. These classes of structure are distinguished from one another by a set of common characteristics. For example, a mangrove habitat type is defined by plant species (and its specific location in relation to water level) and is therefore distinguishable from seagrasses. This type of classification process is widespread, particularly in resource management where this approach has allowed simplification of a complex spatial pattern. In ecology, a problem occurs when a single habitat type is selected to represent the scale of a study regardless of how the animal(s) under investigation use their environment. The misleading tendency that has sometimes followed this approach is that

investigators (and subsequent users of the results) have assigned animals to a habitat type (e.g. 'salt marsh fish community'), without information on the actual importance or dependence on other neighbouring habitat types. This error has occurred in studies that have focused on fish and crustaceans that use upper intertidal habitat types through tidal excursions (e.g. saltmarsh, mangroves, rocky shore etc.). For many animals, the upper intertidal is only a small part of the home range and may only be accessible for short periods at high tide. The importance of these areas to the animals is often not known and the arbitrary assignment of a single habitat type descriptor is misleading. Clearly, these animals are not saltmarsh or mangrove fish communities but are a product of a mosaic of adjacent subtidal and intertidal patterns and processes, which combine to maintain a population in a particular area. Very few animal assemblages can be appropriately assigned to a particular habitat type since very few spatially discrete environments exist, with perhaps the exception of lakes and ponds that are discrete for at least some of their inhabitants. In most other aquatic environments, communities intergrade, interact and exist within more complex spatial delimitations.

In summary, measuring attributes in a single habitat type for multi-habitat species will confound any meaningful conclusions on correlates and provide misleading information for resource management strategies. As argued by Roughgarden *et al.* (1988), "studies at only one of the habitats tell no more than half the story". Therefore, if information on animal movement is not available, the assumption of single habitat use should be considered carefully or rejected entirely. If an assumption is to be made, then a multi-habitat type assumption may be more suitable, thus allowing for the consideration of broader-scale movement and potential linkages between component habitat types. This argument is also important in relation to the limitations of some traditional sampling strategies.

3.3. Mismatched scale in sampling strategies

As we have already highlighted, sampling strategies and the selection of techniques and equipment for data capture are often designed without *a priori* information on the scales relevant to the dynamic spatial distribution of animals. For example, Epifanio *et al.* (1989) sampled the spatial distribution of crab zoea at weekly intervals and found that this was insufficient to resolve the details of zoeal transport. Subsequent analyses of wind vector and surface current patterns indicated that the distance a parcel of surface water would have travelled during any week was greater than the radius of the study area. Scale mismatching also commonly occurs in studies that aim to investigate environmental correlates for fishes found using coral reefs. Most surveys of coral reef fish and associated benthic structure have involved daytime counts along line transects (e.g. 50 or

100 m long and 5 or 10 m wide) or stationary counts within a known area and time frame (Samoilys and Carlos, 2000). The methods of visual census have received extensive evaluation but critiques have focused primarily on fish movement as it relates to the accuracy and precision of the technique. This is usually defined as bias introduced by fish swimming speed (and body size), their direction of travel and their position in the water column (Thresher and Gunn, 1986; Watson *et al.*, 1995). The appropriateness of the scale of sample unit area or scheduling of the survey with respect to the spatial and temporal patterns of fish movement are generally not discussed. The key problem is that many of the fish that use coral reefs have broader-scale movements than previously assumed. During a visual census, fish are recorded as they pass through the field of vision of an observer and it is assumed that the underlying substratum (if significantly correlated) has some relevance to the fish. However, the abundance and species richness recorded may in fact be a function of other attributes such as the proximity of suitable night resting areas or food resources in some other part of their home range possibly some distance outside the study area. Equally, animals can be affected by changes occurring in a portion of a home range that is not included in the survey area and will therefore be undetected. To ameliorate this problem, sampling strategies and techniques should be carefully evaluated with regard to variability in temporal activity patterns and the spatial scale of animal movements.

Scale mismatching can also occur when attempting to examine animal use of tidally dominated inshore areas. For instance, when sampling fish undergoing tidal excursions, sampling should be spatially distributed over a range of depths, taking into account the changing phase of the tide (Gibson *et al.*, 1996; Rozas and Minello, 1997). Combinations of techniques may be necessary to achieve this and care must be taken with regard to their suitability for comparative purposes. Only a few studies have attempted to compare two or more inshore habitat types, but these have often been done at the same stage of the tide and have generated non-comparable data sets because of inappropriate sampling strategies.

3.3.1. Case study

An example of how an anthropocentric perspective of habitat can disadvantage research is exemplified by the studies of Morton (1990) and Laegdsgaard and Johnson (1995), who sought to evaluate the importance of several adjacent intertidal habitat types in Moreton Bay, Queensland. They sampled fish in mangroves, adjacent seagrasses and unvegetated mudflats using a combination of semi-quantitative and non-quantitative sampling methods at spring high tide. Comparatively higher yields from mangroves led the authors to attribute greater importance to this habitat type. Morton (1990) reported one of the

highest 'standing crops' ever recorded in mangroves and considered those animals part of mangrove productivity. Laegdsgaard and Johnson (1995) also concluded that mangroves offered a more important nursery function than adjacent seagrasses and mudflats. In these studies, comparisons between habitat types should not have been made for at least three reasons, all relating to animal behaviour. First, there are inherent differences in gear selectivity and catch efficiency between block nets used in the mangroves and seine nets used in adjacent habitat types. Second, all samples were collected at peak high tide when many animals (particularly juveniles of larger tri-phasic species) had moved into the shallowest waters (i.e. upper intertidal and mangroves). At this phase of the tide, adjacent deeper waters are utilised less by those species. Third, mangroves at these sites are only available (inundated) to most nekton for approximately 8–10 hours in any 24-hour period. Furthermore, one of us (SJP) examined sites used in these studies and found that extensive areas of intertidal and subtidal seagrasses surrounded mangrove areas in both studies. It is likely, therefore, that both intertidal and adjacent subtidal vegetated areas provided a complementary range of resources during tidal excursions and throughout home ranges. Despite these limitations, results from such studies have still contributed information that has influenced decision-making in resource management. To address this problem, future comparative studies should compare a range of habitat types at scales appropriate to the way that animals use them (i.e. mosaics of mangrove with adjacent seagrasses, *vs.* mosaics of mangroves without seagrasses etc.) (Parrish, 1989). Stratified sampling designs are also needed that incorporate the animal response to fluctuations in water level. If different sampling techniques are employed for comparative evaluations, then comparisons must be made within strata (habitat type) at different locations and not between strata. For example, Nagelkerken *et al.* (2001) studied fish use pattern around Curaçao in the Caribbean Sea. In order to compare the effect of the surrounding mosaics on patch type use, they sampled assemblages of fish using seagrasses and mudflats within different mosaic structures. Seine nets were used to sample fish that used seagrasses with and without adjacent mangroves, and fish that used mudflats with and without adjacent mangroves and seagrasses.

4. THEORETICAL CONSTRUCTS OF THE ANIMAL–ENVIRONMENT LINKAGE

In this section, we examine the historical development of fundamental concepts in animal ecology and their application. We begin by examining the definitions of traditional concepts of habitat and niche. Then we develop a scale-explicit conceptual model that defines an alternative hierarchical organism-based

perspective of the animal–environment interrelationship. This conceptual framework then drives the formulation of an operational approach presented in Section 5.

4.1. Habitat and niche

The concept of habitat is one of the oldest and most fundamental concepts in ecology, yet its meaning is often taken for granted. Yapp (1922) noted that the usage of habitat often “varies according to the concept in the mind of the individual”. In the English language, habitat has been broadly defined as “a living or dwelling place of an organism” equivalent to the Greek *Oikos*. However, there are many perspectives and definitions of habitat in use, most of which have originated in plant ecology. Most commonly, definitions have been elaborations of the basic definition, often with reference to interacting biotic and abiotic processes. Corsi *et al.* (2000) reviewed the term habitat and found that definitions ranged from “the place where a species lives”, which they considered a Cartesian space-related concept, to “the environment in which it lives”. Morrison (1992) considered both Cartesian and non-Cartesian aspects by defining habitat as “the area that has specific environmental conditions that allow the survival of a species”. This definition is somewhat similar to the “ecological niche concept”, which has often been used interchangeably with habitat and therefore requires brief mention. Hutchinson (1957) defined niche as a “multidimensional hypervolume” (an abstract graph) representing the set of all conditions needed to ensure the successful survival and reproduction of a species. There are many different interpretations (see review by Kolasa and Waltho, 1998) but overall, the ecological niche remains something that cannot be seen or directly measured and therefore is as difficult to scale to the real world as the previously discussed concepts of habitat. Further ambiguity was also introduced with the term ‘habitat type’. Habitat type refers to a unit of land usually described by a dominant vegetation community. The term has received wide use, particularly in resource management, where habitat mapping requires the creation of discrete and homogeneous units (Corsi *et al.* 2000).

In a synthesis of definitions, Rejmanek and Jenik (1975) presented a complex of three interrelated aspects of an ‘organism–environment linkage’ based on the original definitions of habitat and niche (Figure 9). In their synthesis, the response of an organism to its environment lies at the heart of the concept of habitat and niche. The habitat is referred to as the ‘operational environment’ (Spomer, 1973) a subset of environmental factors that interact directly with the organism (MacMahon *et al.*, 1981). In their model, the organism and habitat are parts of a system linked with feedback (Southwood, 1977). While useful in its emphasis on functional interactions between the environment and organism activity, it still does not integrate scale. The ‘organism–environment linkage’

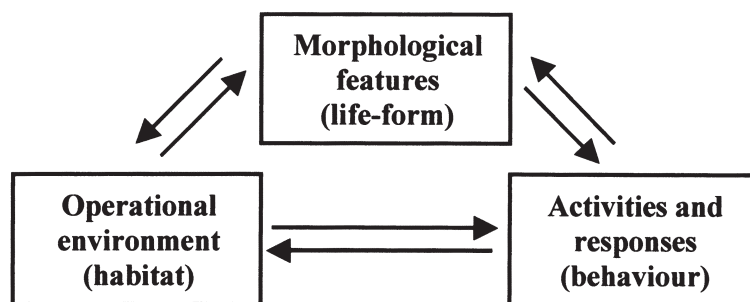


Figure 9 Rejmánek and Jenik's (1975) synthesis of three interrelated aspects of the organism–environment link that are most frequently the basis for the various concepts of habitat and niche. This synthesis offered a more holistic concept of the organism–environment relationship.

concept is closely allied to that of the 'ecotope' (Whittaker *et al.*, 1973), which views niche and habitat as complementary terms for different sets of attributes that combine to represent the species' relation to the environment. Whittaker *et al.* (1973), however, did make note of the complication presented by highly mobile animals and while not explicit about movement in their definition, they suggest that an ecotope may include "population movement between two different habitats occupied at different times".

Overall, most of the definitions that have been used appear inappropriate and overly simplistic for their application to the study of highly mobile animals with complex life cycles. Instead, concepts and definitions are required that acknowledge animal behaviour and at least two important dimensions: space and time. More appropriately, Baker (1978) defined habitat specifically as, "the area that provides the resource requirements for a discrete phase of an animal's life". Resource refers to both consumables (e.g. food) and non-consumables (e.g. settlement substratum, refuge etc.) (Wiens, 1984). In terms of movement, Southwood (1981) added that habitat is also, "the area traversed by the animal's trivial movements, that is, those within its sensory range where it forages" (and hides, rests or defends territory). Temporal phases of space-use are emphasised within these concepts, thus making them more appropriate for application to highly mobile animals with multiple phases of development (e.g. eggs, larvae, post-larvae, juvenile, adult).

4.2. Home range and ecological neighbourhood

With the emphasis on movement patterns, Aebischer *et al.* (1993) offered an appropriately broad organism-scaled perspective of habitat use, whereby "an animal's movements determine a trajectory through space and time and its use of

habitat is the proportion of the trajectory contained within each home range". The home range of Aebischer *et al.* (1993) is the "area within which an animal's trajectory is located during a given period". As discussed earlier, home range estimation techniques are well developed in ecology and have been used in behavioural studies of juvenile and adult marine animals. The concept of home range, however, has not generally been applied to include the infrequent and often broad-scale migratory movements of animals or the movement of planktonic life stages for which the total area used over time may not reach an asymptote (Figure 10).

The advantages of considering the home range of an animal is that it does allow, at least initially, for habitat to be operationally defined and scaled using measurements or estimations of an animal's daily movement pattern. The appropriate scales of habitat used are then determined from the observer's interpretation of the

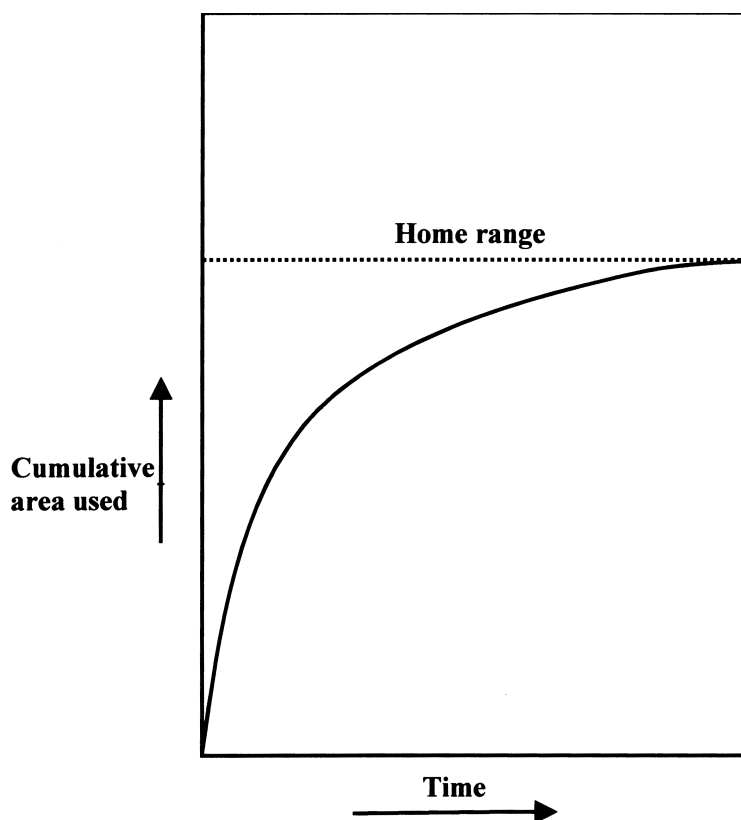


Figure 10 Animal movements will describe a home range if cumulative area used ceases to increase with greater time (i.e. an asymptotic value is approached) (adapted from McLoughlin and Ferguson, 2000).

animal's movements over time. In order to encompass more fully the life cycle dynamics, the concept of home range may be considered as, *the area typically used over some specified period of time or ontogenetic phase* (e.g. planktonic period or benthic nursery period) *or activity* (e.g. foraging, tidal excursion, spawning migration). Activity-based or functional descriptors of habitat are widespread in ecology and resource management. For instance, a species may have 'settlement', 'nursery', 'adult' and 'spawning' habitat all of which form 'essential habitat'. With the emphasis on function or process (Figure 11), the concept is somewhat similar to that of a spatial ambit, applied for scaling the activity spaces of pelagic nekton (Haury *et al.*, 1978) and the better-known process-oriented concept of the ecological neighbourhood (Southwood, 1977; Antonovics and Levin, 1980; Addicott *et al.*, 1987).

The ecological neighbourhood of an organism is "the region within which that organism is active or has some influence during an appropriate period of time" (Addicott *et al.*, 1987). For a given ecological process, there will be an appropriate time scale over which to measure neighbourhood size. Addicott *et al.*

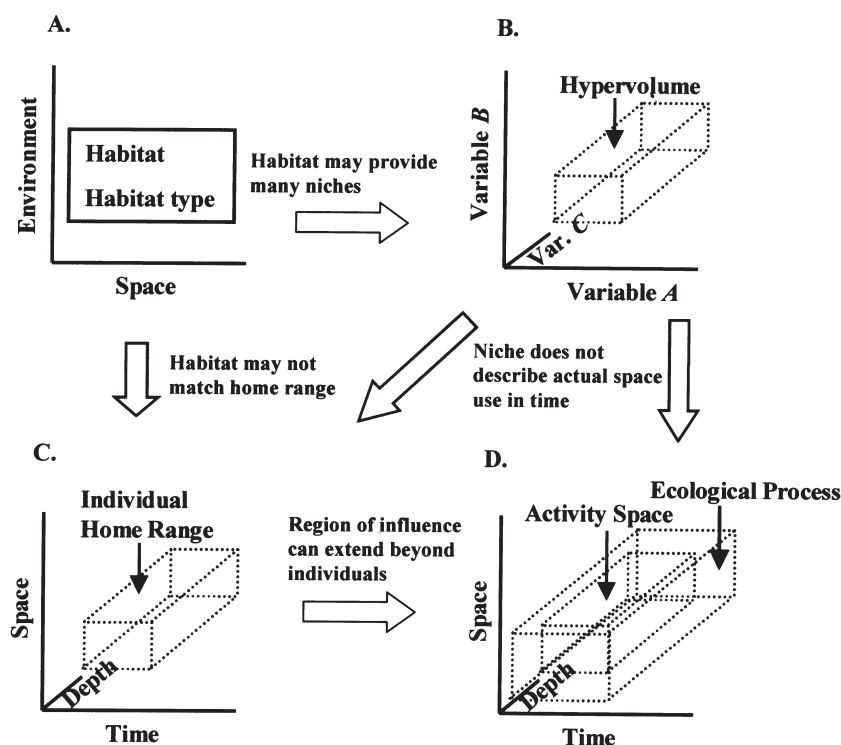


Figure 11 Relationships between four key concepts in animal ecology. (A) habitat and habitat type; (B) ecological niche; (C) home range and (D) ecological neighbourhood.

(1987) also proposed that for relatively mobile organisms, the movement of individuals would usually define the neighbourhood. From this perspective, there can be more than one ecological neighbourhood for an individual, hence a life cycle could be perceived as a multi-movement process and therefore a multi-neighbourhood event. For instance, for a foraging portunid crab, moving between patches of seagrasses, the scale of the foraging neighbourhood would be defined by the period of foraging and the spatial extent of foraging movements. For the planktonic zoea and megalopa life stages of crabs, the study of the neighbourhood may include measures of physical hydrodynamics and the spatio-temporal structure of its chemical aquatic 'landscape' during its planktonic phase from the spawning site to settlement substratum. The process of transition to a benthic phase would be another process-defined neighbourhood, with post-settlement home ranges and adult spawning migrations being others. It may be meaningful to compartmentalise ontogeny, together with associated movements within a characteristic spatio-temporal domain (for example see Figure 2). Applying this reductionist approach to lifetime use of habitat by an animal would also make fieldwork more logistically feasible, whilst maintaining an organism-based perspective. Alternatively, for a more holistic approach, one would need to couple separate neighbourhoods or consider the whole life cycle (Roughgarden *et al.*, 1988; Eckman, 1996) as a single spatio-temporal domain. The life-cycle neighbourhood would then be scaled using the spatial and temporal dimensions appropriate to the total trajectory of movement throughout the life cycle. Whatever the spatio-temporal unit may be, the important aspect of an organism-based approach is that the movement process is the scaling mechanism, thus allowing us to describe the relative scales, specific to organisms and their life stages. The value of this approach is that it encourages us to evaluate ecological structure in the context of ecological function.

Generally, these concepts are based on the activities of individuals. However, assemblages may also exhibit predictable activity, for instance, in tidally synchronous movements where even multi-species behaviour is entrained enough to allow a meaningful scale generalisation to be made. Nevertheless, while useful for its placement of the organism at the centre of the scaling process, ecological neighbourhoods alone are limited in their application in ecology since the neighbourhood itself is influenced by broader and finer scale processes.

4.3. Spatial hierarchy

One of the most significant contributions that hierarchy theory has made in ecology has been to enhance the awareness of scale and facilitate operational measures of scale (Wu and Loucks, 1995). It allows one to focus on an event at a particular scale, while recognising that there are other scales relevant to that event (Urban *et al.*, 1987). Furthermore, hierarchy theory emphasises the need

to distinguish between the spatio-temporal scale of a structure and the more arbitrary 'type' or 'category' of a structure (Allen, 1998). Spatial and temporal scaling is not an easy concept to grasp, but one way to conceptualise multi-scale pattern in the environment is by framing it within a nested (triadic) hierarchy (Allen and Starr, 1982) (Figure 12). Spatial hierarchies of structure (Kotliar and Wiens, 1990) have been described for several inshore habitat types such as coral reefs (Hatcher, 1997), saltmarshes (Kneib, 1994), seagrass systems (Robbins and Bell, 1994) and mussel beds (Kostylev and Erlandsson, 2001). For instance, Robbins and Bell (1994) described seagrasses as a hierarchy of nested structures, ranging from the individual shoot composed of multiple leaves (millimetres), to clumps (centimetres-metres) arranged in patches (1–100 metres), emerging as meadows (kilometres) surrounded by a coastal mosaic of component habitat types.

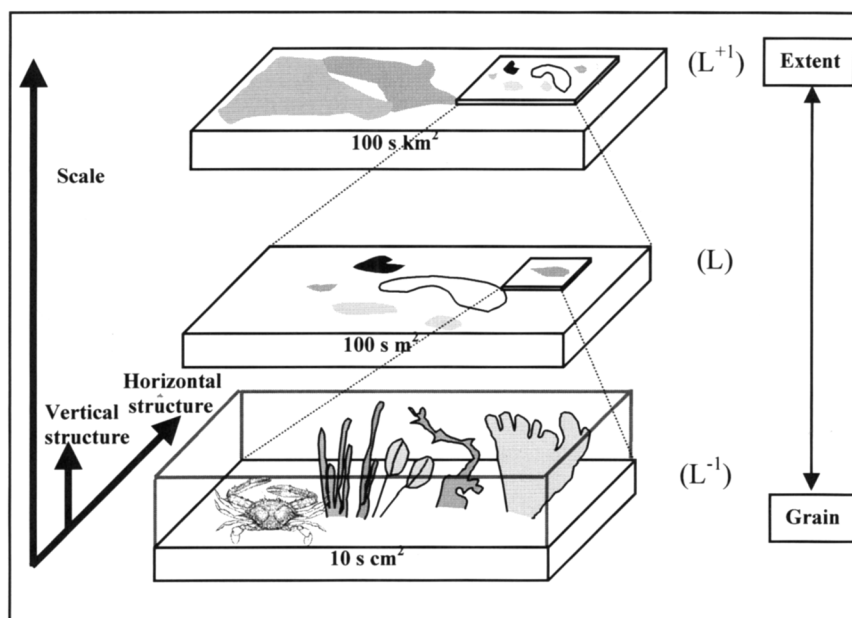


Figure 12 Scaling functional habitat structure in the context of a nested spatial hierarchy. Lower levels, $L^{(-1)}$, occupy less space and are characterised by processes operating at faster rates and finer time scales. Higher levels, $L^{(+1)}$, are of broader temporal and spatial scales (King, 1997). Spatial hierarchies can be used as interpretive tools to develop models of habitat structure at multiple scales (left-hand axis), contextualise relevant processes and to examine related pattern in the responses of animals (right-hand axis showing scale-dependent grain and extent). Vertical structure may include water depth and for aquatic vegetation, features such as canopy height. Horizontal structure may include shoot density and various measures of spatial pattern, such as the size and shape of a patch and its proximity to other patches or the diversity of patch types in a mosaic.

For an example of how this might be relevant to defining the environment for highly mobile animals, consider an assemblage of juvenile fish using a tidally dominated inshore area. In order to evade predators in deeper water and to forage amongst intertidal seagrasses or mangroves, the animals move back and forth with the flooding and ebbing tide through a mosaic of patches from the subtidal at low tide to the intertidal at high tide. A conceptual framework can be constructed with the home range or ecological neighbourhood as the focal level (L) and intermediate in the hierarchy. The focal level is the level at which the phenomenon or process under study characteristically operates (Wu and Loucks, 1995) and is a functional part of a higher and lower level. At any single level, the consequences and significance can only be understood at a higher level(s) and the mechanistic explanation must be investigated at a lower level(s) (O'Neill *et al.*, 1986). The finer scale $L^{(-1)}$ components of the mosaic may consist of structure such as seagrass leaf length, epiphyte biomass and patch size and these may explain some of the fish distribution patterns found at high tide. For instance, some animals may have a preference for relatively large patches of long seagrasses. This relationship, however, may not adequately explain the patterns at the broader scale of the home range, which may also include unvegetated subtidal areas where animals spend considerable time at low tide, possibly exposed to a very different environment. At the extent of the home range, distributions may also be influenced by the spatial arrangement of patches of seagrasses and the relative proximity of seagrasses to complementary resources in adjacent mangroves and coral reefs. Lower level explanations may be further lost at the $L^{(+1)}$ level, which would include the environment surrounding the home range, i.e. where animal distributions and abundance respond to a suite of physico-chemical constraints such as a gradient in wave action, salinity, temperature, turbidity etc. These higher-level factors can be treated as constants when viewed from the focal level, though they may be quite variable at broader-scales (Urban *et al.*, 1987). At the L and $L^{(+1)}$ levels, the composition and spatial arrangement of components, such as habitat types, may emerge as a significant determinant of animal distribution and abundance.

In this way, the intermediate level of the hierarchy is defined by the spatial activity patterns of the animal(s) within relevant time periods, thus anchoring the hierarchy to an ecologically meaningful scale in time and space. The hierarchical approach presented here can be considered as 'middle out', in contrast to the conventional 'top-down' or 'bottom-up' approaches that tend to be polarised either towards reductionism or holism (Wu and Loucks, 1995). Clearly, though there is no single correct scale or level for observations and ultimately, the appropriate scales will depend on the questions asked, the organisms studied and the time period considered (Wiens, 1989). Studies conducted over several scales, however, will integrate scale-dependent relationships into a more ecologically meaningful investigation of animal-habitat relationships.

Furthermore, a hierarchical model allows the relative scales of animal response to be built into the model, so that $L^{(-1)}$ corresponds to the grain (finest scale of response) and $L^{(+1)}$ to the ecological extent (broadest scale of response) (Kotliar and Wiens, 1990; Kolasa and Waltho, 1998). The lower threshold of heterogeneity is the level of resolution at which an animal no longer responds to structure, while extent is the coarsest scale of heterogeneity to which an animal responds. Response is a broad term that can mean physiological, behavioural or morphological reaction of an individual to the environment. It may be species or life-stage specific (Levin, 1992) and will emerge in patterns of populations and metapopulations (Hanski, 1998). Within a multi-species assemblage the animal response to multi-scale spatial pattern will be diverse owing to the range of behaviours, morphology and physiology. For example, a crab megalopa may respond to relatively fine-scale patchiness that may be unimportant to an older megalopa or a megalopa of another species (Eggleston *et al.*, 1998). Likewise, heterogeneity important to the crab may be insignificant to a cod or a shark. However, some generality may be found, since groups of species may respond similarly. Such patterns may emerge within and between functional groups, such as trophic generalists vs. specialists, species with broad geographical distributions vs. narrow ranging species or large vs. relatively small body sizes. For example, Kolasa *et al.* (1996) found a positive relationship between ecological range, abundance and spatial distribution for a total of 42 species of invertebrates inhabiting 49 rock pools in Jamaica. Discontinuities were interpreted as forming groupings of species within three levels; narrow range specialists, intermediate range species and broad range generalists. The framework of hierarchical response may be a useful interpretive tool if there is a relationship between the hierarchical structure of the environment and the responses of species to that structure (Kotliar and Wiens, 1990; Kolasa and Waltho, 1998).

The conceptual basis for this hierarchical and organism-based approach is derived from landscape ecology, which explicitly focuses on scale and the linkages between structure, function and change (Forman and Godron, 1986; Turner, 1989; Wiens, 1995). Researchers that practice landscape ecology recognise that ecological patterns and processes operate at a range of scales in time and space and that many organisms respond to this hierarchically. This organism-based perspective means that 'habitat' and the relevant patterns and processes in the surrounding environment are defined and scaled by the activities and responses of the organisms of interest (Wiens, 1976; Harris, 1980; Addicott *et al.*, 1987; Morris, 1987; Wiens and Milne, 1989; Kotliar and Wiens, 1990; Pearson *et al.*, 1996; McAlpine *et al.*, 1999).

In landscape ecology, the underlying assumption is that the environment is a mosaic of interacting components and the composition and arrangement of these components (in both time and space) determine how a system operates (Wiens, 1995). Valuable early contributions to the conceptualisation of ecological systems as "dynamic mosaics of patches" took place in benthic and pelagic

marine environments (e.g. Levin and Paine, 1974; Steele, 1978; Paine and Levin, 1981; Sousa, 1984; 1985). It is in terrestrial environments, however, that the quantification of landscape pattern and the study of the effect of pattern on ecological processes have made significant advances in understanding animal movement and persistence, the effects of disturbance, the importance of broad-scale environmental change and the design of resource management strategies (Turner, 1989; Saunders *et al.*, 1991; Hobbs, 1994; Forman, 1995; Farina, 1998). Landscape ecology principles and tools are applicable throughout ecology and recent reviews have outlined the usefulness of a landscape ecology approach for the marine environment (Kneib, 1994; Robbins and Bell, 1994; Bell *et al.*, 1997; Irlandi and Crawford, 1997; Eggleston, 1999). These reviews have rekindled interest in spatial pattern in the marine environment, with a number of researchers now applying and further developing concepts and analytical tools that have been used successfully in terrestrial landscape ecology.

With these concepts in mind, we propose that the living space for all animals, whether terrestrial or aquatic, can be considered to occur within a mosaic structure characterised by multi-dimensional heterogeneity of abiotic and biotic features. We present a definition of habitat that is both holistic and organism-centered; whereby *the habitat (or environment) of an animal is the interacting biotic and abiotic patterns and processes that an animal responds to in the course of its life-cycle trajectory*.

Operationally, the identification of habitat requires at least an estimate of the actual movement patterns. In addition, the traditional 'habitat types' (e.g. seagrasses, mangroves, coral reefs) are considered in the context of the amount of time that an animal uses that habitat type as well as its functional importance to the ecology of the animal.

5. APPLICATION AND TOOLS

This section presents an operational framework for studies of animal–environment relationships that is based on the conceptual framework outlined above. We first explain the logical sequence of the procedures that are necessary to ensure appropriately scaled studies. Then we examine a range of techniques that can be used to measure movement patterns for marine animals, followed by a range of techniques for quantifying and mapping environmental variability at multiple spatial scales.

5.1. Operational framework

The first step in any research strategy is to define the research questions (Figure 13). The second step involves the development of a scale-explicit

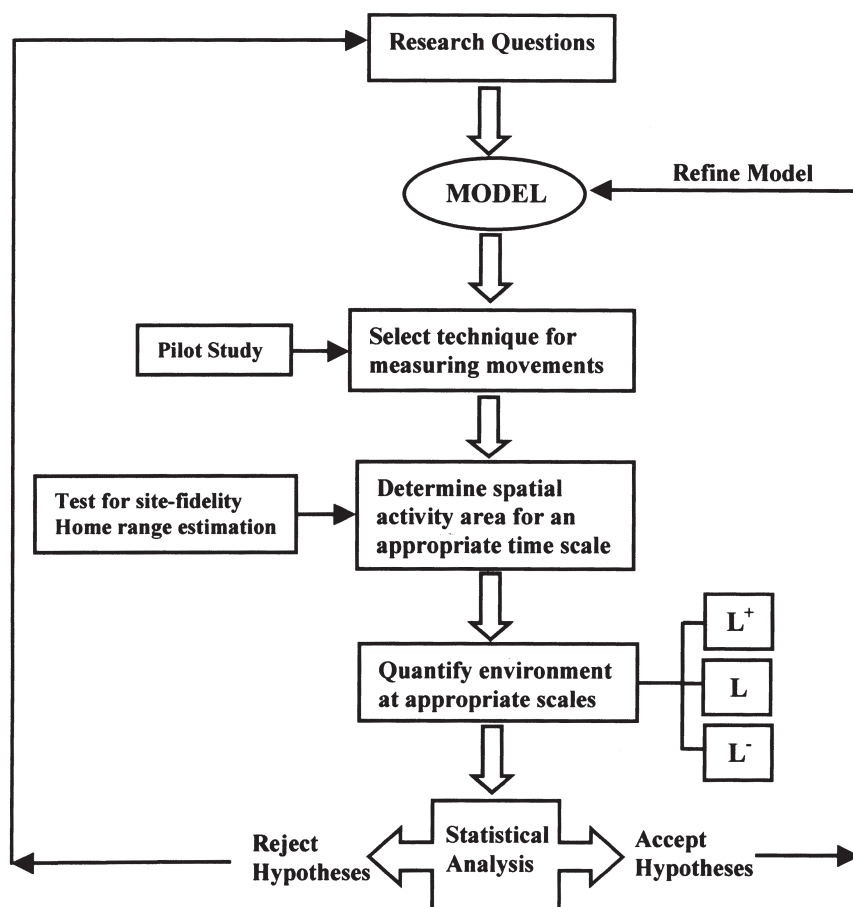


Figure 13 Operational framework showing a logical sequence of components in an experimental procedure for examining animal–environment relations at multiple spatial scales. The model is constructed to make predictions about ecological relations that are then presented as hypotheses. This component involves the development of a conceptual framework that considers temporal and spatial scale. To determine operationally appropriate scales for focal animals, field studies are usually required that involve tracking or fixed-point sampling to collect data on movement patterns. Environmental variables are then quantified at multiple scales including the activity area (L), within the activity area (L^{-1}) and beyond the activity area (L^{+1}). The procedure culminates in the testing of hypotheses that lead to refinement of the model or more observations and experiments.

conceptual framework that will define the approach and generate testable hypotheses. Next, it is necessary to select the appropriate scales at which to investigate the research questions. In studies of highly mobile animals, the movement patterns provide the mechanism for the initial identification of

meaningful scales and an appropriate technique must be selected for quantifying movements at time scales relevant to the research questions. Construction of space–time diagrams (Schneider, 1994, 2001) may prove useful in the early stages of planning for scale selection (see Figures 2 and 3 for examples). The scale selected will then contribute to the rationale for determining the relevant environmental variables and the techniques suitable for their quantification. The data generated through multi-scale animal–environment studies are likely to be in a range of formats (i.e. point measures, map trajectories, aerial photographs, multi-spectral satellite data etc.), with data on movement and multi-scale environmental attributes all needing to be temporally and spatially referenced. This not only provides context but it also provides mappable data that facilitate spatial and temporal statistical analyses.

5.2. Measuring animal movement

Quantification of animal movement in time and space is an essential first step of any attempt at scaling the environment from the perspective of an organism. There are many techniques available (both low- and high-technology) for directly and indirectly measuring and estimating movements (Table 2). It is useful, therefore to separate them into two main approaches: (1) tracking techniques; and (2) fixed-point sampling. Tracking techniques include telemetry or complex Lagrangian computer models, which provide high spatial and temporal resolution data (relative to other techniques) on the individual trajectories of free-ranging animals or virtual animals in computer simulations. In this approach, the individual is the unit of study and raw data usually consist of a series of x–y coordinates collected in the field or predicted over time. Observation above and below the water surface, where an observer follows and records the direction and geographic position of an individual, is also considered a tracking technique. Fixed-point techniques are a “multiple snap-shot” approach involving discrete measurements taken from a set of specific predetermined points in time and space, including extractive sampling, mark and recapture/resight, chemical signatures (such as the microchemistry of otoliths), still photography and fixed position underwater video. Techniques from the two categories have been applied to both planktonic (Levin, 1990) and post-planktonic stages of fish and decapod crustaceans.

5.2.1. *Eggs and larvae*

Mapping the trajectory of eggs and larvae presents a particularly difficult problem because of their small size, relatively long planktonic duration and complex behaviour (Levin, 1990; DiBacco and Levin, 2000). Scheltema (1986) remarked that “although it is quite impossible to follow individual larvae over

long distances at sea, one can nonetheless, from knowing the location of its capture, gain an insight about the probable origin, as well as the route a larva may have taken". In attempts to collect information on movement pathways many early studies used traditional zooplankton capture techniques (e.g. towed nets; settlement collectors) to examine larval distributions. However, even when used intensively these capture techniques have provided only minimal information about larval trajectories (Levin, 1990) and require that scientists infer potential trajectories from physical oceanographic data (DiBacco and Levin, 2000). Attempts have been made at tagging eggs and larvae using chemical markers but advection and mixing, as well as heavy mortality experienced by most larvae often make the recovery impractical, limiting the application of such methods (Levin *et al.*, 1993). More recently, Jones *et al.* (1999) demonstrated the utility of chemical marking in a mark-recapture experiment that showed that some juveniles return to their natal reef (Lizard Island, Great Barrier Reef, Australia). The authors marked the otoliths of an estimated 10 million developing embryos laid (on artificial surfaces used as nesting sites) by the damselfish, *Pomacentrus amboinensis*, by immersing them *in situ* into a tetracycline solution. Subsequent sampling of juveniles in the same location revealed that 15 of 5 000 individuals examined were marked.

Larvae with calcified body parts have also been examined for naturally incorporated trace-elements (see also Section 5.2.2.). DiBacco and Levin (2000) applied trace-elemental fingerprinting to stage I zoeae of the striped shore crab, *Pachygrapsus crassipes* to examine the tidally driven movements of the larvae into and out of San Diego Bay, California, USA. Swearer *et al.* (1999) used similar techniques on the bluehead wrasse (*Thalassoma bifasciatum*) in the Caribbean Sea to show that, in some areas, a significant proportion of newly-settled individuals have been locally spawned and retained as planktonic larvae in nearshore waters. While these fixed-point techniques provide invaluable information on the origins of individuals and coarse resolution data on movements that contribute to the understanding of local and regional population dynamics, they provide no direct coordinate data with which to reconstruct a trajectory in time and space.

One of the first attempts to track successfully a patch of plankton in the open water was carried out by Cushing and Tungate (1963). Their team coordinated two ships in a relay of nine cruises in an attempt to continuously track a patch of copepods (*Calanus finmarchicus*) for 66 days over 140 km off the north-east coast of England. The study was designed to examine changes in patch composition and structure and demonstrated that it was possible to follow planktonic animals if the patch is large enough, observations are near-continuous and weather conditions are not severe. In a series of studies undertaken in the mid 1980s (Heath and MacLachlan, 1987; Heath *et al.*, 1989; Heath and Rankine, 1988), patches of herring (*Clupea harengus*) larvae were tracked for periods of 2 to 13 days after leaving spawning grounds in the north-west of Scotland. These studies were designed to examine feeding, growth and mortality and showed that

some of the difficulties in tracking free-living larvae at sea could be overcome with the use of drifting marker buoys. Broad-scale sampling was first carried out to identify, measure and map a patch of newly hatched herring. Following this initial survey, a satellite-tracked parachute drogue buoy was deployed in the centre of the patch and on successive days samples were collected around the buoy. Natunewicz and Epifanio (2001) and Natunewicz *et al.* (2001) used a similar technique to follow patches of newly hatched blue crab (*Callinectes sapidus*) larvae for up to 11 days near the mouth of Delaware Bay, USA.

Other techniques have included visual tracking of individual larvae underwater, although such studies have usually focused on large invertebrate larvae with short (several metres) dispersal distances (Levin, 1990). Studies that have visually tracked and recorded the trajectories of individual larval fish are rare. Leis and Carson-Ewart (1997) followed (using SCUBA) individual larvae of coral reef fish on the Great Barrier Reef and recorded their direction, depth and speed every 30 seconds. The authors found that there were inherent difficulties in visually tracking underwater since human observers have limited mobility in water compared to larval fish, with fish swimming speeds ranging from ~ 2 to 65 cm s^{-1} and occasional rapid bursts of acceleration (Leis and Carson-Ewart, 1997). Underwater visual tracking is also limited to studies of animals that inhabit calm, clear and warm waters. It may not be feasible for tracking animals in rough, turbid or cold waters, with trajectories of hundreds of kilometres or where their position in the water column varies in depth, from the surface to several hundred meters below. Furthermore, it is not known whether the pursuit of a larval fish alters its behaviour (i.e. swimming speed and direction).

Because of the difficulties in tracking live larvae at sea, most studies have addressed the mechanisms underlying their transport (Werner *et al.*, 2001). Technological developments in biotelemetry, global positioning systems, computer modelling and remote sensing have rapidly increased the feasibility of accurately predicting trajectories in the marine environment. Werner *et al.* (1993) applied a 3-D circulation model to explore the influences of a range of physical and biological processes on the distribution and passive transport of cod and haddock larvae spawned on Georges Bank. Simulations demonstrated that a range of conditions (physical forcing, spawning location and position in the water column) determined whether larvae were retained in an area or advected away to neighbouring regions. Quinlan *et al.* (1999) also used a passive transport approach to develop a physical model that suggested the importance of seasonal changes in circulation and temperature on the life-history strategy and population dynamics of Atlantic menhaden (*Brevoortia tyrannus*) along the Atlantic coast of North America. Simulations led to the formulation of testable hypotheses on the function of alongshore transport and the location of spawning sites in relation to nursery areas.

The integration of remote sensing technology, together with complex hydrodynamic modelling can be especially useful where broad scale oceanographic patterns and processes are important (e.g. chlorophyll *a*, surface

temperature, sea-surface height, surface roughness, ice) (Roughgarden *et al.*, 1988). Polovina *et al.* (1999) modelled the trajectory of larvae of the spiny lobster (*Panulirus marginatus*) in the Hawaiian Islands using data from space-borne satellites. The authors used time series data of sea surface height (TOPEX-POSEIDON satellite altimetry) to estimate geostrophic current and to run a simulation model of the transport of lobster larvae released from selected banks. Individual larvae were tracked for a series of time steps starting from a given location by iteratively applying advective displacements (due to water flow) and additional random displacements caused by diffusion. Simulations released 5000 larvae in pulses throughout the spawning season and tracked their spatial distributions for a year, after which they would (in real life) metamorphose into free-swimming pueruli.

Although hydrodynamics can explain distributions without provision for larval behaviour (Reiss *et al.*, 2000), lack of consideration of behaviour (and morphology) that may enable larvae to move differently from the motion of the surrounding water will limit their application. Models assuming passive transport are limited by the absence of any behavioural responses (e.g. vertical behaviour) and complex biological interactions, including any feedback mechanisms that may be experienced by the animals (e.g. predation and starvation and density-dependence). Modern computer modelling, however, provides a tool for the integration of biological and physical processes occurring at multiple scales (e.g. larval behaviour and broad-scale circulation). Spatially explicit individual-based models (IBMs) (Judson, 1994) have been developed to incorporate the trajectories of individual animals that experience and respond to complex horizontal and vertical patterns in time and space (reviewed by Werner *et al.*, 2001).

The inclusion of spatial history is crucial for many marine species since different life stages may occupy substantially different physical environments. Hinckley *et al.* (1996) developed a spatially explicit biophysical model for walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. The model combined a three-dimensional hydrodynamic model (physical) with a probabilistic life-stage model (biological) for young fish. The physical model reproduced broad-scale circulation features and spatial distributions of important physical factors such as temperature and salinity. The biological model was divided into three life stages: egg, yolk-sac larvae and feeding larval stage. Each interaction of an individual with the abiotic factors was modelled and the unique trajectory mapped through time and space, as well as its growth and survival. Similarly complex IBMs that recognise heterogeneity in biological entities have been developed for north-eastern Atlantic populations of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (Heath and Gallego, 1997). Incze and Naimie (2000) provide another example of the utility of coupling biological and physical models in order to compute the predicted near-surface trajectories of larval and postlarval lobsters (*Homarus americanus*) in the Gulf of Maine, USA. The authors used an IBM that coupled a model of physical advection with a

biological model of temperature-dependent development to reveal that 'numerical lobster' larvae exhibit high temporal and spatial variability in the distances travelled (19 – 280 km) between hatching and settlement. This was attributed to a combination of spatial and temporal differences in hydrographic features, sea breezes and water temperature effects on development.

However sophisticated the software, these modelling techniques require actual tracking in order to validate predictions. In the absence of tracking real animals, ground-truthing can be achieved by incorporating the use of instruments such as fixed depth drifters and drogues, which can track actual patches of eggs and larvae while describing their environment and transmitting their positions via satellite. One of the principal attractions of drifters and drogues is that broad geographical areas can be sampled. Recently, investigators have modified drifters to mimic the behavioural response of an animal to the environment. Wolcott and Wolcott (1996) developed a 'larval mimic' for the study of the transport of decapod larvae. Their drifter senses water pressure changes, diel and tidal cycles, temperature, light, contact with the substratum, salinity and vertical velocity through the water. It is programmed to compare environmental measurements with its programmed behavioural pattern and to respond accordingly by altering its buoyancy. The machine stores depth profiles and transmits an acoustic signal for tracking. De Robertis and Ohman (1999) used an autonomous vertically-migrating drifter (VMD) to mimic diel vertical migrations in zooplankton. Their mimic used radio telemetry of GPS positions and allowed two-way communication for data telemetry and instrument reprogramming. Whilst even these mimics may be too simplistic for tracking some animals, they are the first step in a new generation of organism-based tracking devices.

5.2.2. *Juveniles and adults*

For larger individuals, such as post-planktonic juveniles and adults, telemetry is a powerful tool for an ecologist because of its potential for providing unbiased data on how a free-ranging animal utilises space in time. Telemetric tracking techniques commonly utilise five technologies: acoustic, radio, electromagnetic, data storage tags (archival) and satellite-based geolocation (e.g. Argos), some of which can be used most effectively in conjunction with one another (e.g. radio acoustic positioning and telemetry [Solomon and Potter, 1988; O'Dor *et al.*, 1998] or ultrasonic telemetry and data storage tags [Stone and Kraus, 1998; Freire and González-Gurriarán, 1998]) (Table 2). Receivers can be hand-held or ship-, water-, air- and shore-based. Transmitters can be fixed externally, lodged internally within the gut or surgically implanted in a body cavity or intramuscularly. Manufacturers of tracking technology are continually pushing the limits, with respect to the size of tags, their longevity and the accuracy of mapped trajectories. Some of the tags and transmitters

that are now being used are as small as 8×19 mm and weigh 2.39 g in air. In all telemetry studies, transmitter size is an important consideration and smaller transmitters are less likely to adversely affect the behaviour and health of an animal. The information gained from tracking assumes that the movements of an animal are unaffected by the transmitter. However, some transmitters (and other tags) have been found to influence mortality and behaviour (Jepson *et al.*, 2002). For example, predation trials with tagged and untagged juvenile Chinook salmon (*Oncorhynchus tshawytscha*) revealed a reduced swimming speed and higher susceptibility to predation for fish with surgically implanted transmitters (Adams *et al.*, 1998). However, individual animals are likely to respond differently to the tag itself and the tagging procedure and therefore whenever possible it is necessary that devices be experimentally evaluated in a pilot study before being deployed for tracking (Murray and Fuller, 2000).

Most studies using transmitters have been autecological (on single species) and based on only a few individuals. However, engineers have now developed multi-channel telemetry techniques, which involve digital encoding to allow simultaneous tracking of large numbers of animals (Wolcott, 1995; Cote *et al.*, 1998; Smith *et al.*, 2000). Position data typically are collected but it is also possible to telemeter information on physiological variables such as heart rate, body temperature and respiration rate, as well as environmental variables such as salinity, light, depth and temperature (Klimley, 1993; González-Gurriarán and Freire, 1994; Wolcott, 1995). The majority of studies on marine fish and decapod crustaceans use acoustics, such as ultrasonic telemetry (see examples in Table 1), which can provide fine resolution data with automated, continuous position fixing. The advantages and disadvantages of using acoustic telemetry methods in studies of both fish and decapod crustaceans have been reviewed by Wolcott (1995); Freire and González-Gurriarán (1998); Zeller (1999) and Smith *et al.*, (2000) (and Table 2).

Continuous tracking of animals over very long distances has also limited the application of conventional ultrasonic telemetry. For instance, González-Gurriarán and Friere (1994) lost detailed tracking information (using ultrasonic telemetry) when spider crabs (*Maja squinado*) migrated to deeper and colder offshore waters. The application of multidirectional hydrophone arrays that can be towed by ship coupled with independent acoustic receivers may improve data capture for animals undertaking movements over several kilometres (Block *et al.*, 1997). Alternatively, fixed position automated 'listening stations' can be deployed on moorings (Klimley *et al.*, 1998; Arendt *et al.*, 2001). Klimley and Holloway (1999) attached an acoustic receiver, with a detection range of 1.10 km, to a concrete mooring to log positions of tagged yellowfin tuna (*Thunnus albacares*). Righton *et al.* (2001) monitored the movement activity of North Sea cod (*Gadus morhua*) during the summer months (June to August) using a listening station with a 500 m detection range. This study combined data from individually coded acoustic tags together with Data Storage Tags (DST) attached to

cod in the North Sea and in the Irish Sea revealing that seasonal patterns of activity (possibly foraging movements) differ between individuals in different geographical regions. However, acoustic techniques may be limited when tracking burrowing animals or animals over rocky substratum, as sound transmission is adversely affected by attenuation and reflection (Smith *et al.*, 2000).

Electromagnetic telemetry has been used to study cryptic, crevice dwelling decapod crustaceans, such as lobsters, in topographically complex environments, which are not amenable to ultrasonic telemetry (Phillips *et al.*, 1984; Jernakoff, 1987; Smith *et al.*, 1998, 2000). The system uses low frequency signals that can be detected through seawater, rock and sediment via a grid of aerials set out on the seabed (Smith *et al.*, 2000) but is limited to site-attached individuals by a relatively short (a few metres) range of detection.

Flat-bed Passive Integrated Transponder (PIT) technology may also be appropriate for site-attached animals. The technique involves inserting a PIT tag into the body cavity of an animal and setting up an antenna or series of antennae to create a local energy field (400 kHz). When the transponder enters the field, it is energised to retransmit (40–50 kHz) an ID code that is then decoded and recorded. This technique has been used mainly for small freshwater fish (<11 cm standard length) (Armstrong, *et al.*, 1997; Greenberg and Giller, 2000) but also offers some potential for monitoring the movements of site-attached epibenthic marine animals. The main factor limiting the application of the PIT system is the range at which tags can be detected, since with current techniques, the tag is only detected when fish pass within 15–20 cm of the antenna thereby limiting its application for continuous monitoring.

For exploited species, where recapture is likely, DSTs or archival tags have been used for mapping movement patterns. DSTs allow us to reconstruct the tracks of individual animals for longer periods than would usually be feasible with acoustic tags. For example, tags engineered by CEFAS (Centre for Environment, Fisheries and Aquaculture Science, UK) and Lotek Marine Technologies Inc. are capable of storing over 500 000 data samples for periods of up to 25 years (Metcalf and Arnold, 1997; Turner *et al.*, 2002). The continuous monitoring of environmental variables, such as depth, light, salinity and temperature make it possible to reconstruct the tracks of animals, estimating the time, place and directionality of movements (Friere and González-Gurriarán, 1998). Welch and Eveson (1999) reviewed the techniques used for geopositioning based on variations in light and Gunn and Block (2001) discuss the limitations with regard to geolocating free-ranging fish.

Using DSTs Metcalfe and Arnold (1997) revealed that some mature female plaice (*Pleuronectes platessa*) visited more than one spawning area within a single spawning season and that rates of movement were often as much as ten times faster than those estimated using conventional mark-recapture experiments. Arnold and Holford (1995) combined information from DSTs from several fish species with interpolated tidal stream vectors to predict rates and scales of movement of demersal fish in the North Sea and English Channel.

An example of a data set retrieved from a DST attached to a female plaice (*Pleuronectes platessa*) is shown in Figure 14.

Some DSTs have been designed to transmit information via satellite using the Argos system. The Argos system provides world-wide position fixes of a mobile UHF transmitter via an orbiting satellite (Taillade, 1992). Transmission of data via satellite, however, requires that the transmitter be positioned above the surface of the water. Traditionally, this has limited the use of Argos to air-breathing marine animals such as mammals and turtles (Marsh and Rathbun, 1990; Priede and French, 1991; Plotkin, 1998; Gillespie, 2001) and some surface-dwelling fish (Priede, 1984). However, the necessity for understanding the movements of fast swimming and deep diving (> 1000 m) pelagic fish that are being exploited by fisheries has resulted in the invention of 'pop-off' transmitter tags that are programmed to detach from the animal and float to the surface to transmit position and archived data (Priede and French, 1991; Gunn and Block, 2001). Together with implanted DSTs these have been used successfully for studies of bluefin tuna (*Thunnus thynnus*) (Block *et al.*, 1998, 2001) and swordfish (*Xiphias gladius*) (Sedberry and Loefer, 2001). For example, data were retrieved from 95% (Block *et al.*, 1998) and 90% (Block *et al.*, 2001) of tags detached from bluefin tuna.

DSTs have also been used in conjunction with integrated video and audio systems to simultaneously examine animal–environment linkages by examining the interaction between space use patterns and animal behaviour such as locomotor effort, social interactions and hunting behaviour (Marshall, 1998 and Heithaus *et al.*, 2001 for tiger sharks; Davis *et al.*, 1999 and 2001 for seals). So far, such systems have only been applied to large vertebrates such as sharks, cetaceans and pinnipeds but in the future, micro-cameras with smaller batteries and longer life will no doubt provide new insights into the behavioral and physiological interactions of small-bodied animals with their environment.

Extractive sampling techniques using combinations of conventional fishing gears could also be used to examine spatial and temporal patterns of distribution. For instance, to estimate the spatial extent of tidal migrations it would be necessary to sample repetitively at various distances (depths) from the shore at all stages of the tide. Another fixed-point technique, mark–recapture, has been used extensively to map movements. Such studies provide information on the locations of release and recovery from which movement patterns can be inferred (Hilborn, 1990). Generally, however, the probability of recapture is low and multiple recapture extremely rare and largely a function of both animal movement and the catch or search effort of the investigator (Whitehead, 2001). Nevertheless, it is this form of data that provides most of our current knowledge of movement in marine animals. Hastein *et al.* (2001) have reviewed innovative methods for marking fish and crustaceans. Mark–resight can also be used, whereby an observer records the position of a marked animal underwater (Zeller and Russ, 1998) or uses *in situ* video recordings. For example, Burrows *et al.*

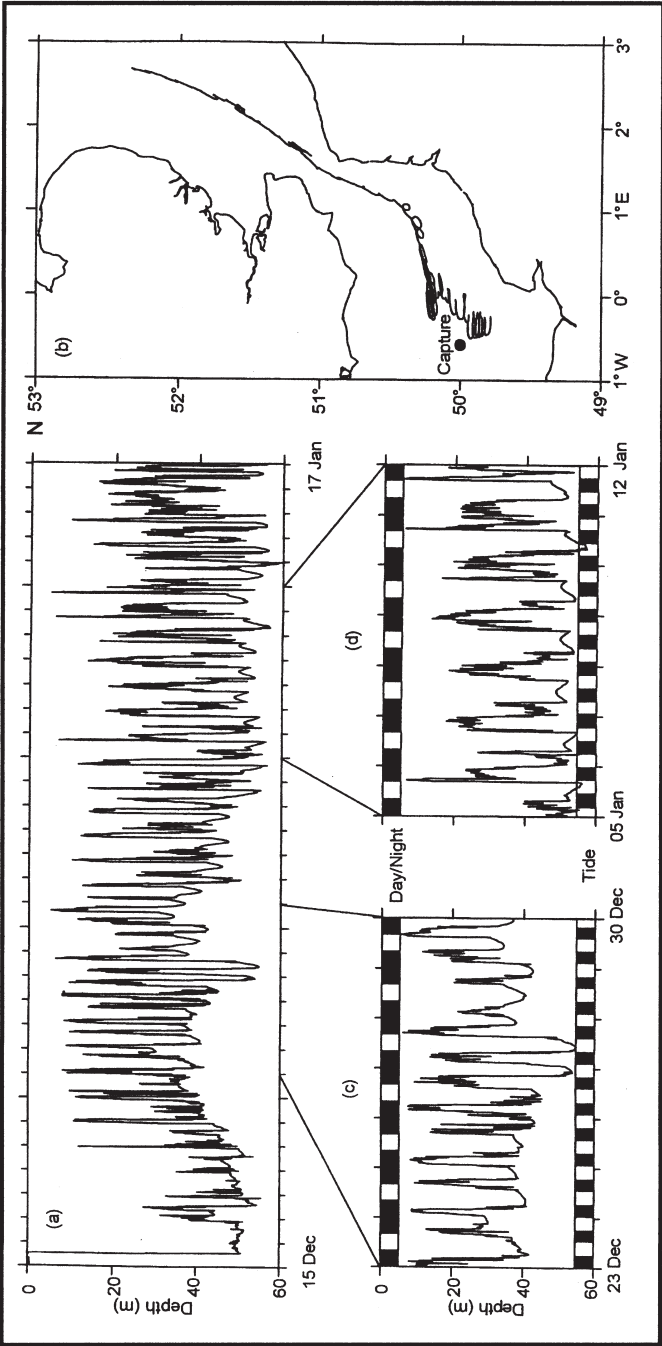


Figure 14 Continuous information on the vertical movement patterns and reconstructed track of a female plaice (*Pleuronectes platessa*) tagged with a CEFAS data storage tag in the North Sea from 15 December 1993 to 17 January 1994. Plaice use the tidal stream to facilitate movements. The DST depth record shows a plaice moving up into mid water on a flowing tide, returning to the seabed when the tide turns (Arnold, 2001). Fish were geolocated using information on geographic variability in the tidal range and times of high and low tide incorporated into a computer simulation model of the tidal streams. Data reproduced by permission of CEFAS, Lowestoft. © Crown copyright.

Table 2 Techniques used to examine animal movement patterns in the marine environment. Techniques are grouped as tracking techniques and fixed-point sampling techniques.

Technique	Advantages	Disadvantages	Life stage(s) studied	References
<i>Tracking techniques</i>				
Acoustic	Multi-channel allows multiple individuals to be tracked simultaneously.	Sound can be attenuated and reflected by rocky substratum. Limited to shorter range than radio telemetry.	Juvenile Adult	Wolcott (1995) Freire and Gonzalez-Gurriaran (1998)
Radio	Tracks over broad-scales even global coverage via satellite.	Transmitter large, short battery life. Signal transmitted from the surface.	Juvenile Adult	Gillespie (2001)
Electromagnetic	Signals detected through water, sediment or rock.	Shorter range than acoustic telemetry.	Juvenile Adult	Smith <i>et al.</i> (2000)
Passive integrated transponder (PIT)	Small size. Useful for mapping of movements for site-attached animals	Requires animal to pass close (15-20 cm) to aerial.	Juvenile	Armstrong <i>et al.</i> (1997)
Data Storage Tags (DSTs)	Continuous environmental data for track reconstruction.	Size of tag Retrieval may be difficult Geolocation requires auxiliary data	Juvenile Adult	Metcalf and Arnold (1997)
Pop-off satellite archival transmitters (PSATs)	Retrieval of archival data from broad-ranging and deep diving animals.	Track reconstruction requires auxiliary data.	Juvenile Adults	Block <i>et al.</i> (1997)

Optical tracking (eye, video, photography)	Continuous tracking of a wide range of animals.	Usually requires a motorized platform. Difficult to follow deep diving animals.	Larvae Juvenile Adult	Leis and Carson- Ewart (1997) Sims and Quayle (1998)
Lagrangian computer simulations	Non-invasive and tracks many individuals over broad-scales.	Complex and needs field data to parameterise and validate.	Eggs Larvae	Hood <i>et al.</i> (1999)
<i>Fixed-point samples</i>				
Mark/recapture	Marking is low cost, large numbers can be marked.	Intensive sampling required to recapture. Low recapture rate.	All life stages	Levin (1990) Hilborn (1990)
Capture device for study of distributions	Devices are low cost, low maintenance and widely available.	Intensive sampling required to build trajectory, particularly if no <i>a priori</i> information are available. Highly selective.	All life stages	Levin (1990) Rozas and Minello (1997)
Fixed position optical sampling (eye, video, photography)	Permanent visual record, non-destructive remote sensing approach.	Coarse taxonomic resolution, limited field of view and focal length.	All life stages	Samoilys and Carlos (2000) Burrows <i>et al.</i> (1994)
Elemental fingerprinting	Low cost, non-invasive	Interpretation requires extensive reference data. Trajectory difficult to determine for multi- habitat users. Requires mass- spectrometer.	All life stages	Gillanders and Kingsford (2000) Fry <i>et al.</i> (1999)

(1994) used a series of underwater video cameras fixed to the intertidal and subtidal substratum surface to record patterns of tidal movements for fish. Cameras were placed in the centre of a radiating array of nets designed to guide moving animals past the camera, with time-lapse video recordings (3.43 and 2.67 frames per second) made over sixteen 24-h periods.

The microchemical analyses of body parts, such as fish otoliths, which incorporate chemicals from the surrounding environment ("elemental fingerprints") have been used to estimate movement patterns for marine animals (Campana *et al.*, 1995 for fish; DiBacco and Levin, 2000 for crustaceans). Thorrold *et al.* (1997) and Gillanders and Kingsford (1996, 2000) suggested that these permanent records of environmental conditions experienced by highly mobile animals could be used to determine the offshore–inshore movement of larvae and specific nursery areas for adult populations. Quinlan *et al.* (1999) suggested that a cohort could be 'tracked' as it arrived at estuaries, using information from both otolith microchemistry and birth-date distributions. Thorrold *et al.* (2001) compared geochemical signatures in whole otoliths of juvenile weakfish (*Cynoscion regalis*) with otolith cores of reproductively mature adult weakfish to reveal that many adults were returning to their natal estuary to spawn.

Secor and Piccoli (1996) used levels of strontium (which are higher in sea water than fresh water) in otoliths to investigate the distances of up-estuary and down-estuary movement during the growth of striped bass (*Morone saxatilis*). Another potentially useful technology involves measurement of stable isotopes (Fry, 1983; Hobson, 1999) acquired from the diet. The range of isotope values (^{13}C , ^{15}N) for animals varies depending on the source of nutrients (e.g. seagrasses and mangroves). Therefore, animals moving between isotopically distinct foodwebs can carry with them information on the location of previous feeding. For example, Fry *et al.* (1999) used isotope signatures to show that seagrass meadows were the main contributor to the diet of pink shrimp (*Farfantepenaeus duorarum*) that moved to join offshore populations in Florida. The difficulty in stable isotope studies comes from variability introduced from animals that have consumed a diet having a range of isotope values. Together with extensive environmental reference data, tissue assay techniques hold great potential for investigating the origins and broad-scale movement patterns, particularly for animals too small for telemetry and unsuitable for mark–recapture experiments.

Clearly, fixed-point techniques cannot easily provide detail of movements that may occur between measurements and therefore the resulting estimate of a trajectory is heavily dependent upon sufficient samples to piece together a movement pattern. Some telemetry techniques can also suffer this limitation, whereby trajectories are largely dependent on the time interval between readings (Swihart and Slade, 1985; Spencer *et al.*, 1990). Therefore in all movement studies, a time component must be explicitly stated, for instance, the frequency of observations and the duration of the study (e.g. second, hour, day, season etc.).

This is important in relation to the scaling of habitat use, since individuals do not use their spatial domains evenly and will likely have a core area or several core areas where they spend a significant proportion of time.

In summary, the choice of technique ultimately depends on the animal concerned and the objectives of the study. In some instances quantifying movement patterns for marine animals may require combinations of both tracking and fixed-point techniques and the application of a range of statistical techniques. Telemetry provides detailed tracking of a few larger individuals, whereas chemical markers can generate information on the likely extent of movements for many individuals of a range of sizes. Alternatively, low-technology extractive sampling (e.g. beam trawling or drop-netting) may be the only option available. It is important to appreciate that the spatial and temporal resolution and extent of the data will determine the resulting model of animal movements.

5.3. Analysis of animal movement data

Establishing linkages between animals and their environment at appropriate scales requires that movement patterns such as pathways and home range size be quantified. Telemetry and tracking studies of free-ranging animals typically generate empirical data in the form of a time series of x , y or x , y , z coordinates. Analysis of coordinate data is a rapidly growing area of biostatistics (Powell, 2000) and spatial statistics (Legendre and Fortin 1989; Fortin 1999). There are numerous techniques available to analyse tracking (and fixed-point) geolocal data in order to estimate movement and home range size, shape and structure. Movement patterns for individual animals can be characterised by simple measures such as length, direction, duration, speed and turning angle, each of which reveals something different about movement behaviour (Turchin *et al.*, 1991; Wiens *et al.*, 1993). Techniques such as re-normalisation (Wiens *et al.*, 1993) can also be applied to the data to obtain independence among successive observations (e.g. aggregating a pathway by renormalisation). For home range estimation, frequently-used statistical models include utilisation distributions (Ford and Krumme, 1979), the Fourier transform method, the minimum convex polygon, the harmonic mean and the adaptive kernel method (reviewed by Powell, 2000). These statistical techniques each have specific sensitivities regarding sample size, and the distribution and independence of data. One of the first steps in operationally defining a home range is to test for site fidelity, which can be performed using a robust Monte Carlo random walk test (Spencer *et al.*, 1990).

Much software for home range estimation is in the public domain and available via the World Wide Web for both Macintosh and MS-DOS operating systems. CalhomeTM, WildtrackTM, Home RangeTM and AntelopeTM are just a few programs widely used for home range estimation. AntelopeTM (University of

California, San Diego) for instance, performs spatial statistics on data generated by mapping a group of individuals or from tracking an individual over time. Hooge and Eichenlaub (1997) have created an Animal Movement Analyst Extension (AMAE) to ArcView® GIS for the statistical analysis and modelling of animal movements. This software permits the user to conduct a wide range of spatial analyses and hypothesis testing on movement data taken from both observation and telemetric-tracking data. The program offers more than 50 functions including several to examine habitat selection (e.g. compositional analysis and availability analysis). Compositional analysis (Aebischer *et al.*, 1993) uses the utilisation distribution of the animal to determine resource use, with the habitat types within the home range expressed as a proportion of the total range area. The technique also compares habitat use with the availability of habitat. Four widely-used functions in the preliminary analyses of movement data have been demonstrated on data from a sonic-tracking study of Pacific halibut (*Hippoglossus stenolepis*) in Glacier Bay, Alaska (Hooge *et al.*, 1999) (Figure 15). For overviews of the advantages and disadvantages of the many home range estimation techniques, refer to Boulanger and White (1990), Harris *et al.* (1990), Larkin and Halkin (1994), Hooge *et al.* (1999) and Powell (2000).

Moorcroft *et al.* (1999) argued that while the majority of traditional statistical models provided useful information, they are purely descriptive, with no mechanistic basis. Instead, they advocate a mechanistic home range model that uses partial differential equations to form simple behavioural rules, which have been derived from field observations of animal behaviour. Such models can be used to evaluate hypotheses for the factors underlying animal home range patterns and to obtain predictions on the changes to home range patterns following perturbations. Application to marine animals, however, may be more challenging since for many species, insufficient details are available on predictable behaviour with which to parameterise models. Nevertheless, mechanistic models would complement traditional statistical models of home range use. Using several methods may overcome the biases in any one method, allow cross-validation of model results, and enable comparisons with other studies.

In contrast to most statistical models, fractal analysis is relatively insensitive to sample size, measurement error and to measurement scale (Loehle, 1990). The fractal dimension (D) has increasingly been applied to studies of movement including home range movements (e.g. Dicke and Burrough, 1988; Wiens and Milne, 1989; Crist *et al.*, 1992). Loehle (1990) calculated D for both the path taken by an animal (measure of tortuosity) and for the pattern of the patches used by the animal. The technique involved building a 3-D surface of spatial activity over a mapped area and calculating the fractal dimension of the surface at multiple scales. Mouillet and Viale (2001) calculated D for trajectories of satellite-tracked fin whale in the north-western Mediterranean Sea and revealed relatively linear paths ($D = 1.03$). Long straight movements by whales were explained in relation to the movement between aggregated patches of

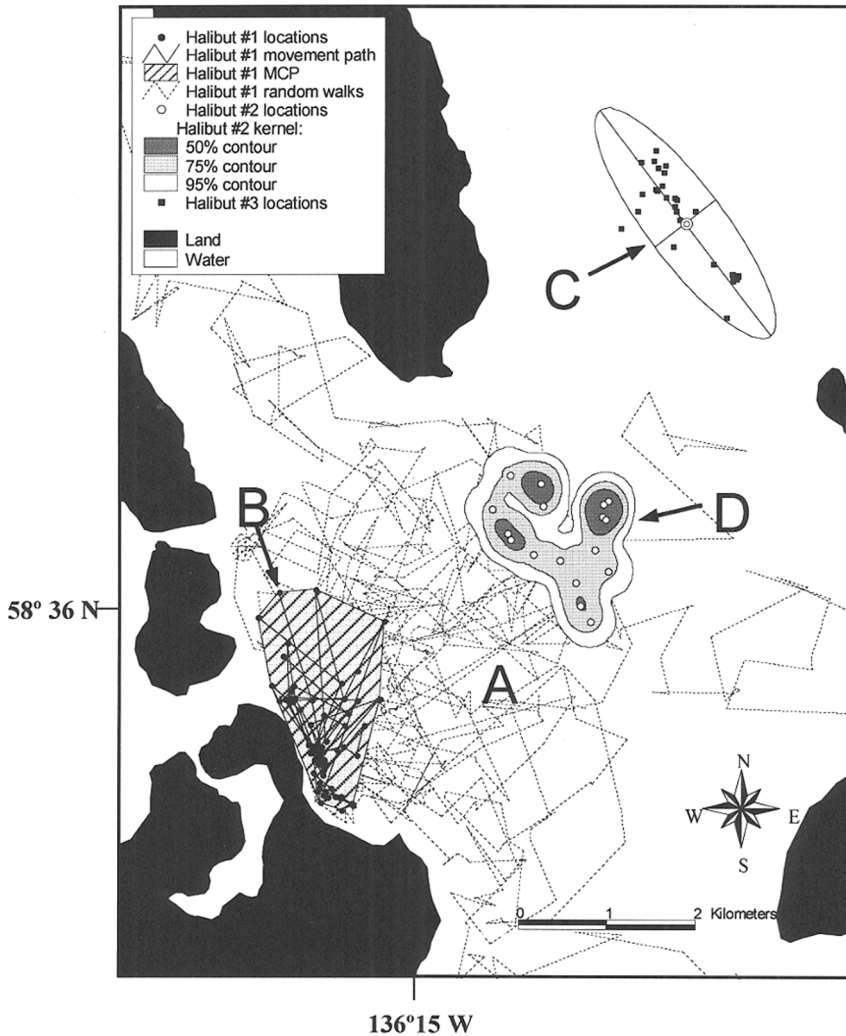


Figure 15 Analyses of acoustic telemetry data from three Pacific halibut in Glacier Bay, Alaska using the Movement Analyst Extension to ArcView® GIS. (A) A test for site-fidelity and the existence of a home range using a Monte Carlo random walk test with land as a constraining polygon for ten random walks. The values of the actual movement path are then compared to the ranked values of the random walks to determine significance. (B) Minimum convex polygon (MCP) home range shown enclosing the actual movement path of the animal tested in (A). Areas can be clipped out of the polygon by ArcView® to more accurately represent the areas used. (C) Jennrich-Turner 95% home range with the major and minor axes of the data shown. (D) Fixed kernel home range with the smoothing factor calculated via least-squares cross validation, showing the 50%, 75% and 95% utilization distribution contours. Data reproduced with permission of Philip Hooge, USGS, Glacier Bay Field Station, Alaska, USA.

zooplankton prey providing information on the way these whales perceive and use their environment. The authors hypothesised that trajectories composed of linear segments correspond to low prey densities (searching) and segments with relatively tight loops correspond to higher prey densities (feeding). With this perspective, it is likely that uni-directional movements such as migrations will exhibit low D , while multi-directional movements such as foraging will exhibit highly tortuous movements or high D values. If D is scale-independent then its use may facilitate ecologically meaningful extrapolations across spatial scales and provide insights into pattern–process relationships when linked to a multi-scale analysis (Crist *et al.*, 1992). Turchin (1996) argues that if scale-independence cannot be demonstrated an alternative random-walk model should be used in place of fractal analyses with which to examine animal movement. The correlated random walk model is a theoretical model used to evaluate movement pathways. The model produces pathways in a series of discrete time steps with a net directional bias. It is compared with observations so that correspondence indicates random movement, overpredicted displacement indicates preference for a region and underpredicted displacement indicates avoidance of a region. Deviations from correlated random walk model assumptions may reveal specific behaviour such as changes in turn direction to move along a straightened path or positive correlation in sequential turn direction in area restricted movements (Kareiva and Shigesada, 1983; Bergman *et al.*, 2000).

In addition to its great utility in the calculation of and visualisation of home range estimators (Hooge *et al.*, 1999) and other statistical models that can be applied to movement data, GIS provides a powerful tool for linking animal movement models with models of environmental heterogeneity. Tischendorf (1997) describes the development of an hierarchical grid-based spatial data model coupled with an object-orientated model of individual movements, which combine to permit simulation experiments to investigate the effects of spatial patterning in the environment on animal movements over a wide range of spatial and temporal scales. Furthermore, species-specific responses to patch attributes such as edge permeability can be assigned to pattern-orientated models, which then act as a template over which movement responses can be simulated. For example, if the foraging movements of a crab are known to be inhibited by a specific gap size between patches of seagrasses, then that spatial information can be programmed into the model.

5.4. Quantifying environmental data at multiple spatial scales

Examining animal–environment linkages for small and highly mobile animals that use a spatially heterogeneous environment requires spatially intensive quantitative environmental data, with both fine resolution and broad extent. It is unlikely that any single technique currently available would be capable of

discriminating structural features at the range of scales that are likely to be important to many fish and decapod crustaceans. Typically, techniques that provide fine scale measures are limited in their spatial coverage by time demands, whilst remote sensing devices, able to record pattern at broad spatial extents (i.e., aerial and space-borne sensors) have fixed limits of spectral sensitivity, spatial resolution and descriptive resolution (Green *et al.*, 1996). To address this problem, a range of techniques is needed, each with a unique ability to discriminate pattern. Each technique has advantages and limitations defined by their design, but are complementary when used in an integrated approach.

5.4.1. Mapping

A selection of commonly used techniques is reviewed here, with particular emphasis on techniques applicable for benthic mapping. Measures can be ground-based or remote, such as water-, air- and space-borne sensors. Ground-based measurements are usually point samples delineated with cores, quadrats and transect and are well known to most ecologists. Continuous spatial data (i.e. maps), however, are needed to represent the environmental template (*sensu* Southwood, 1977) over which an animal operates. Underwater videography used in conjunction with Global Positioning System (GPS) data can provide continuous geo-referenced images covering broader areas than could be achieved using point sampling, whilst retaining the ability to identify positively substratum composition (albeit not necessarily with high taxonomic resolution). Underwater videography of benthic structure is an increasingly commonly used tool in marine science and is one of the few techniques that can effectively map subtidal substratum in waters with variable depth, turbidity and substratum composition. The camera can either be hand-held, attached to a mobile platform such as a manta-tow board (Carleton and Done, 1995), a benthic sled (Bergstedt and Anderson, 1990), a remotely-operated submersible (Anderson, 1994), or at the surface attached to a boat (Norris *et al.*, 1997; Riegl *et al.*, 2001). However, video usually requires human visual interpretation and therefore bias can be introduced through variability in water depth and turbidity and in the ability of an observer to discriminate structure (i.e., vegetated from unvegetated).

Acoustic techniques such as sonar are not limited by variable light and such techniques have been shown to provide accurate sediment and vegetation mapping information for marine environments that are not suitable for optical sensors (Bernhardt *et al.*, 1998; Lee Long *et al.*, 1998; Pasqualini *et al.*, 2000). High resolution multibeam sonar and digital sidescan sonar survey techniques are rapidly developing to provide high resolution (<1 metre) images through a range of water depths (Armstrong *et al.*, 1998; McRea *et al.*, 1999). Interpretation of sonograms usually requires extensive ground-truthing but when coupled with diver

observations, the method can provide accurate maps over broader areas in shorter time than diver surveys or videography alone. However, even water-based videography and acoustic surveys may not easily map the environment at the spatial scales relevant to many marine nekton using shallow inshore areas. Higher altitude sensors are therefore required. Elevated platforms such as balloons, aeroplanes, helicopters, spacecraft and satellites have been used extensively for the mounting of still and video cameras and multispectral and hyperspectral scanners. The applications of air and space-borne remote sensing techniques for acquiring data on marine systems have been extensively reviewed elsewhere (Green, *et al.*, 1996, 2000; Mumby *et al.*, 1998, 1999; Santos, 2000; Hedley and Mumby, 2002; Mumby and Edwards, 2002). Most animal–environment studies of fish and decapod crustaceans will require a combination of integrated remote sensing techniques. For example (although not specifically for mapping animal environments), Pasquatini *et al.* (1998) mapped seagrasses around Corsica by combining aerial photography for the waters less than 20 m deep with sidescan sonar for waters 20–50 m deep. Our own studies in Moreton Bay, Australia, have used a GIS to integrate geo-referenced samples from multiple scales, ranging from fine-scale point samples for water quality and substratum structure to video-graphic transects, aerial photographs and Landsat Thematic Mapper data. These data represented environmental variability at multiple scales (including the extent of the home range) to which animals in our study area were likely to respond. An example of a framework for an integrated approach to collecting, classifying and mapping environmental data at multiple spatial scales is shown in Figure 16.

5.4.2. *Delineating functionally-meaningful pattern*

The discrimination of spatial themes or classes can be achieved objectively using various clustering and ordination algorithms (e.g., Sheppard *et al.* 1995; Mumby and Harbourne, 1999; Green *et al.* 2000). The aim of any classification is to simplify heterogeneity by subsuming it within a representative entity that carries a class name or descriptor. Typically, in the production of a thematic or categorical map, an artificial line network supersedes information about fine-scale structure and all accurate quantitative information about within-map unit variation is lost (Burrough and McDonnell, 1998). However, in animal ecology the resulting classification is integrated into a digital map from which to quantify spatial pattern and therefore the map must represent classes that are meaningful to the animal(s) of interest. Otherwise, the output from spatial pattern statistics will be difficult to interpret. The recognition of meaningful structure for any animal requires that a functional interaction be established (Kolasa and Rollo, 1991; McCoy and Bell, 1991; Cale and Hobbs, 1994), which means that *a priori* information on finer-scale relationships must be established through carefully designed mensurative or manipulative experiments.

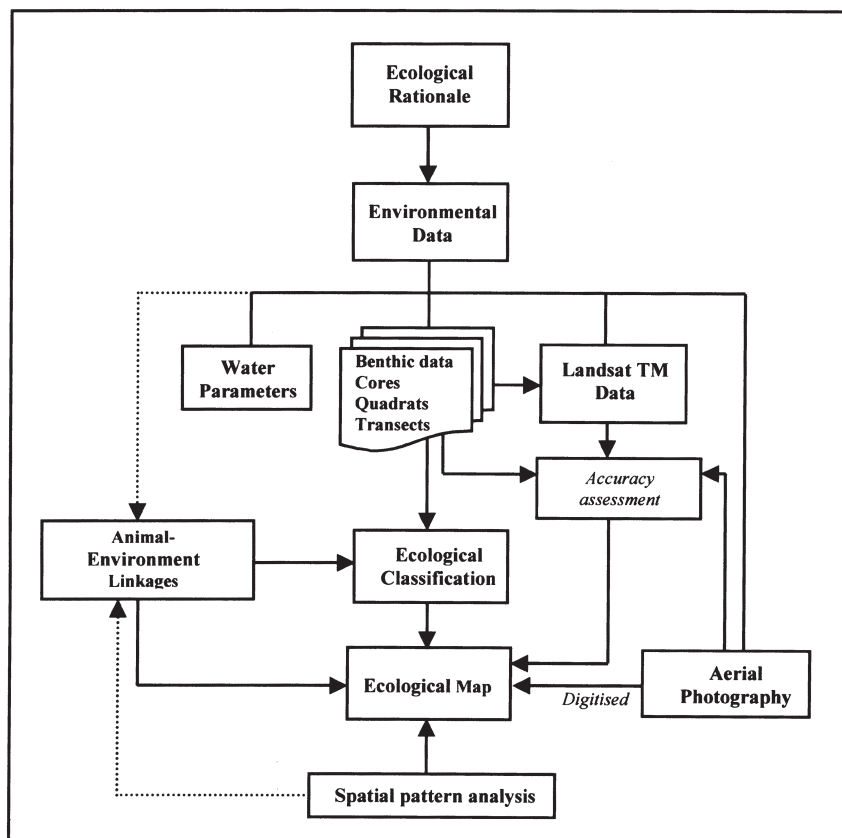


Figure 16 Overview of the structure and flow of information in an integrated multi-scale approach to collecting, classifying and mapping benthic structure. The rationale provides a conceptual framework with which to approach the quantification and analysis of environmental data. The high resolution data (cores, quadrats, transects) provide information for the examination of fine scale linkages and for the composition of the broader scale patterns distinguished through aerial photography and Landsat TM data. Information from all scales contributes to the ecological map, which is a digital thematic map based on the integration of pattern that was digitised directly from the aerial photography, with themes derived from the ecological classification.

The selection of an appropriate minimum mapping unit (MMU) is also an important consideration, since this constrains the lower limits of resolution (Li and Reynolds, 1994; McGarigal and McComb, 1995; Gustafson, 1998) and influences the behaviour of spatial pattern metrics (Saura, 2002). Furthermore, delineating boundaries requires careful consideration, since the production of a categorical map using statistical clustering algorithms typically results in an

abrupt division between groupings. The representation of classes with sharp edges, however, is not necessarily unrealistic since in tidally-dominated inshore areas, gradients in environmental conditions are often characterised by abrupt discontinuity in the distribution of benthic plants and animals. This well recognised pattern of intertidal 'zonation' (Stephenson and Stephenson, 1949; Lewis, 1964; Ranwell, 1972) is a consequence of the responses of benthic plants and animals to variation in the environment (e.g. water depth, immersion/emersion times, grazing etc.). Burrough (1986) and Fortin and Drapeau, (1995) advocated using statistics to detect boundaries by identifying the location where the measured variables (biotic/abiotic) show the highest shifts (or maximum rate of change). Furthermore, to validate functional meaningfulness to the proposed biophysical boundaries (from the point of view of the animals of interest), the animal response – in terms of the spatial distribution of abundance, mass or species diversity or the trajectory of an individual – could be examined for concomitant discontinuities. Therefore, at every stage in the mapping process, decisions must be made about scale and about which structures and which attributes are meaningful. The challenge for the mapping process is to incorporate functionally meaningful structure at a range of spatial scales, whilst also selecting an appropriate level of simplification that retains sufficient detail to address the problem.

5.4.3. *Quantifying spatial pattern*

Since a suite of complementary and integrated spatial technologies is required to analyse and display data in animal–environment studies, a Geographical Information System (GIS) would be an invaluable tool. Free standing and GIS-integrated spatial pattern analysis programs such as FRAGSTATS®ARC and Patch Analyst, can be used to quantify and model spatial pattern. For studies in terrestrial systems, an extensive set of indices or metrics has been developed and applied to measure the composition and spatial pattern of mosaic structure (e.g. O'Neill *et al.*, 1988; Turner, 1989; Gustafson *et al.*, 1994; McGarigal and Marks, 1994; McGarigal and McComb, 1995; Haines-Young and Chopping, 1996; Gustafson, 1998; Hargis *et al.*, 1998). Mosaic composition encompasses the variety and abundance of patch types, without being spatially explicit and includes the proportion of each class (patch type), as well as richness, evenness and diversity indices. The spatial pattern (physical distribution of patches) is measured by shape, area, amount of edge, patch isolation and contagion. The metrics developed to measure the various aspects of structure are interrelated by their dependency on the same underlying measures of patch area, edge length and inter-patch distance (Riitters *et al.*, 1995; Hargis *et al.*, 1998). As a result, some partial or complete redundancy occurs (Riitters *et al.*, 1995; Haines-Young and Chopping, 1996; Cain *et al.*, 1997).

Using Factor Analyses (a principal components analysis based on correlation coefficients between pairs of metrics), Riitters *et al.* (1995) found that six factors explained 87% of the variation among 26 metrics. In animal ecology, however, the process must also ensure that the chosen metrics capture all dimensions of spatial pattern relevant to an animal. For exploratory studies of the influence of mosaic pattern on animals, a suite of metrics is typically used (26 metrics by McGarigal and McComb (1995) for bird assemblages; 17 metrics by McAlpine *et al.* (1999) for kangaroos and eight metrics by Hansen *et al.* (2001) for caribou). For marine systems, however, this type of approach remains largely theoretical (Robbins and Bell, 1994), with few attempts to quantify spatial pattern (Garrahou *et al.*, 1998 for rocky shores; Robbins and Bell, 2000 for seagrasses; Teixidó *et al.*, 2002, for Antarctic benthic communities).

In addition, exploratory studies undertaken on a wide range of highly mobile animals including hoverflies (Haslett, 1994), birds (Pearson, 1993; McGarigal and McComb, 1995), kangaroos (McAlpine *et al.*, 1999) and Florida panther (Kerkhoff *et al.*, 2000) have recognised that investigation of a species response to spatial pattern must take place at multiple scales. These previous studies have quantified mosaic structure within a range of spatial extents, delineated around an observation area for a particular species or group of species. For example, from studies of wintering bird populations in Georgia (USA), Pearson (1993) showed a species-specific response to pattern measured at different distances (five concentric bands of 100 m) from a sample transect. In the Alps of southern Germany, Haslett (1994) quantified mosaic complexity by computing fractal dimensions within circles of 300 m radius that were estimated to have incorporated hoverfly home ranges. In Queensland, Australia, McAlpine *et al.* (1999) quantified mosaic structure for kangaroos at a number of radial extents from 5 to 15 km surrounding each 10 km line transect. In Florida, USA, Kerkhoff *et al.* (2000) quantified forest cover at multiple scales using fractal dimensions and assessed the association with known panther locations (telemetry) via conditional mapping. In Moreton Bay, Queensland, benthic mosaic structure was quantified at radial extents of 100 and 300 m around beam trawl and buoyant pop-net samples of marine nekton (Pittman, Ph.D. thesis) (Figure 17).

Although few studies have examined the effect of spatial pattern on nekton, studies that link detailed movement patterns with detailed benthic mapping using spatial statistics are now emerging. Cote *et al.* (1998) investigated the spatial and temporal animal–environment linkages for juvenile cod in Newfoundland through the continuous and simultaneous tracking of a number of fish ($n=28$). This was coupled to high-resolution mapping of bathymetry, substratum structure, currents and tides as well as spatial and temporal variation in temperature and salinity. Benthic mapping was accomplished using an acoustic seabed mapping system, together with baseline mapping undertaken by scuba divers carrying transmitters and tracing out the various environments within the study area. Fish position was associated with mapped environmental

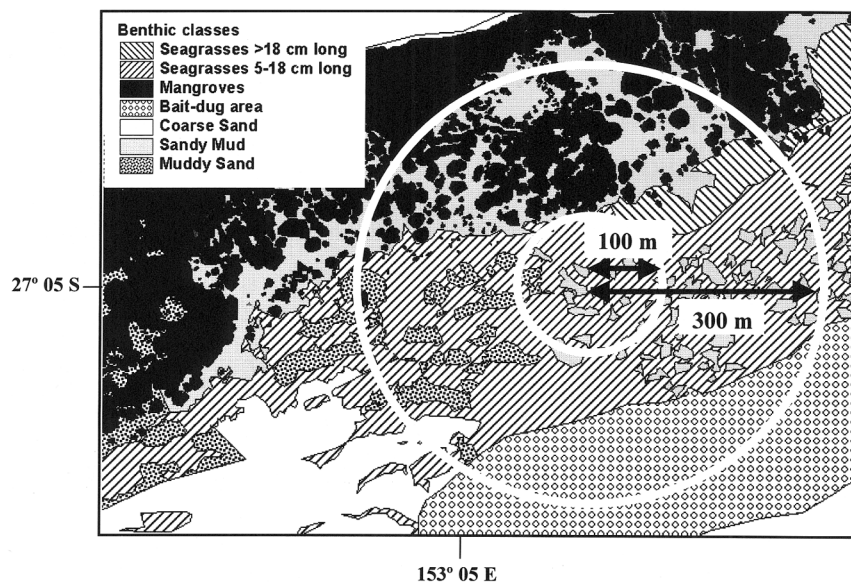


Figure 17 An example of mosaic patterns delineated at two spatial extents (100 and 300 m radii) around a beam trawl sample of 50 m length in Moreton Bay, Australia. Spatial extents were selected to explore the influence of spatial scale (the estimated home range and within the home range scale) on relations between mosaic structure and a number of attributes of the nekton assemblage (e.g., diversity, taxonomic distinctness, live mass, species composition, abundance, etc.). Benthic classes were determined using cluster analysis based on core samples. Boundaries were delineated using a combination of Landsat TM data, aerial photography, underwater videography and ground surveys as well as overlaying animal distributions to examine correlation between proposed biophysical boundaries and those meaningful to the animals of interest. Delineated circles were then clipped out and spatial pattern analysed using FRAGSTATS software (McGarigal and Marks, 1994).

features in a GIS using a point/polygon routine to link features to each fish position. Such an approach would reduce the bias associated with an arbitrary choice of scale and would also facilitate multi-scale spatial pattern analyses of benthic structure.

6. IMPLICATIONS FOR CONSERVATION AND RESOURCE MANAGEMENT

Animal movement is a mechanistic element of many ecological processes and therefore, understanding animal movement patterns throughout their life cycle is

fundamental to the effective design of conservation and resource management strategies (Acosta, 1999; Warner *et al.*, 2000). For heavily exploited species, this information is crucial if populations are to be maintained or enhanced (Dugan and Davies, 1993; Zeller and Russ, 1998; Willis *et al.*, 2001). The size, shape and geographical placement of management strategies such as reserves or marine parks must be driven by information on animal movement and the locations of key activities that allow a population to persist in an area. Furthermore, management strategies are unlikely to be effective without knowing how the component parts are connected (Wolanski *et al.*, 1997). When establishing a reserve the objectives are usually to protect a region of high diversity or specific resource requirements for a threatened species or commercially valuable species (Tuck and Possingham, 2000). However, most reserve designs and site selection procedures have involved little scientific justification (Allinson *et al.*, 1998) and rarely do plans for marine reserves incorporate specific movement patterns for key species for scaling reserve area and determining its shape and placement (Botsford *et al.*, 2001). Modelling approaches for examining the structure and function of fishery reserves have also tended to assume high site fidelity or limited movements of animals in relation to reserve area (e.g. Sladek Nowlis and Roberts, 1999). This is largely a result of the fact that research has focused primarily on a few relatively site-attached individuals and because trajectories for most species are unknown or only poorly understood.

Where biological information has been used, it is traditionally based on knowledge of the requirements for single life stages (St Mary *et al.*, 2000). However, strategies that are designed to consider only single segments of the life-cycle trajectory (e.g. adult or larvae; reproduction or settlement) are likely to be less effective than strategies that consider whole life cycle processes, particularly for exploited populations (Sladek Nowlis and Roberts, 1999). For instance, it may be counterproductive to manage only for locations of high larval retention or known settlement substratum that have no available resources in adjacent areas to support subsequent ontogenetic shifts (Acosta, 1999). Following extensive observations of spiny lobster distributions in the Caribbean Sea, Acosta (1999) recommended that the limited goals of marine reserves "must be expanded to the protection of all important habitats that will support an intact life history". The author also stated, "Shelter, foraging grounds, or movement corridors for exploited species must be quantified and incorporated into the design of protected areas". If a reserve is geographically placed in order to optimise survival for a particular species that uses inshore areas as a "nursery", but distant spawning grounds where mature adults aggregate are heavily exploited (or *vice versa*), then abrupt changes can be expected in overall abundance, regardless of the efforts put into the management strategy. The spatial and temporal domains of larval trajectories, ontogenetic shifts, home ranges, home range relocations and spawning and non-spawning migrations all have implications for reserve design. Essentially, when the home range of an animal is broader than the scale of the refuge, an animal will not receive full protection (Kramer and Chapman, 1999).

Research has shown that some species have evolved life-cycle movements that operate at scales of 10s to 100s km. In contrast, most management strategies operate at much finer-scales. In most parts of the world, matching such broad-scale movements with a single reserve is unlikely to occur. Instead, a system of marine reserves is required that covers locations of essential activities and includes pathways that link these locations. Sladek Nowlis and Roberts (1999) have argued that fish movement across boundaries will decrease the predicted yield from reserves. Consequently, reserves must be designed large enough or in large enough units to contain populations, particularly during the phase of their life in which they are most vulnerable to fishing. Furthermore, scales of movement patterns differ between species and between individuals of the same species. For example, several tagging studies of exploited species have shown both long-term site-fidelity by some individuals and extensive distances travelled by others (Attwood and Bennet, 1994; Beentjes and Francis, 1999). An acoustic telemetry study by Eristhee and Oxenford (2001) on space use of Bermuda chub (*Kyphosus sectatrix*) within a marine reserve, revealed that several individuals spent more than 60% of the their time outside the reserve boundaries. The implications of this variability are that one reserve design will be unlikely to function optimally for all species or all individuals (Allison *et al.*, 1998; Sladek Nowlis and Roberts, 1999). Designing optimal strategies for multi-species assemblages is a significant problem that requires substantially more information on movement patterns than is currently available. However, in addition to tracking and tagging studies, it may be possible to use general models of movement parameterised by biological characteristics, such as life-history strategy or allometric scaling relationships or combinations of characteristics, to estimate relevant scales for reserve design (Kramer and Chapman, 1999).

Understanding movement also allows the opportunity to evaluate reserve function (Hixon *et al.* 2001). Reserve function can be examined directly through quantifying movement into and out of reserves, as well as the animal movement response to boundary placement that often occurs along physical discontinuities. For the management of exploited species, the main aim of a refuge or a no-take reserve is that animal biomass will increase within the protected area and eventually high density forces relocation, resulting in "spillover" into surrounding waters where they are fished (Russ and Alcala, 1996; McClanahan and Mangi, 2000). For some reserves, the contribution a relocating individual makes to nearby fisheries will be a function of its mobility and resource requirements. Indirect evidence of the spillover phenomenon can be found through observed changes in abundance and anecdotal reports from fishers. However, direct and more detailed evidence requires the application of tracking and tagging techniques (see Section 5.2 this paper and see Cole *et al.*, 2000; Chapman and Kramer, 2000). Computer simulation combined with tracking techniques also provide an unprecedented ability to examine connectivity within networks of

marine reserves and to predict the spatial and temporal dynamics of source and sink areas (Arnold and Holford, 1995; Roberts, 1997; Botsford *et al.*, 2001).

As argued here, the management of resources based on a purely anthropocentric perspective may not be sufficient to achieve goals related to effective ecological function. With current spatial technologies and rapid advances in tracking technologies, it is not unrealistic for movement patterns to be quantified and incorporated into management strategies. This information may encourage decision makers to look beyond evaluations of single habitat types and observation at arbitrary scales. For example, for fisheries based on tri-phasic species, the question should not be whether mangroves are more important than adjacent seagrasses, but how mosaics of habitat type, both inshore and offshore, combine to influence populations.

In addition to guiding scale selection in resource management evaluations and reserve design, analysis of movement data (particularly from advanced telemetry), can begin to answer some of the most challenging problems in marine ecology. Often observations of considerable temporal variability are reported to occur seasonally and on a lunar cycle, yet we rarely are able to sample widely enough to know where animals have gone. For instance, it should now be possible to track many species all year therefore allowing the identification of overwintering areas and spawning grounds as well as the trajectories linking these areas of essential activity. With the development of smaller transmitters, it will also be possible to directly quantify the patterns of movement between inshore nurseries and offshore adult populations. Furthermore, little is known of the movement response to changing environmental conditions and we speculate that the application of tracking techniques will provide great insights here. For instance, the dynamics of the response of highly mobile animals to a disturbance have important implications for impact assessment, since species-specific mobility may significantly influence the rate of recolonisation and therefore evaluations of the magnitude of the impact (Breitburg and Loher, 1994).

7. CONCLUSIONS

Differences in the scales of animal movement are the result of the evolutionary and ecological interaction with complex patterns and processes in the environment. Knowledge of the actual distances travelled as well as the directions of movement and movement pathways, is particularly useful in animal ecology, conservation and resource management. Using animal activity patterns to select appropriate scales with which to anchor our observations in time and space will improve sampling design, particularly in comparative studies. The application of a hierarchical approach, together with the coordinated integration of spatial

technologies offers an unprecedented opportunity for researchers to tackle a range of animal–environment related questions for highly mobile marine animals. Technological advances in tracking devices now allow us to fill in the gaps in the movements of animals with increasingly broad extent and fine resolution. This information complements existing studies and forms the basis of studies that aim to determine habitat suitability.

Overexploitation of marine animals is a global problem (Jackson *et al.* 2001) with no foreseeable solution in the near future. Nevertheless, it is clear that some management strategies are constrained by a lack of fundamental data on the scales relevant to the way animals use their environment throughout the life cycle. For exploited populations, it appears likely that maintenance of long-term sustainability will in part depend on understanding the relationship between animal movement patterns and management strategies, such as reserve design, size and placement. The use of computer-based spatial technologies such as GIS and advances in complementary technologies such as mathematical modelling and telemetry will facilitate the implementation of ecological information into planning strategies. Life-cycle trajectories and multi-scale environmental maps must become essential modules in the decision making process for ecologically meaningful resource management strategies. A concomitant shift in perspective toward a multi-scale organism-based approach to resource management will advance any attempts to understand both animal ecology and ensure a diverse and productive marine environment through ecological information-based management strategies.

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