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Linking habitat selection, emigration and population dynamics of freshwater fishes: a synthesis of ideas and approaches

Abstract – The consequences of individual behaviour to dynamics of populations has been a critical question in fish ecology, but linking the two has proven difficult. A modification of Sale's habitat selection model provides a conceptual linkage for relating resource availability and individual habitat selection to exploratory behaviour, emigration and population-level responses. Whole-population experiments with pupfish *Cyprinodon macularius* that linked all factors along this resource to population continuum lend support to this conceptual model, and illustrate that emigration may be much more common in fish populations than considered in most individual- or population-based models. Accommodating emigration can enhance the ecological appropriateness of behavioural experiments and increase confidence in extrapolation of experimental observations to population-level effects. New experimental designs and advancing technologies offer avenues for assessing population consequences of habitat selection and emigration by individual fish. Emigration often is the key linkage between individual behaviour and population responses, and greater understanding of the underlying factors affecting this often-overlooked demographic parameter could offer new approaches for management and conservation of fishes.

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Life, and the freedom to move, are one. (Haida proverb)

Introduction

Population biologists justifiably tend to be more interested in population-level processes than in the behaviour and fates of individual organisms. Whereas populations have demographic features, such as birth rate, death rate and population growth rate that individuals within the population do not have, it is increasingly recognised that these demographic features ultimately are the result of the behaviours of individual animals, behaviours that influence growth, survival, reproductive success and movements (Lomnicki 1988; Sutherland 1996).

Despite the increased interest in the role of individual behaviour in population dynamics, details of the link between the two are poorly understood (Sutherland 1996; Lidicker 2002). For example, biologists know that population growth must be the result of additions of individuals through birth and immigration and removal of individuals through death and emigration. However, immigration and emigration frequently are discounted in population dynamics models – that typically focus on birth and death rates as primary driving forces – partly because immigration and emigration are so inherently difficult to measure

(Lomnicki 1988; Lidicker 2002). Yet immigration and emigration may be numerically important and vital to normal population processes (Hanski 2001), including responses to management actions (Riley & Fausch 1995). However, biologists know surprisingly little about what conditions trigger emigration, which individuals are likely to become emigrants, and how emigration and immigration influence population dynamics (Nathan 2001).

The importance of emigration came to the forefront of population ecology with the discovery that populations of a diverse assortment of animals rapidly overpopulate when emigration is prevented (see list in McMahon & Tash 1988). In addition, emigration has received renewed attention in the recent development of metapopulation theory and source–sink dynamics (e.g. Kristan 2003), and is viewed as a vital factor for maintaining biodiversity in fragmented landscapes through recolonisation, demographic support and gene flow (Hanski 2001).

For freshwater fishes, movement among habitats is now recognised as the norm rather than the exception across many taxa (Lucas & Baras 2001). As with all animals, the difficulty of measuring emigration and of unambiguously distinguishing it from normal foraging movements, local exploratory behaviours and migration are major impediments to unravelling its causes and consequences (Matter et al. 1989). Moreover, there is much uncertainty in extrapolating from mechanistic, small-scale studies of habitat selection and emigration, to the larger scale context of temporal and spatial population dynamics, and vice versa (Lidicker 2002; Lowe 2003). However, as Humston et al. (2004) noted, realistic models of large-scale movements and spatial structure and population dynamics of fishes require a thorough understanding of the proximate mechanisms eliciting movement at small scales.

We present a conceptual model that links resource availability, habitat selection, exploratory behaviour and emigration of individual animals at small scales, to the spatial and temporal dynamics of populations at larger scales. We use whole-population experiments on emigration in a freshwater fish to test this model, and present approaches for measuring emigration in the laboratory and the field. We define *emigration* as the one-way movement away from a home area (Lidicker & Stenseth 1992), as a special type of *dispersal*, which is typically used more broadly to define all types of nonmigratory movement outside a home range (Hendry et al. 2004). Our focus is on the movement of individuals away from a home area that equates to 'loss' of individuals from a site and thereby affects local population density as well as the population characteristics of the area where immigrants settle. A distinction between 'facultative' and

'obligative' movement is also important (Bell 1991). We focus on factors influencing facultative or condition-dependent movement – voluntary movement made in response to changes in resource needs or resource access from such factors as increased density, reduced food, need for cover or mate seeking (Ims & Hjermann 2001; Massot et al. 2002) – in contrast to obligative movement, an innate movement in response to some external cue or endogenous clock (e.g. posthatching dispersal in larvae or downstream smolt migration) (Howard 1960; Dytham 2003).

Linking habitat selection, emigration and population dynamics: a conceptual model

One of the most important attributes of fish and other mobile animals is the ability to move away from unsuitable conditions. However, for mobility to have its greatest adaptive advantage, organisms must be able to assess biotic and abiotic conditions such that exploratory behaviour is triggered 'on' by inadequate or unsuitable conditions, and triggered 'off' when individuals encounter suitable conditions (Sale 1969a; Bell 1991). To do this, animals must be able to perceive environmental features that, over evolutionary time, have been associated with survival and reproductive success for the species (Kristan 2003).

During habitat selection, animals respond by remaining in areas that hold the proper suite of environmental cues, but continuing to search more widely when these cues are not present in a local area, even if this requires that they move through areas unsuitable for the species (Matter et al. 1989; Bonte et al. 2004). Cues that trigger exploratory behaviour may include unfavourable environmental conditions, inadequacy of resources or unacceptable interactions with resident animals, including intra- and interspecific competitors and predators (Bell 1991). In this way, movement is viewed as a condition-dependent trait that can be triggered by many different cues (Ims & Hjermann 2001).

Sale (1969a)) provided an early conceptual model linking resource availability, motivation and exploratory behaviour in fish (Fig. 1). Sale theorised that habitat selection is a continually active process governed by the intensity of exploratory (appetitive or searching) behaviour via a negative feedback loop, with exploratory behaviour governed by the interaction of internal drives (motivation) for needed resources (A) with the perceived availability of those resources in the environment (B). External and internal stimuli perceived by the central nervous system serve to regulate exploratory behaviour (C).

Sale hypothesised that exploratory behaviour leads to variation in the immediate environment (D) experienced by an individual, which, in turn, leads to
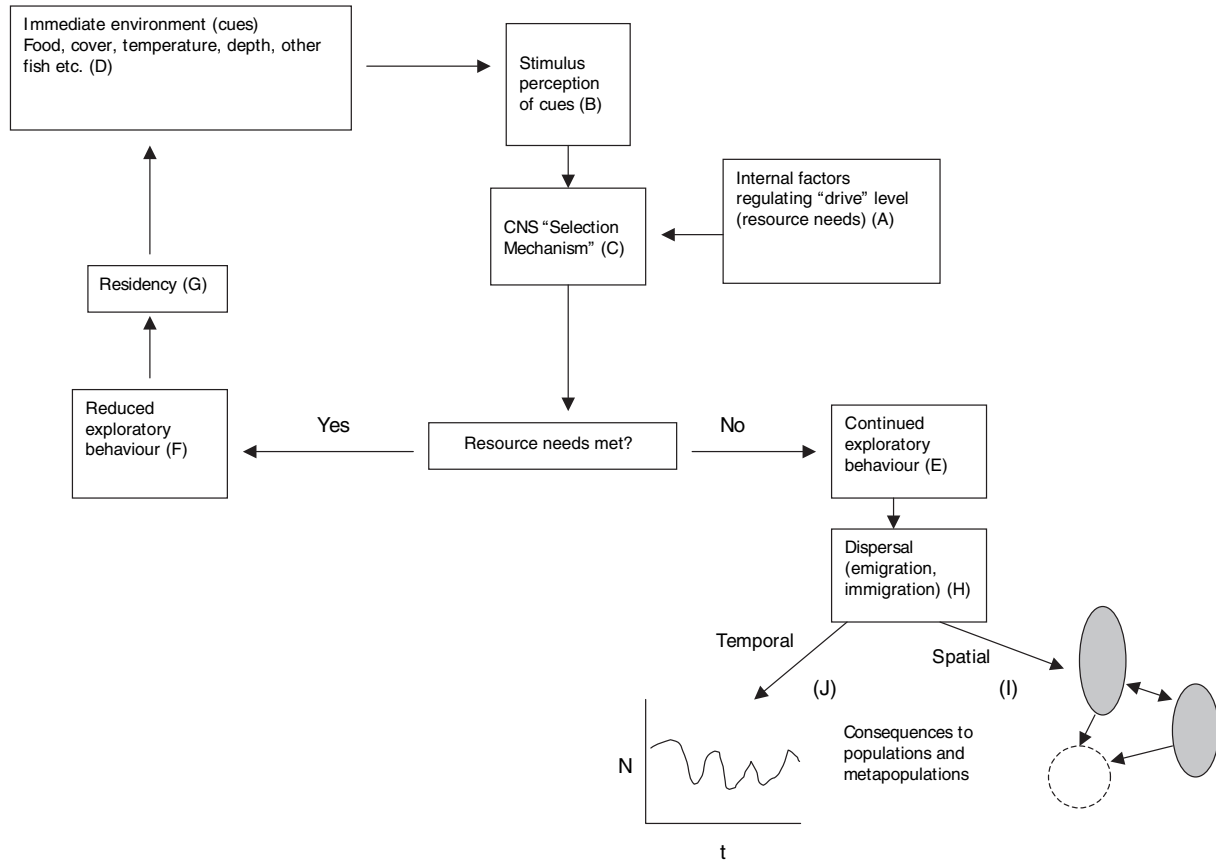
Fig. 1. Schematic representation of the habitat selection-emigration model modified from Sale (1969a). CNS, central nervous system. Letters referenced in the text.

changes in the level of stimuli (B) animals use to assess availability or access to needed resources. Thus, the model predicts that exploratory behaviour will be most intense when environments are perceived as less adequate (E), and exploration will diminish when an environment is perceived as suitable (F), leading to residency (G). As a result of this process, the intensity of exploratory behaviour (movement rate) is inversely proportional to the quality of available habitat (Winker et al. 1995). Furthermore, the model suggests that exploratory behaviour can be triggered by a host of factors affecting both resource needs and availability. Tests of the model in the laboratory with manini (*Acanthurus triostegus sandvicensis*), a tropical reef fish, confirmed that the intensity of searching behaviour varied greatly dependent on water depth and presence of cover. Searching behaviour was lowest when fish had access to shallow water with cover, the preferred habitat of manini in the field (Sale 1969b).

Sale did not address emigration directly in his model, so the question remains: How does exploratory behaviour relate to emigration? We hypothesise that emigratory behaviour can be viewed as a more intense form of exploratory behaviour (H). This is analogous to Sale's observation that searching behaviour was expressed nearly continuously in the presence of deep water with no cover – the least preferred conditions in the field. Thus, emigration events are likely to occur when environments that lack adequate resources (or access thereof) trigger continued exploration until animals eventually emigrate from an area in search of suitable conditions elsewhere. Experiments with several different animals support this hypothesis (Matter et al. 1989; Nelson et al. 2002). Viewed in this way, the decision to stay in an area or emigrate represents two ends of a continuum of complementary behavioural responses that may be elicited from any individual of a mobile animal species in response to the adequacy of the site currently occupied. The summation of the many such individual behavioural responses of fish to local conditions in relation to their environmental and physiological requirements will not only be a key determinant of the density of individuals occupying a site but, in turn, the resulting emigration will drive the larger scale spatial (I) and temporal (J) population dynamics within a landscape (Fig. 1) (Lidicker 2002; Humston et al. 2004; Kritzer & Sale 2004).

Although this habitat selection-emigration model is conceptually simple, we believe it provides a useful

explanatory tool for linking individual behaviour to population dynamics. To date, habitat selection has been explained primarily through the optimisation models based on ideal-free and ideal-despotic theories. According to optimisation models, well summarised for fishes by Kramer et al. (1997), population density in concert with habitat quality is the main driver of the decision of individuals to settle in or move away from habitat patches of differing quality. These models have been used profitably to predict local fish distributions in the field based on balancing survival and net energy functions (e.g. Hughes 2000; Railsback & Harvey 2002). However, in these studies it is frequently unclear which proximate environmental cues or stimuli individual animals are using to assess habitat suitability (Grossman et al. 1995). In addition, few habitat selection studies have explored the relationship of local movement within habitat patches to emigration and large-scale population dynamics (Doncaster 2000). Furthermore, an important assumption of optimality models is that animals 'sample' all available habitats before settling, yet animals often leave a site, in some cases moving across expanses of unsuitable conditions, without knowledge of the quality nor availability of other sites (McMahon & Tash 1988; Matter et al. 1989; Bonte et al. 2004). Our model suggests that the quality of the local site in relation to current resource needs and access is the primary driver of habitat selection and exploration decisions, rather than information about conditions at distant sites.

Detailed observations of fish habitat selection and movement in nature also show a great deal of complexity and individual variation (e.g. Armstrong et al. 1997, 1999; Smithson & Johnston 1999; Diana et al. 2004) that are not readily explained by optimisation models (Thorpe et al. 1998). For example, marked seasonal habitat shifts of fishes during autumn may occur abruptly, without any apparent changes in food availability or habitat quality (Riehle & Griffith 1993; Jakober et al. 1998). Similarly, nutritional or hormonal state can trigger movement away from a site of residence (Forseth et al. 1999), movement that is not strictly dependent on density or resource availability *per se*, but rather reflects changes in physiological needs of individuals (Bell 1991). Thus we believe that our model complements current habitat selection theory by extending it to include the underlying motivations and proximate environmental cues that govern habitat selection, and to explore the population dynamics consequences of habitat selection and movement patterns (see also Grossman et al. 1995).

The degree to which fish movement is a rather fixed trait has been the subject of much discussion among fish ecologists (Gowan et al. 1994; Rodríguez 2002), and the idea that there are 'mobile' and 'resident'

factions among individuals within populations is common (see Gowan et al. 1994 for discussion). Indeed, dispersal has generally been viewed as an adaptive trait that evolved for colonisation of new environments, prevention of inbreeding depression or risk spreading in stochastic environments (e.g. Kisdi 2002; Hendry et al. 2004). In our model, individual differences in access to resources or changes in environmental or physiological requirements could elicit variation in movement among individuals from very limited to very mobile, thereby accounting for the wide variation in movement observed both within and among fish populations (Smithson & Johnston 1999; Gowan & Fausch 2002; Rodríguez 2002; Hilderbrand & Kershner 2004). Experiments with fishes and other animals demonstrating that individual emigrants readily become residents when needed resources are supplied and that residents become emigrants when resources are limited (Matter et al. 1989; Nelson et al. 2002), lend support to this inherent flexibility in switching between residency and emigratory behaviour. We hypothesise that emigration is primarily an adaptive response to the inadequacy of conditions at the site of residency, and other benefits of movement to species persistence (risk spreading, gene flow, colonisation of open habitat, rescue effect in meta-populations) accrue largely as a by-product of the movement resulting from habitat selection decisions as portrayed in our model.

Case study: emigration and population dynamics of desert pupfish

Linkage of individual behaviours to population-level responses often is hampered by the small scale of behavioural studies (laboratory or stream section) and by their short-term nature and focus on a particular time or phase of the life cycle (Lowe 2003). These limitations have contributed to the view that findings from studies of individual behaviour are of limited value for extrapolation to overall population dynamics (Lima & Zollner 1996). In particular, a major impediment to examining the role of emigration in population dynamics has been the difficulty in unambiguously accounting for all individuals that leave a population and measuring the overall effects of these losses on population size in the light of the array of other additions and losses.

Our work with desert pupfish (*Cyprinodon macularius*) from western North American deserts has shown them to be ideal species for comprehensive study of mechanisms underlying population dynamics, and specifically the role of emigration (McMahon & Tash 1988). The small, relatively simple systems they inhabit – likely among the smallest occupied by an entire vertebrate population – can be readily duplicated

in small pools where pupfish exhibit behaviours and population dynamics indistinguishable from those in nature. Although this work was reported previously, we summarise its main results here because they come from one of the few studies of dispersal and population dynamics in fishes at the whole-population level.

The magnitude and timing of emigration and its overall relation to population vital parameters was examined experimentally by (i) comparing the dynamics of pupfish populations in pools open and closed to emigration over several generations; and (ii) measuring the emigration response to direct manipulation of resource levels. We mimicked immigration into a new environment by adding several adult male and female pupfish to outdoor pools that approximated the size of some of the smallest known pupfish habitats, and fish readily reproduced. Four pools were kept 'closed' to emigration. In four 'open' pools, pupfish were allowed to emigrate for 2 days every 2-3 weeks. To emigrate, pupfish had to swim across a shallow, exposed shelf and over a small, shallow spillway notch and fall into a holding tank. This means of emigrating from open pools seemed to mimic conditions of natural spring pools and provide a sufficient challenge that only certain fish were motivated to move through this gauntlet, supporting classification of these individuals as emigrants (Matter et al. 1989). Populations were censused every 2 months over the 22-month test period. No supplemental food was provided.

Initially, abundance of pupfish in open and closed pools grew exponentially, but populations in closed pools grew at a faster rate, peaked at a level 40% higher than populations in open pools, and then declined rapidly. During the decline, pupfish in closed pools were in poor condition – weighing 20% less than fish in open pools – grew slowly, had low recruitment rate and exhibited the narrow length–frequency distributions characteristic of stunted fish populations (McMahon & Tash 1988). In contrast, during this same period, large numbers of pupfish in open pools emigrated, and resident fish maintained high condition and growth, and exhibited no signs of stunting.

Although population sizes in open and closed pools were similar in the second year of the study, population parameters were very different in pools open and closed to emigration (Table 1). In open pools, emigration accounted for a much larger proportion of losses than did mortality, and net production (reproduction – mortality) was over 2.5 times higher in open pools than in closed pools. Overall, 84% of the pupfish produced in open pools emigrated. The low reproduction and high mortality of fish in closed pools (Table 1) clearly illustrated that the chances of survival and reproduction of fish that do not emigrate may be quite low in an area where access to resources by these 'excess' individuals is limited.

Table 1. Differences in population parameters (mean ± SE per pool) between pupfish populations held in pools with and without emigration outlets. Reproduction includes gains in population numbers plus number of emigrants counted between censuses. Net production refers to the average numbers produced per pool (total reproduction – mortality) during the 22-month study. Adapted from McMahon & Tash (1988).

	Open	Closed
Reproduction		
Year 1	283.2 (6.7)	268.5 (23.4)
Year 2	116.5 (60.7)	18.5 (6.5)
Mortality	36.2 (11.8)	164.0 (29.3)
Net production	331.5 (56.7)	127.0 (3.6)
Emigration	293.7 (55.3)	–

Emigration was similar among all four open pools, occurring at high levels during summer recruitment, at very low levels during winter, and increasing sharply in early spring coinciding with rising temperature and initiation of spawning. Emigration showed no direct relation to density. These patterns suggest that both environmental and behavioural cues were involved in triggering individuals to emigrate (McMahon & Tash 1988). Many of the adult fish first added to experimental pools were still present at the end of trials. This indicates that individuals whose resource needs were met did not attempt to leave open pools, but other individuals (especially young males) without access to sufficient resources readily navigated the shallow-water exit.

To test the link between emigration and resource availability more directly, we erected a barrier across the middle of two open pools, confining the population to one half of the pool and effectively doubling the density:resource ratio. Despite wide differences in initial population size, almost half (42%) of pupfish emigrated from the two manipulated pools, most leaving within the first 2 days of the 8-day trial, whereas only 16% emigrated from two control pools. These results, coupled with the consistent seasonal pattern of emigration among all four open pools, indicated that emigration was neither random, rare nor solely a product of a simple wandering response, but likely a direct response to changes in resource availability and resource demands of individual fish.

But how applicable are these results to other fishes? At first glance pupfishes appear unique from most other fishes that occur in much larger systems and as members of more diverse assemblages. However, just as the simplified environments on the Galapagos Islands have provided a window on the underpinnings of evolutionary processes in more complex communities (Weiner 1994), the small and relatively simple aquatic islands that pupfishes inhabit offer the opportunity to observe the effects of individual behaviour on population dynamics at a level of detail typically not possible in most other systems or species. Given that a

diverse assortment of animals exhibit similar population responses to prevention of emigration as do pupfish (McMahon & Tash 1988) and that pupfishes currently and in the past occurred within more diverse assemblages in larger lakes and estuaries (Miller 1981), we believe that the significant effects of emigration on population dynamics of this species are unlikely to be distinctive to this group. Similar experiments with other species that inhabit ponds, small streams and other environments amenable to experimental manipulation and precise measurement of emigration and other demographic rates are needed to test the generality of our hypothesised linkage between habitat selection, emigration and population dynamics (Fig. 1).

Measuring emigration

Emigration experiments with pupfish and other fish species (e.g. Matter et al. 1989; He & Kitchell 1990; Dunham et al. 2000) indicate that emigration is common, arguably more so than perhaps currently recognised, and has profound effects on population dynamics. Yet the difficulty in reliably differentiating emigrating individuals from individuals undergoing other types of movement remains a major hurdle for assessing its causes and consequences. Recent technological advancements in detecting fish movement (Lucas & Baras 2000, 2001), along with increasing recognition of its importance in population processes at the local and landscape scale (e.g. Schlosser & Angermeier 1995; Gowan & Fausch 2002), have led to the development of a number of different designs useful for measuring the interaction among habitat selection, emigration and population dynamics in the field, and in more controlled settings.

Field studies

Despite the large number of movement studies in fishes (e.g. Gowan et al. 1994; Lucas & Baras 2001; Hilderbrand & Kershner 2004), most tagging studies are unable to reliably distinguish emigration from other types of movement. Seasonal migrations and daily home range movements (e.g. Diana et al. 2004) could easily be confused with true emigration movements. Moreover, low recovery of tagged animals that move long distances from sites of tagging can confound interpretation of the effects of emigration on population dynamics and interconnection among populations. However, we found several study designs (Table 2) that could be tailored to differentiate local, exploratory-type movement from emigration, and to better estimate the magnitude of emigration on local and landscape-level population dynamics.
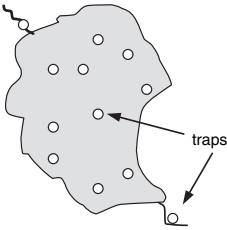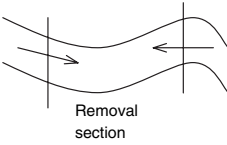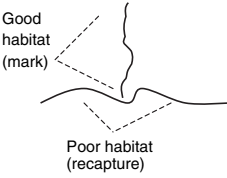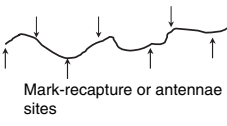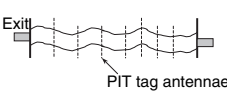
He & Kitchell (1990) employed an innovative design to measure the effects of a predator introduction on a prey fish assemblage in a small North American lake (Table 2A). Traps within the lake and within inlet and outlet tributaries measured changes in prey fish abundance and species composition in the lake and the timing and magnitude of what He & Kitchell (1990) called outmigration. Tributaries were small and often had unsuitable conditions in summer because of frequent oxygen depletion, and therefore movement into these sites could be distinguished from normal exploratory or home range movement in a way analogous to pupfish emigration from outdoor pools described above. Furthermore, the before-and-after experimental design allowed comparison of normal 'background' levels of outmigration to those following the predator introduction, thereby allowing a distinction between a seasonal, obligative-type of emigration and true facultative emigration.

The decrease in prey fish biomass due to a sharp increase in outmigration immediately following the introduction of pike (*Esox lucius*) was at least as great as the estimated loss from direct consumption. Outmigration was eight times greater following pike introduction compared to that during the same period the previous year, supporting classification of outmigration as a true emigration from the population.

Movement of new individuals into experimentally defaunated areas is another design that could be used to assess the degree of emigration (Table 2B), and is especially useful for assessing recolonisation potential and source–sink dynamics. If the removal area is large, most colonists can be assumed to primarily represent emigrants, although some animals living in home ranges adjacent to the removal area may move into the removal area. To date, this design has been deployed primarily to measure immigration rates (e.g. Adams et al. 2000), and we found no studies with fishes that explored the consequences to population dynamics in source and 'sink' (removal) habitat, nor how habitat quality in source areas influences the degree of movement, as has been the case with small mammals (Gundersen et al. 2001). Such studies are needed to assess how rates of emigration among source and sink patches influence spatial population dynamics within and between drainages (Schlosser & Angermeier 1995; Travis & French 2000).

Movement into areas of unsuitable conditions (Table 2C) is another design for measuring emigration (Matter et al. 1989; Nelson et al. 2002). For example, Fraser et al. (1999) recorded movement of killifish (*Rivulus hartii*) tagged in a small tributary with preferred habitat conditions into apparently unsuitable conditions of a main river corridor, where preferred habitat was rare and predation risk was markedly higher. Presumably, individuals would enter such

Table 2. Types of study designs for measuring emigration in the field and in controlled settings.

Design	Example	References
Field studies		
A. Comparison of within-population movement to emigration	traps	He & Kitchell (1990)
B. Experimental removal–immigration	Removal section	Adams et al. (2000)
C. Emigration into low quality habitat	Good habitat (mark) / Poor habitat (recapture)	Fraser et al. (1999)
D. Local versus long-distance movement	Mark-recapture or antennae sites	Bélanger & Rodríguez (2002), Dananacher et al. (2004), Ibbotson et al. (2004)
E. Retrospective analysis using hard parts	Individual variation in movement and effects on adult recruitment	Arai et al. (2003), Elsdon & Gillanders (2003)
Experiments in controlled settings		
F. Experimental enclosures	Exit PIT tag antennae	Matter et al. (1989), Armstrong et al. (1999)

PIT, passive integrated transponder.

unsuitable areas, strictly avoided by resident individuals, only when lack of access to resources strongly motivates them to do so (Fig. 1), thereby operationally identifying themselves as emigrants. Coupling this design with simultaneous measurement of local movement within the 'source' habitat would be an effective way to examine the relationship between habitat quality, exploratory behaviour and emigration in the field. For example, as predicted by our model, Bonte et al. (2004) found that increased rates of local movement within low quality habitat were correlated with increased emigration rates.

Recapture or detection of tagged fish at fixed sites along a stream course have also been used to assess the degree of immigration and emigration in relation to habitat quality within and between habitat patches of varying distances (Bélanger & Rodríguez 2002; Dananacher et al. 2004). For example, studies with Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) demonstrated that apparently preferred areas had higher immigration and residence times and lower emigration rates than less preferred areas (Bélanger & Rodríguez 2002). Arrays of 'recapture' or 'detection' sites could be deployed, using individual marks, radiotags, or passive integrated transponder (PIT) tags, to differentiate short distance exploratory and home range movement from long-distance emigration, and for examining the rates of movement among population units. In particular, the advent of remotely deployed PIT tag detecting

antenna technology, coupled with the opportunity to PIT tag many individuals (Barbin Zydlewski et al. 2001; Ibbotson et al. 2004), offers great promise for assessing movement of many individual fish in relation to environmental factors in real-time over both small and large spatial scales to a degree that has been nigh impossible to date.

Chemical analysis of hard parts to retrospectively determine movement patterns of fish (Table 2E) offers another important tool for analysis of movement (Thorrold et al. 2001; Arai et al. 2003; Elsdon & Gillanders 2003). Natural chemical tags can overcome some of the limitations of traditional tagging because movement and habitat use can be assessed over an entire life cycle and the contribution of different movement patterns or 'contingents' (Secor 1999) to adult recruitment can be determined.

Experiments in controlled settings

The use of laboratory or field enclosures with emigration exits offers several important advantages over observational field studies for measuring the impact of emigration on population dynamics: (i) the ability to accurately identify and enumerate emigrants and residents, (ii) direct testing of triggers to emigration via manipulation of potential environmental and social factors such as fish density and resource availability, and (iii) the potential to isolate the effects of emigration from other demographic parameters (Matter et al. 1989). To ensure such experiments do not produce artefactual behavioural and population responses, a common concern of controlled ecological experiments, Matter et al. (1989) (see also Nelson et al. 2002) set forth several key criteria that must be met. First, all test animals must have the ability to find and use exits, thereby having the same freedom of movement available in nature: to stay when conditions are perceived as suitable and to leave when conditions are unsuitable (Fig. 1). Second, enclosure exits must readily allow the passage of animals with sufficient motivation to emigrate (Fig. 1E,H), but must be sufficiently challenging that residents do not inadvertently wander out during routine exploratory movements. Exits that require fish to swim through narrow passageways and over a shallow shelf have proven effective at meeting these test criteria (McMahon & Tash 1988; Matter et al. 1989).

Such controlled settings offer great potential for experimentally evaluating how variation in emigration responds to variation in habitat conditions and contributes to subsequent population responses to a degree not possible in field settings. For example, such a study design could by used to experimentally evaluate the 'movement rules' which form the basis for individual-based models of fish population dynamics

(Bélanger & Rodríguez 2002; Railsback & Harvey 2002), and provide clearer insight into the mechanisms underlying fish movement and its consequences. We believe that simultaneously measuring within-enclosure movement with emigration out of an enclosure (Table 2F) would be a particularly useful approach for linking individual behaviour to manipulations of resource availability and density. We found no examples of studies that have adopted this design, but studies of movement of fish with PIT tags within enclosures (without exits) having an array of tag-detecting antennae, attest to its potential value for measuring individual variation in exploratory behaviour and emigration in direct relation to changes in abiotic and biotic conditions (Armstrong et al. 1997, 1999; Brännäs et al. 2003).

Despite such distinct advantages, use of such 'open' experimental enclosures for study of fish habitat selection and emigration has been limited. Direct comparison of populations 'open' and 'closed' to emigration, similar to that noted above for pupfish, can yield important insight into the overall impact of emigration on population dynamics for a species, yet in our review of the fish ecology literature from 1988 to 2004, we found only three studies that employed this approach (McMahon & Tash 1988; Dunham et al. 2000; Keeley 2001). Of 16 studies published during this period that used experimental enclosures in the laboratory or the field to study habitat selection and behaviour of fishes, nine (56%) were conducted in enclosures that lacked exits. As experiments by Matter et al. (1989) demonstrate, affording animals the choice of staying or leaving a site is a minimal requirement of proper enclosure design; otherwise results from closed system experiments may not be truly representative of natural responses.

Emigration in many natural aquatic systems that at first glance appear 'closed' to emigration (e.g. small lakes, desert springs and cave pools) may in fact be more common than realised (McMahon & Tash 1988; He & Kitchell 1990), further emphasising the need to incorporate exits in experimental enclosures to increase confidence in the 'naturalness' of the results from tests conducted therein. The importance of conducting habitat selection and other fish behaviour experiments in enclosures with exits is illustrated by studies of winter cover selection in juvenile coho salmon (*Oncorhynchus kisutch*) conducted in outdoor stream channels (McMahon & Hartman 1989). Coho added to channels first selected the lowest current velocity available during the day, but later emigrated from experimental channels at twilight unless overhead cover and woody debris were present. If enclosures had prevented emigration, behaviour of fish would have indicated that low velocity areas were preferred habitat conditions, when in fact, such

conditions were inadequate to trigger residency when fish had the opportunity to emigrate.

Conclusions

Linking individual decisions of fish to stay or leave a site to the larger-scale dynamics of populations over space and time poses significant conceptual and logistical hurdles for fish ecologists. Yet, overcoming such hurdles is needed to fully understand the consequences of movement to populations, metapopulations, and species persistence. Resolving these difficulties requires integration of both mechanistic and contextual viewpoints (Lima & Zollner 1996; Lidicker 2002; Humston et al. 2004). Our conceptual model provides a framework for understanding how resource needs and resource availability at the scale of individual fish (mechanistic view) influences populations and population connectivity and persistence at much larger scales (contextual view).

There has been great progress in fish ecology over the past two decades in the development of hierarchical models that link fish habitat requirements from the small (microhabitat) to large (drainage basin) habitat scale (Rabeni & Sowa 1996). Applications of such hierarchical models (Hölker & Breckling 2002) of fish habitat have shown that all scales are interconnected and each provides a unique perspective for habitat conservation and management (Rabeni & Sowa 1996). In a similar fashion, our habitat selection-emigration model could prove profitable for placing individual behaviour within the context of the temporal dynamics and spatial distribution of populations (see also Humston et al. 2004). A significant outcome of development of hierarchical perspectives is increased communication among ecologists working at different scales (Lima & Zollner 1996). Emigration is often the key linkage between the scale of individual behaviour to the scale of population responses, and greater understanding of the underlying factors affecting this often-overlooked demographic parameter could offer new approaches for management and conservation of fishes.

Acknowledgements

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