Lecture 6: Habitat selection, Population, Niche Concept

Aquatic fisheries science is currently undergoing a conceptual shift in understanding of fish-habitat linkages, assessment, and management. In the present models, habitat is identified using relatively static indicators: e.g. depth, cover, substrate, and to a lesser extent velocity, which depend on geology, physiography and landscape – variables used in the Aquatic Ecosystem Classification. Emerging science links aquatic species life history traits and rate processes – hatching success, growth rate, survival – to dynamic habitat features that influence species more directly – temperature, light and water movements (currents, turbulence etc.). These dynamic habitat features are energy based and are driven by climate and hydrological processes and phenomena and draw more explicit links between physiology and habitat.

Every organism has a place to live in nature, a functional role in that place, and a complex set of adaptations for reproducing its kind. On the surface, this observation might seem to be obvious, even trivial. However, in order to understand our biological world—the biosphere, how it operates and ultimately how to protect it—we need to understand at a deep level how organisms interact with each other and with their physical environment.

The most fundamental and perhaps most difficult of these concepts is that of the **ecological niche**. A niche refers to the way in which an organism fits into an ecological community or ecosystem. Through the process of natural selection, a niche is the evolutionary result of a species' morphological (morphology refers to an organism's physical structure), physiological, and behavioral adaptations to its surroundings. A **habitat** is the actual location in the environment where an organism lives and consists of all the physical and biological resources available to a species.

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 unfavorable environmental conditions, inadequacy of resources, or unacceptable interactions with resident animals, including intraand interspecific competitors and predators (Bell 1991). In this way, movement is viewed as a conditiondependent 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 theorized 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 hypothesized that exploratory behaviour leads to variation in the immediate environment (D) experienced by an individual, which, in turn, leads to 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 hypothesize 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 optimization models based on ideal-free and ideal-despotic
theories. According to optimization models, well summarized 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). Also, few habitat selection studies have explored the relationship of
local movement within habitat patches to emigration and larger-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 optimization 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

colonization 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 hypothesize 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,

colonization of open habitat, rescue effect in metapopulations) accrue largely as a byproduct of the

movement resulting from habitat selection decisions as portrayed in our mod