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Title	Is there confusion over what is meant by 'open population'?
Author(s)	Johnson, Mark
Publication Date	2005
Publication Information	Johnson, M. P. 2005. Is there confusion over what is meant by 'open population'? <i>Hydrobiologia</i> 533, 333-338.
Publisher	Springer Verlag
Link to publisher's version	http://www.springerlink.com/content/wh42057573wh1q44/
Item record	http://hdl.handle.net/10379/364

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Is there confusion over what is meant by 'open population'?

Mark P. Johnson

School of Biology and Biochemistry, The Queen's University of Belfast, 97 Lisburn Road,
Belfast, BT9 7BL, Northern Ireland, UK

m.johnson@qub.ac.uk

Phone: 028 90272297

Fax: 028 90335877

Running title: types of open population

Key words: larvae, demographic, genetic, definitions, models

This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to *Hydrobiologia*

Abstract

Marine species possessing widely dispersing larvae are often considered to have open populations. However, two concepts are covered by the phrase 'open population'. One concept stresses the supply of recruits from outside the local population (genetically open) while the alternative use describes situations where recruitment rate is independent of the local population size (demographically open). These two concepts are not necessarily equivalent. A review of recent literature suggests that there is no consensus on whether a demographic or genetic concept is associated with the use of the phrase 'open population'. The different meanings of open population are never formally acknowledged. Explicit recognition of the different concepts of openness would remove an ambiguity from the literature and may aid communication between disciplines. Processes in natural populations, such as gregarious settlement and homing behaviour, are more clearly described by distinguishing between demographic and genetic degrees of openness. Changes in spatial scale will affect the degree of population openness. However, demographic and genetic aspects of population structure will not necessarily respond in the same ways to changes in scale. This provides further support for the explicit separation of genetic and demographic concepts of openness.

Separate concepts of openness

The degree to which a population can be considered 'open' is a central debate in marine ecology (Jones et al., 1999; Hixon et al., 2002; Mora & Sale, 2002). This debate about population structure has implications for both conservation and fisheries. For example, coral reefs with 'upstream' sources of recruits may be more protected against overfishing and less influenced by local management schemes than more isolated reefs (Roberts, 1997). Clarity of terminology is essential for the resolution of scientific debates. Unfortunately, use of the phrase 'open population' is undermined by a persistent problem in definition. A careful examination of the influential paper by Roughgarden et al. (1985) reveals two separate views of an open population. The text in the paper by Roughgarden et al. (1985) defines an open system as one where the majority of recruits are supplied from distant sources (defined below as a genetically open population). This definition is repeated in more recent work (Hixon et al., 2002; Mora & Sale, 2002). Roughgarden's model formulation is, however, unequivocal: recruits arrive at a rate defined not by the adult population size, but by a settling constant, s . This is a demographic definition, very different to one concerning the geographic origins of the recruits.

Among population modellers, the demographic definition and its mathematical formulation are uncontroversial. Most modelling studies use the same assumption (e.g. Hixon et al. (2002), ' R_t is the number of new recruits ... R_t is independent of local dynamics'). Consistent with current usage, a definition for a demographically open population can therefore be given as: a population where the number of recruits arriving is independent of the local population size. In practice, recruitment to marine populations is often measured some time after settlement from a planktonic larval stage (e.g., in barnacles, Jenkins et al., 2000). Hence studies of any particular population require careful definition of settlement and

recruitment to avoid confounding pre and post settlement processes (e.g. Schmitt & Holbrook, 1999).

The definition of a demographically open population given above (and as described in the models of Roughgarden et al., 1985; Hixon et al., 2002) emphasizes the swamping of any population dynamic signal attributable to the local production of recruits. This focus on the forcing of population dynamics has been important in the recognition of the role of spatially and temporally variable larval supply ('supply side ecology', Lewin, 1986; Hughes et al., 2000). Supply side ecology has widened the perspective of marine ecologists, shifting the focus from local interactions to include a broader range of interacting phenomena (Sale, 1990; Shkedy & Roughgarden, 1997; Camus & Lima, 2002).

It is perhaps straightforward to see how an emphasis on 'supply' to open populations has led to genetic and demographic concepts being combined. To evaluate this combination of concepts, we can consider the demographic processes that affect population size. Local population size increases through local births and immigration and decreases through local deaths and emigration. A demographically open population could therefore result from either local births or net immigration being uncoupled from the population size. Debate over the source of recruits (local or immigrants) is additional to the population dynamic definition of a demographically open population. I would argue that it is clearer to have a simple definition of demographically open than to include implicitly or explicitly ideas about the source of recruits within the same definition. The scatter around a stock-recruitment curve is a measure of demographic openness of relevance to predictions of population size. A separate concept of openness is needed to describe the source of recruits.

An emphasis on the geographical origins of recruits implies that gene flow is occurring between different locations. Population geneticists use measures of the genetic difference between local populations to estimate variables such as Nm (the effective number

of migrants, Avise, 1994. For other approaches see Emerson et al., 2001). In most marine species with limited adult mobility the individuals exchanged between local populations (migrants) are larval recruits. The proportion of non-indigenous recruits affects the genetic composition of a local population. Hence definitions of open populations that focus on the source or origins of recruits can be thought of as a genetic concept of openness. An example of this is given by Hixon et al (2002): 'An appropriate measure of openness is one minus the mean probability that an arriving recruit was born within the population boundaries'. A genetically open population can therefore be defined as one that receives all of its recruits from distant sources. For example, barnacle larvae have been considered 'nearly certain to be carried away from the system where they were released' (Roughgarden et al. 1985), meaning that virtually all the local recruitment is from other populations. Many authors relax the definition of a genetically open population to include populations where the majority, but not necessarily all, of the recruits are from distant sources (e.g. Mora and Sale 2002). In practice, few populations are likely to be so open as to receive no locally produced recruits. In this context, debates on whether populations are open or closed are rather artificial; of more interest is the wider application of continuous measures of openness such as that proposed by Hixon et al. (2002).

Published uses of 'open population'

Both genetic and demographic concepts of openness are widely used in the literature. The quotations from Hixon et al. (2002) show that both concepts can occur within the same paper. To quantify the recent trends, papers on open populations published in the years 1999-2003 were identified. The search was based on use of the words 'open', 'recruit' and 'population'. The sample of papers may not represent an exhaustive review, as the search only identified papers with the target words in the title, abstract or key words. However, the

manuscripts are representative of recent uses of the phrase 'open population'. Only papers that made specific reference to marine populations were used. Of particular interest were cases where an explicit definition of an open population was made. Explicit definitions could be given by a statement in the text of the form: 'An open population is ...'. As mathematical models are unambiguous formulae, an explicit definition can also be taken from the way recruitment is specified (as in Roughgarden et al., 1985). Where no explicit definition was given in a paper, judgements were made based on key phrases or implicit meanings. For example, references to connectivity, sources and sinks or larval retention suggest a genetically open interpretation while statements about independent dynamics or decoupled supply suggest a demographically open context.

Of twenty five papers classified in the literature search, twelve articles gave explicit definitions for an open population. There was no consensus over the preferred open population concept (Fig 1). Approximately one third of papers referred to both a genetic and a demographic concept of openness. None of the papers reviewed made a distinction between the genetic and demographic concepts of openness. Demographic models were always accompanied by a genetic concept in the text. Clearly there are likely to be papers where model formulation and text consistently describe the demographic concept, but the absence of any such papers in the sample of twenty five publications is surprising. Certain key papers were repeatedly cited by authors writing about open populations. Just under half the papers reviewed cited Roughgarden et al. (1985). As discussed above, the Roughgarden paper contains both a demographic and a genetic concept of openness, but does not explicitly distinguish between the two. Most frequently cited (by 52% of papers) was Caley et al. (1996), which also uses both demographic and genetic views of openness.

The equivalence of demographic and genetic concepts

Communication between scientists will clearly be hindered where one term involves two separate concepts. Such confusion may not be important if the two concepts of openness have a clear equivalence. However, an influential example from the 'supply side' ecology literature suggests that the two definitions of openness are not interchangeable. Gaines & Bertness (1992) describe settlement variation of the barnacle *Semibalanus balanoides* (L.) in Narragansett Bay and on the open coast. The populations inside the bay and on the open coast appear to be distinct. Larvae inside the bay were larger than those found on the open coast. The absence of small larvae inside the bay implies that open coast populations do not supply recruits to the bay population (Gaines & Bertness, 1992). This distinction between open coast and bay populations is also supported by differences between the thermal tolerances of open coast and bay recruits (Bertness & Gaines, 1993). By reference to the genetic concept of openness, the population in the bay is a closed population as recruits are produced locally. However, a key finding of Gaines & Bertness (1992: 580, line 11) was 'no correlation between the interannual variation in settlement and stocks of reproductive adults'. The independence between the supply of potential recruits and the adult population size defines the population as demographically open. Gaines and Bertness (1992) therefore describe a situation where a population is demographically open but genetically closed. The barnacle population in Narragansett Bay can only be described if two independent definitions of openness are used.

The relationships between genetic and demographic concepts of openness can be illustrated in a simple graphical model (Fig. 2). Populations may be placed in different positions relative to the axes. For example, Narragansett Bay would be in the top left quadrant. The exact position of any population will reflect factors such as the scale of the study, local hydrography, and larval life span. If the degrees of genetic and demographic openness in a population are equivalent, populations are restricted to points along the

diagonal. However, the equivalence of genetic and demographic degrees of openness may not be common. Various processes may shift populations away from the diagonal. For example, even with careful definition of settlement and recruitment, pre-settlement processes can decouple larval production and recruitment without altering the genetic identity of recruits (Gaines & Bertness, 1992; Danilowicz & Sale, 1999). Alternatively, gregarious settlement may induce a relationship between adult density and recruitment even where larvae are from distant sources (Jeffery, 2000). Homing behaviour may also affect the genetic composition of recruits without an equivalent demographic effect. A separation of concepts of openness is therefore more inclusive of the processes observed in natural populations than any single definition.

Developing the debate on open populations

The issue of scale also suggests that the different concepts of open population (demographic and genetic) should be considered separately. The choice of spatial and temporal scales fundamentally affects the description of population structure. For example, many populations of species with pelagic larvae are likely to be demographically open at the scale of metres (Hixon et al., 2002; Mora & Sale, 2002), but the population structure will move towards demographic closure at larger spatial scales (Hughes et al., 2000). However, there is no *a priori* reason to assume that the relative change in demographic openness will be matched by an equivalent change in genetic openness (a situation that would be implied if genetic and demographic concepts are not distinguished). At the largest spatial scale (biogeographic range), a species must be genetically closed, but there may still be considerable scatter around the stock-recruit relationship. Climatic events at the same scale as the population range may still disrupt any predictive relationship between stock and recruits. Alternatively, the population dynamics at large scales may still reflect the (local scale)

dynamics of a limited number of source or mainland populations that are responsible for providing the majority of recruits (James et al., 2002). Under such circumstances recruitment at the large scale may be uncoupled from population size even though the population is genetically closed.

The categories of closed or open population are unlikely to be satisfactory descriptions for many populations. Most populations will lie somewhere between the extremes. Hence a sample of local populations may be plotted as a cloud of points in figure 2. This would allow identification of structures such as larval sources and sinks (a scatter of points from closed to genetically open) to be combined with information on population dynamics. Thomas & Kunin (1999) use a similar approach to describe the spatial structure of populations in terms of demographic balance and individual mobility. The advantage of such perspectives is that the focus shifts from unsatisfactory classifications of pattern to descriptions of process. Hence the debate can move on from arguments about the classification of populations into open or closed (which are unlikely to fit many natural populations) to a debate that looks at changes in the influence of different processes at a range of spatial scales (Johnson, 2000; Hixon et al., 2002).

Explicit recognition of the difference between genetic and demographic concepts of openness is currently lacking from the literature. Some marine scientists may not have commented previously on the distinction between demographic and genetic concepts because they view it as obvious. Other scientists may be more familiar with one or other approach and have no need for both concepts within their sub-discipline. What is undoubtedly clear from the literature is that different definitions of an open population are in use, potentially hindering communication between scientists. Given the results of Gaines & Bertness (1992), the issues discussed with figure 2 and the potential role of scale, it seems unwise to use genetic and demographic concepts as though they are equivalents. A wider acceptance of this

should aid communication between disciplines and remove a source of confusion. Clarity over definitions is particularly important given recent calls for the open population concept to be re-evaluated (e.g Swearer et al., 2002).

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Figure legends

Figure 1. Venn diagram classification of the concepts associated with the phrase 'open population' in publications from 1999-2002. Papers were classified into four sets: Dm includes papers where a demographic concept was used in a model, Dt includes papers where a demographic concept was referred to in the text, Gm includes papers where a genetic concept was used in a model and Gt includes papers where the text used a genetic concept of openness. The shaded area emphasizes all the papers where a demographic concept of openness was used. One paper lies outside the sets, as no clear definition of open population concept was given. The sample of publications was comprised of Cropper & DiResta, 1999; Danilowicz & Sale, 1999; Dixon et al., 1999; Gilmour, 1999; Jones et al., 1999; Schmitt & Holbrook, 1999; Schmitt et al., 1999; Shima, 1999; Swearer et al., 1999; Cowen et al., 2000; Etherington & Eggleston, 2000; Hughes & Tanner, 2000; Hughes et al., 2000; Muko et al., 2001; Wright & Steinberg, 2001; Armsworth, 2002 ; Forde, 2002; Hixon et al., 2002; Mora & Sale, 2002; Paine, 2002; Yund & Stires, 2002; Barnay et al., 2003; Gilg & Hilbish, 2003; Lambert et al., 2003 and Shanks et al., 2003.

Figure 2. A graphical model of local population structure. The degree of genetic openness reflects the proportion of recruits that are locally produced. A population is genetically open when all recruits are supplied from other locations. The extent of demographic openness can be defined statistically from repeated surveys of reproductive adults and recruits. For example, the correlation between adults and recruits will be zero in demographically open populations. A population with the same degree of genetic and demographic openness will lie at a point along the 45° diagonal. Various processes can move a population away from the diagonal to occupy other areas of the graph: a) decoupling pre-settlement factors, b) homing behaviour, c) gregarious settlement (these processes are not necessarily parallel to either axis).

Figure 1.

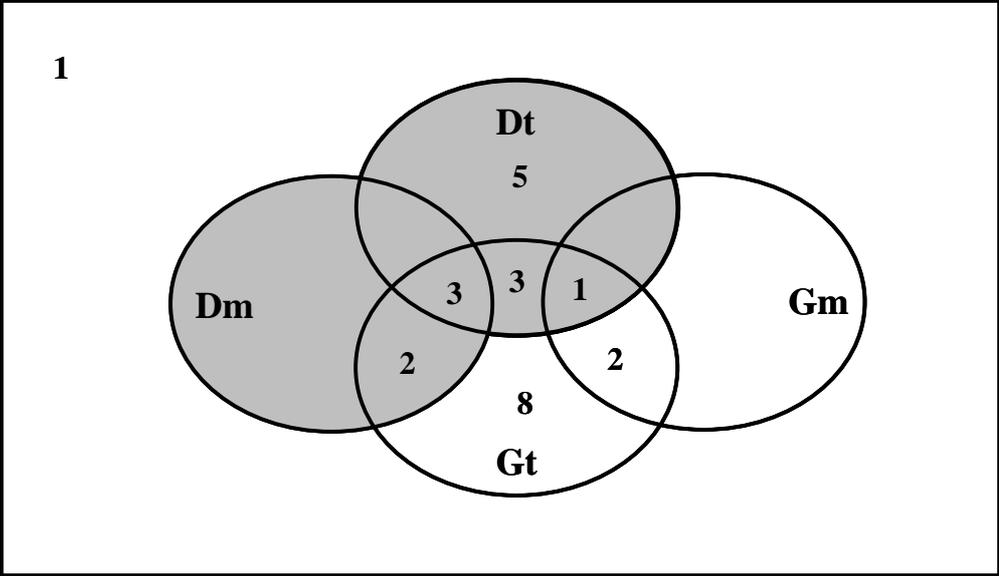


Figure 2.

