ORIGINAL ARTICLE

Volker Grimm · Karsten Reise · Matthias Strasser

Marine metapopulations: a useful concept?

Abstract We discuss the potential and limitations of the metapopulation concept in marine ecology. The usefulness of the concept in terrestrial ecology is neither based on its simplicity or generality nor on overwhelming empirical evidence. The usefulness is in the questions which are asked when the metapopulation concept is applied. These questions address spatial phenomena and processes on different spatial scales. They help in acknowledging that every population, be it terrestrial or marine, has a spatial organization. Understanding this spatial organization is also important for tackling specific applied problems, i.e. to avoid overexploitation of living marine resources or for configuring marine reserves. The 'openness' of coastal populations, whose larvae enter larval pools or which are holoplanktonic, is no reason for not asking the questions implied by the metapopulation concept. For marine ecology, the real problem is to delineate populations, which then may possibly correspond to the 'local populations' of metapopulations. Thus, the answer to the question in the title of this paper, whether 'marine metapopulation' is a useful concept, is 'yes', if the concept is considered a working hypotheses, if the concept is explicitly defined, and if the questions linked to the concept are clearly stated. Even if it eventually transpires that only very few marine metapopulations actually exist, marine ecology would still have gained some important new insights.

Keywords Metapopulation · Population ecology · Dispersal · Coastal

Communicated by W. Armonies, M. Strasser and K. Reise

V. Grimm (✉)
UFZ Umweltforschungszentrum Leipzig-Halle,
Sektion Ökosystemanalyse, PF 500 136, 04301 Leipzig,
Germany
e-mail: vogri@oesa.ufz.de
Tel.: +49-341-2352903, Fax: +49-341-2353500

K. Reise · M. Strasser
Alfred-Wegener-Institut für Polar- und Meeresforschung,
Wattenmeerstation Sylt, 25992 List, Germany

Introduction

The concept of a metapopulation as a "population of populations that go extinct and recolonize" (Levins 1970) has become a major paradigm in conservation biology and terrestrial animal population ecology (Harrison 1991; Hanski 1999). The number of publications using the metapopulation concept has increased exponentially since the mid 1980s (Hanski 1999, p. 180), which indicates that the concept must be useful for a wide range of systems and problems. The concept applies to situations where the habitat in which individuals reproduce and preferably live is not homogeneous but consists of discrete islands or patches. Due to isolation from other patches, the populations on individual patches have their own dynamics. This means that they are largely independent of the dynamics of other populations. On the other hand, the patches are not completely isolated because dispersers may occasionally cross the distance between patches. In fact, the basic question behind the metapopulation concept is the question of persistence: the patches may be too small for their populations to persist in the long term. The populations die out sooner or later due to random variations in their environment and demographic processes. However, a patch that becomes empty may be recolonized by dispersers from other, still occupied, patches. This metapopulation effect can be expressed in terms of a 'local' and a 'regional' scale: in metapopulations, regional persistence is possible despite local extinctions.

There are many natural populations which, at least in parts of their distribution, are organized as metapopulations, but the success of the metapopulation concept reflects the major anthropogenic threads to most natural populations: loss and fragmentation of habitat. Many populations are now forced to live on a network of habitat patches and the question is whether these networks allow for the metapopulation effect and whether the effect is strong enough to prevent regional extinction. Typical management questions addressing such situations are: should corridors be established to link the
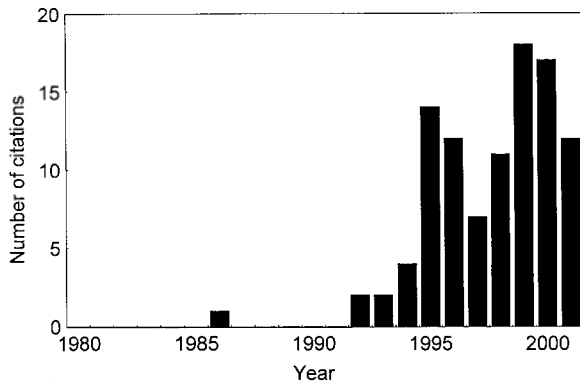
Fig. 1 Numbers of citations to the key words "marine" and "metapopulation" in the database "Aquatic Science and Fisheries Abstract" in 1980–2001

patches? Is a further fragmentation, for example by a new highway, tolerable? Is local habitat management of certain patches required to augment their persistence and their role for the entire network?

However, despite its success and usefulness for terrestrial systems, the question still remains of whether the metapopulation concept is also useful for marine populations. Here, the concept has increasingly been used since the beginning of the 1990s (Fig. 1) but still not as readily as in terrestrial ecology. The main problem in applying the concept to marine systems is to delineate local and regional populations or to delineate populations and their spatial scale in the first place (Camus and Lima 2002). What corresponds to the habitat islands of the terrestrial systems? Obviously, this is hard to determine for purely pelagic species. Also benthic species, which often occupy identifiable habitat patches, may not have local population dynamics because of pelagic larval stages which are dispersed over long distances by oceanic currents. Because of all these open questions, it has been assumed that the metapopulation concept does not apply to marine populations (Reich and Grimm 1996) but nevertheless it *is* used, as Fig. 1 shows. It therefore seems worthwhile to discuss in detail the potential and limitations of the metapopulation concept for marine populations. This is important for two reasons: on the one hand, to prevent the concept from being used uncritically, which could lead research into a blind alley or even to wrong actions regarding managed populations and, on the other hand, to prevent certain aspects of the concept, which might indeed be important and useful for marine systems, from being unnecessarily neglected.

Therefore we will try to answer three questions: Is the metapopulation concept really as clear and unambiguous as it seems at first glance? And if not, what is it that makes the metapopulation concept still so useful for terrestrial systems? And how could these useful elements also be used for marine systems?

When is a metapopulation a metapopulation?

First of all, when discussing successful concepts it is important to realize that usually the reason for the success is not so much in the concept itself but in the scientific environment and, in particular, in societal needs: if there is a strong resonance between these factors and the concept, than the concept has the chance of being successful. For example, the stability concept is so attractive and widely used in ecology not so much because it is clear or useful per se, but because it reflects the dreams and demands of scientists and the society, especially politicians (Grimm 1996; Grimm and Wissel 1997). A successful concept does therefore not necessarily reflect some absolute truth or a predominating phenomenon which previously has been ignored. Let us therefore take a brief look at the history of the metapopulation concept.

The idea that local extinctions might be counterbalanced by regional recolonizations was not new by the time Levins coined the term 'metapopulation' (Levins 1969, 1970). Among others, Andrewartha and Birch (1954) had described this mechanism of regional population dynamics before. However, the question of extinction was largely ignored by theoretical population ecology for many decades. Instead, the focus was on equilibria, stability of these equilibria, and on cyclic population dynamics. All this could easily be described by ordinary differential equations and there seemed to be no need to include random variation or spatial processes which would have made the mathematics involved much more complicated. Accordingly, it took more than 15 years until Levins' concept received broader attention. However, by the beginning of the 1980s, the scientific environment and societal needs had changed: the mass extinction of species caused by human impacts had become a major topic, and the new discipline of conservation biology focused almost entirely on small populations and their survival (Soulé 1987). We learn from this for our attempt to assess the potential usefulness of the metapopulation concept in marine ecology, that it is mainly marine ecology itself, and the societal demands on marine ecology, which determine the usefulness of the concept: how do the elements of the concept fit in with the current issues of marine and coastal ecology? Are, for example, small populations and extinction major topics? How large need marine no-take reserves be to rescue endangered populations?

The next thing to be careful about with successful concepts is the promise of generality and simplicity that they usually entail. The metapopulation effect is so easy to explain and understand and so suggestive that one is tempted to call virtually every population living on a network of habitat patches a metapopulation, just because then the question of regional persistence would seem so easy to answer. However, a closer look at real situations shows that the situation Levins had in mind is only a rather special situation within a wide range of possibilities (Fig. 2). Levins' metapopulation model, which demonstrated that regional persistence is possible if the per
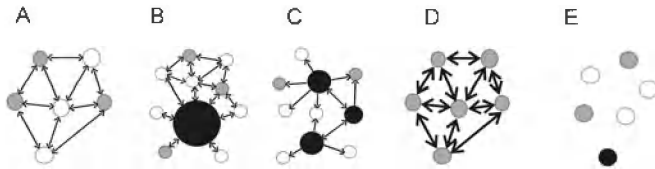
Fig. 2 Different spatial configurations: **A** classical Levins-type metapopulation, **B** mainland–island configuration, **C** source–sink configuration, **D** spatially structured population, **E** isolated populations. *Arrows* indicate weak unidirectional exchange of individuals (←), weak mutual exchange of individuals (↔) and strong mutual exchange of individuals (↔ in bold)

patch rate of recolonization is higher than the rate of extinction, assumed that all patches are the same, that distance between patches does not matter for the chance of mutual recolonization between pairs of patches, and that the number of patches is very high (or, to be precise, infinite in Levins' model).

In reality, however, these assumptions are almost never valid. There may be 'mainland' patches which are so large or whose habitat quality is so good that they allow for a population big or robust enough to persist in the long term. These mainlands may be surrounded by numerous small 'island' patches which, as in Levins' original configuration, are all the same and too small (Fig. 2). However, is this mainland–island situation a metapopulation or not? Owing to the original definition, it clearly is not, because regional persistence is due to the mainland population and does not require any metapopulation effect. It has been argued (Harrison 1991) that the mainland–island situation is more likely to be found in real populations than the 'classical' Levins configuration and that therefore the metapopulation concept is much less relevant to conservation problems than indicated by its success.

Similar to the mainland–island situation, the population may be living on 'source' and 'sink' patches (Pulliam 1988). Source populations are able to persist without immigrants and they produce emigrants, whereas sink populations depend on immigrants from source habitats and do not produce emigrants. Without immigrants, sink populations die out almost immediately. Thus, within the framework of the metapopulation concept, the sink populations do not count at all. Note that such situations may be the case even if all patches are more or less the same size and therefore look like the classical Levins configuration. The decisive parameter determining sink or source status of the patches is habitat quality of the patches.

Another border case is a situation which also looks like the Levins configuration, i.e. without 'mainland' patches or source–sink differences, but with a high exchange rate of individuals between the patches, for example if the individuals are highly mobile (e.g. birds or dragonflies). In such situations the local dynamics on the patches are no longer independent of each other and so we have one large 'spatially structured' population instead of a metapopulation.

Further aspects which cast doubts on the general applicability of the metapopulation concept to terrestrial systems are: both patch configuration and quality may be dynamic instead of static (Stelter et al. 1997); local extinction may be caused by deterministic processes instead of random fluctuations and this may have the consequence that the patch cannot be recolonized immediately (Thomas 1994); identifying an unoccupied habitat patch requires that we are able to predict where a certain species may live and reproduce (McIntosh 1995). In many cases this may be a relatively easy task, but in others it may be mere guesswork.

To summarize: the simplicity and generality of the metapopulation concept are superficial. In the majority of cases of terrestrial populations living on networks of habitat patches, it is not as straightforward to decide whether the population is organized as a metapopulation. We conclude that the usefulness of the metapopulation concept is not based on its general applicability. But even if we broadened the concept to encompass most of the non-classical configurations described above, how good would be the empirical evidence that a metapopulation really is a metapopulation?

Evidence of metapopulation structure in terrestrial systems

Reich and Grimm (1996) were suspicious that much of what is claimed to be a metapopulation in the literature lacks the empirical evidence to support this claim. They therefore formulated a rather broad but precise definition of what constitutes a metapopulation and than reviewed 87 publications and checked for the elements of their definition. Going beyond the rather specific original Levins definition, Reich and Grimm (1996) define a metapopulation as a: "(regional) population of (local) populations which fulfils the following four criteria:

1. The local populations have their own dynamics, i.e. they are clearly able to be delineated from other local populations;
2. At least some of the local populations are so small or so threatened that they face a considerable risk of becoming extinct;
3. The local populations or patches, respectively, are interacting by dispersing individuals;
4. Dispersers are able to establish new local populations on empty patches. 'Establish' means, in particular, that the new population in turn starts to produce dispersers" (Reich and Grimm 1996, p. 126, in the original German).

The rationale of the four criteria is discussed in more detail in Reich and Grimm (1996), but we will here only report the result of the review: in 64% of the publications either the studied population obviously is not a metapopulation, or the empirical evidence is not sufficient. Regarding local extinctions, dispersal, and recolo-

nization only 19% of the studies prove that all three of these processes occur, 17% of the studies only report dispersal, and about a quarter of the studies provide no evidence of any of the three processes at all. These are mainly presence/absence studies over only one season which infer metapopulation dynamics from the fact that some of the potential habitats are not occupied. Of course, most of the lack of empirical evidence is due to insufficiently long study periods. About half of the studies covered only one or two years, and only 19% of the studies covered more than five years. Reich and Grimm (1996) conclude that care has to be taken not to too readily to assume that a population is organized as a metapopulation because this might in some cases lead to making the wrong management decisions.

All this is not to say that in the majority of cases the usage of the metapopulation concept is erroneous (although there are certainly quite a few cases where this seems to be the case), but the lesson to be learnt from this is that the success of the metapopulation concept is not based on overwhelming empirical evidence. There must be other reasons.

The questions behind the metapopulation concept

The metapopulation concept should not be viewed as a means to categorize populations in different classes, but as a working hypothesis. Very often, working hypotheses turn out to be wrong, but in trying to verify the hypothesis, we usually gain important insights about key processes and structures. Likewise, after trying to prove that a population is a metapopulation, we will usually have learned a lot, even if it turns out that it is not a metapopulation according to the definition of, for example, Reich and Grimm (1996). The metapopulation concept forces us to ask important questions which we probably would not have asked without the concept. These questions are:

- Are population dynamics on a patch more or less independent from other populations, i.e. determined by birth and death processes within the patch, or is the population strongly, or even largely, influenced by immigration and emigration? This question is decisive because it delineates the objects of population ecology and also defines the units of management and conservation.
- Is small population size a problem, i.e. are there patches whose populations may become extinct due to random fluctuations? Indicative of this problem are observations of extinction events.
- Are population dynamics on a patch more or less independent from other populations, i.e. determined by birth and death processes within the patch, or is the population strongly, or even largely, influenced by immigration and emigration? This question is decisive because it delineates the objects of population ecology and also defines the units of management and conservation.

- Are there environmental factors which affect more than one patch simultaneously? If so, local population dynamics would be more or less correlated, so that also extinctions are more likely to occur simultaneously. Consequently, the metapopulation effect would hardly emerge because few, if any, occupied patches would exist from which recolonizers could originate.
- Are there source populations which are more productive in terms of emigrants and persistence than other habitats? Such populations would be important to protect if conservation is a concern.
- How far do emigrants go, and where? Where do immigrants come from?
- Which patches are really connected in a network, and which are more or less isolated?

All these questions, and probably a suite of further more detailed questions, are relevant both scientifically and for solving applied problems. Scientifically, they help to acknowledge that population dynamics has to be considered spatially explicit, on more than one spatial scale. Mere number dynamics, which was imposed on us by classical theoretical population ecology, will not be appropriate in most situations. For applied problems, management decisions have to address the appropriate spatial scale or they are bound to fail. Moreover, spatial correlations and differences in habitat quality should be taken into account. However, is all this equally significant for terrestrial and marine populations, or are there fundamental differences?

Are marine populations different?

Insects, birds or bats may fly with the wind swifter than oceanic currents. Nevertheless, these terrestrial organisms are generally considered to have discrete populations or metapopulations, although their ambits are much wider than those of soil nematodes, slugs or snakes. We here propose that the range of spatial population structures is much the same in the marine environment. There are obvious analogues between populations of terrestrial and marine organisms. Whales, herrings, salmon, eels or euphausiid shrimps, for example, perform regular migrations just as mammals, birds and some insects do on land. Usually these migrants have distinct sites for calving or spawning, nurseries and feeding grounds, with a limited interchange between groups or schools imprinted to different sites and routes. However, most species of the marine fauna are holobenthic without regular pelagic dispersal, particularly the diverse meiofauna in mud and in the interstices of sand. Their means of dispersal are rather limited, and adaptations to specific substrates, depths, water qualities and food supplies entail insular populations separated by vast stretches of unsuitable habitat.

We suggest that the probability increases to encounter partially isolated populations when sailing from offshore

towards inshore because habitat diversity increases while average patch size of habitat types decreases. An example of a large and coherent offshore population but with small satellite populations persisting for a couple of years in coastal bays may be the polychaete *Lanice conchilega*, a worm with pelagic larvae and benthic adults (Strasser and Pieloth 2001). Another polychaete, the lugworm *Arenicola marina*, is confined to inshore sediments. Its larval dispersal is rather limited (Reise et al. 2001), and this probably constitutes an adaptation to minimize the loss of propagules towards offshore areas. As a corollary, this also reduces the potential for long-shore dispersal across headlands or from island shore to island shore. Finally, species of marine origin dwelling at the supratidal washline or in salt marshes, such as talitrid amphipods, may show much the same spatial population structures as terrestrial invertebrates in the same habitats. Furthermore, individual rocky outcrops at sedimentary shores, estuaries and coastal lagoons may harbour fairly isolated populations of seagrass, macroalgae and benthic invertebrates, including those with pelagic larvae (Cronin 1982; Eckman 1996; Epifanio and Garvine 2000). In the open sea, parallels to such isolated coastal habitats are submarine mounds or hydrothermal vents. In all these cases we expect spatial population structures to resemble those found in insular or fragmented habitats on land.

Special marine cases are benthic invertebrates with external fertilization and an extended pelagic larval phase as well as holoplanktonic species. In organisms with these modes of dispersal the occurrence of distinct populations depends on particular current regimes such as gyres, permanent fronts or the alternating flow of the tides. In the absence of such hydrodynamic patterns, their spatial population structures may indeed be largely ephemeral and fortuitous. It has been argued that the 'openness' of such marine populations prevents the application of the metapopulation concept because it seems impossible to speak of local population dynamics (e.g. Reich and Grimm 1996). However, the 'openness' is more an artefact of vague definitions and erroneous inferences from the patchy distribution of adult assemblages (Camus and Lima 2002). If a patch of adult, sessile benthic organisms which have meroplanktic larvae is referred to as a 'population', then of course this population would be open because larvae enter a larval pool and are dispersed over wide distances. The relationship between the local adult assemblage and the recruitment into this assemblage is strongly influenced by non-local factors. However, the openness follows from the inappropriate delineation of a population. Camus and Lima (2002) and Berryman (2002) complain that in general ecologists use, if any, only very vague definitions of 'population', for example 'conspecifics in a given area', which make the definition completely arbitrary. Berryman (1999, 2002) claims that populations are "natural units" living on areas "large enough so that immigration and emigration is rare or, at least, balanced" (Berryman 2002, p. 441) and gives the formal definition of a population "as a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and/or migration behavior and in which numerical changes are largely determined by birth and death processes" (p. 441). Although we do not necessarily agree with the notion of populations as being self-defined units (Jax et al. 1998; Grimm 1998), we consider Berryman's definition practical. It corresponds also to the first criterion of the definition of 'metapopulation' by Reich and Grimm (1996; see above). We conclude that there is no compelling reason why the metapopulation concept should not – as a working hypothesis – be applied to marine populations including those with pelagic dispersal. Admittedly, because of the large scale of transports with oceanic currents it will often be not easy to delineate the area of populations, but the delineation is nevertheless important. Regarding the openness of marine populations, Camus and Lima (2002) poignantly argue that "by shifting the focus from local processes to a broader array of spatial phenomena, it is marine ecologists that are becoming more increasingly open, not marine systems" (p. 436).

Applying the metapopulation concept to marine populations

Even more than in terrestrial ecology, due to lack of sufficient data, it will be impossible in most cases to decide whether a marine population is organized as a metapopulation, but spatial organization will be decisive in any case. A good example of this pragmatic attitude to using the metapopulation concept is the modelling study of Morgan and Botsford (2001) who tried to predict the effect of no-take reserves on the fishery of the red sea urchin in northern California. In their conceptual model, they assume a linear array of 24 identical patches of adult assemblages along the coast. They refer to this array as a 'metapopulation' because they, as do many other researchers in both terrestrial and marine ecology, erroneously seem to assume that any patchy distribution of adult habitats is a 'metapopulation'. However, this playing with names is not really relevant, because Morgan and Botsford (2001) make no further reference to the term 'metapopulation' but ask the relevant questions: since the range of larval dispersal is unknown for this species, how would different scenarios of larval dispersal influence the effect of no-take reserves? The four scenarios they model are: limited dispersal (larvae have a limited, local range of dispersal), source–sink (some patches produce larvae with limited dispersal, others only receive larvae), larval pool (all larvae enter the larval pool and are then equally distributed among the patches), headland dispersal (all larvae enter the larval pool, but their distribution among the patches is unequal due to coastal currents and the structure of the coast, with patches near headlands receiving the most larvae). Morgan and Botsford (2001) show that on the one hand the effect of reserves strongly depends on these scenari-

os, but on the other hand this dependency decreases if larger percentages of patches are made reserves.

Barnay et al. (2003) carry such an analysis further. In the English Channel, geographically separated patches of the polychaete *Owenia fusiformis* occur in nearshore muddy sand. Larval dispersal was modelled using tidal forcing alone and coupled with winds of different directions. Without wind there was a high rate of return to the parental patch, while wind considerably increased emigration rates and allowed for long-distance dispersal. Nevertheless, on the 500-km scale of the English Channel, the model suggests three groups with no or very little interchange between but with high interconnectivity within these groups of occupied sites.

Wind and other factors may render larval dispersal in coastal waters a rather hazardous endeavour. Armonies and Reise (2003) estimate that macrobenthic species use less than half of the suitable sites within a semi-enclosed embayment. Such a high proportion of empty habitats indicates that colonization processes often fail and that local extinction may be rather common in most coastal populations. This also implies for marine reserves that these should be either large or many to be effective. On a smaller spatial scale, individuals may have to decide whether to stay in a less suitable area or move to a better one at the cost of an increased risk of mortality during the migration. This may result in spatial distributions deviating from the spatial arrangement of the physiologically optimal sites (van der Meer et al. 2003). Thus, the suitability of an area as a marine reserve needs to be derived from the long-term fitness of a species instead of mere abundance estimates.

The analysis of highly polymorphic microsatellite loci on genomic DNA in benthic adults of the polychaete *Pectinaria koreni* indicates that worms occurring in bays about 100 km apart apparently show little connectivity by larval transport (Jolly et al. 2003). This was surprising because previous demographic comparisons have suggested a large source population for one bay and a sink for the other. Apparently, population genetics are indispensable in the analysis of spatial population structures in the marine environment. By combining genetic data with demographic and geographic information, density-dependent emigration was shown in the dynamics of a grey seal metapopulation (Gaggiotti et al. 2002). However, caution is advised because different genetic methods may generate quite different conclusions (see Hummel 2003).

At the coast, metapopulations are likely to occur in species which are confined to estuaries or lagoons separated from each other. Evidence for this is provided for a bivalve with demersal eggs and a short larval phase (Reise 2003). In this particular case, coastal development has caused habitat fragmentation very similar to what has happened in the terrestrial realm. Knowing about metapopulation dynamics may help to design a conservation scheme at the appropriate spatial scale. Because of long-distance dispersal of larvae, such areas may expand over hundreds or even thousands of kilometres along the coastline while physiological plastic responses may help to buffer environmental variability experienced across such a large area (Giménez 2003).

Metapopulation structure may also be detected in intertidal rock pools. Despite tidal flushing and wave wash, separate local population dynamics were apparent in harpacticoid copepods (Johnson 2001). Pointing to the need to consider time scales, the pools could be regarded as individual systems for about one month. Metapopulations, however, need not to be a strictly coastal phenomenon. Gutow and Franke (2003) predict for the isopod *Idotea metallica*, feeding and reproducing on drifting patches of kelp or other objects, that metapopulation structure may arise mostly in the open sea. Near the shore, these drifting patches with groups of isopods often merge with others, are likely to become stranded or colonized by *I. baltica*, a dominant competitor.

These examples, together with other published case studies (see Fig. 1), show that applications of the metapopulation concept to marine organisms for management purposes as well as for improving basic knowledge on spatial population ecology may be somewhat more difficult than on land but certainly are no less rewarding, and open the gates to a wide field of research.

References

Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. University of Chicago Press, Chicago

Armonies W, Reise K (2003) Empty habitat in coastal sediments for populations of macrozoobenthos. Helgol Mar Res 57 DOI 10.1007/s10152-002-0129-8

Barnay AS, Ellien C, Gentil F, Thiébaut E (2003) A model study in larval supply: are populations of the polychaete *Owenia fusiformis* in the English Channel open or closed? Helgol Mar Res 57 DOI 10.1007/s10152-002-0122-2

Berryman AA (1999) Principles of population dynamics and their application. Stanley Thornes, Cheltenham, UK

Berryman AA (2002) Populations: a central concept for ecology? Oikos 97:439–442

Camus AP, Lima M (2002) Populations, metapopulations, and the open-closed dilemma: the conflict between operational and natural population concepts. Oikos 97:433–438

Cronin T (1982) Estuarine retention of larvae of the crab *Rhithropanopeus harrisi*. Estuar Coastal Shelf Sci 15:207–220

Eckman JE (1996) Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. J Exp Mar Biol Ecol 200:207–237

Epifanio C, Garvine R (2000) Larval transport on the Atlantic continental shelf of North America: a review. Estuar Coastal Shelf Sci 52:51–77

Gaggiotti OE, Jones F, Lee WM, Amos W, Harwood J, Nichols RA (2002) Patterns of colonization in a metapopulation of grey seals. Nature 416:424–427

Giménez L (2003) Potential effects of physiological plastic responses to salinity on population networks of the estuarine crab *Chasmagnathus granulata*. Helgol Mar Res 57 DOI 10.1007/s10152-002-0127-x

Grimm V (1996) A down-to-earth assessment of stability concepts in ecology: dreams, demands, and the real problems. Senckenbergiana Maritima 27:215–226

Grimm V (1998) To be, or to be essentially the same: the "self-identity of ecological units". Trends Ecol Evol 13:298–299

Grimm V, Wissel C (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334

Gutow L, Franke H-D (2003) Metapopulation structure of the marine isopod *Idotea metallica*, a species associated with drifting habitat patches. Helgol Mar Res 57 DOI 10.1007/s10152-002-0126-y

Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford

Harrison S (1991) Local extinction in a metapopulation context: an empirical evaluation. Biol J Linn Soc 42:73–88

Hummel H (2003) Geographical patterns of dominant bivalves and a polychaete in Europe: no metapopulation in the marine coastal zone? Helgol Mar Res 57 DOI 10.1007/s10152-002-0124-0

Jax K, Jones CG, Pickett STA (1998) The self-identity of ecological units. Oikos 82:253–264

Johnson MP (2001) Metapopulation dynamics of *Tigriopsis brevicornis* (Harpacticoida) in intertidal rock pools. Mar Ecol Prog Ser 211:215–224

Jolly MT, Viard F, Weinmayr G, Gentil F, Thiébaut E, Jollivet D (2003) Does the genetic structure of *Pectinaria koreni* (Polychaeta: Pectinariidae) conform to a source–sink metapopulation model at the scale of the Baie des Seine? Helgol Mar Res 57 DOI 10.1007/s10152-002-0123-1

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15:237–240

Levins R (1970) Extinction. In: Gerstenhaber M (ed) Some mathematical questions in biology. American Mathematical Society, Providence, R.I.

McIntosh RP (1995) Metaecology. Bull Ecol Soc Am 76:155–158

Meer J van der, Beukema JJ, Dekker R (2003) Large spatial variability in lifetime egg production in an intertidal Baltic tellin (*Macoma balthica*) population. Helgol Mar Res 57 DOI 10.1007/s10152-002-0128-9

Morgan LE, Botsford LW (2001) Managing with reserves: modeling uncertainty in larval dispersal for a sea urchin fishery. In: Kruse GH, Bez N, Booth A, Dorn MW, Hills S, Lipcius RN, Pelletier D, Roy C, Smith SJ, Witherell D (eds) Spatial processes and management of marine populations. Alaska Sea Grant College Program, Fairbanks, Alaska

Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132:652–661

Reich M, Grimm V (1996) Das Metapopulationskonzept in Ökologie und Naturschutz: Eine kritische Bestandsaufnahme. Z Ökol Natursch 5:123–139

Reise K (2003) Metapopulation structure in the lagoon cockle *Cerastoderma lamarcki* in the northern Wadden Sea. Helgol Mar Res 57 DOI 10.1007/s10152-002-0125-z

Reise K, Simon M, Herre E (2001) Density-dependent recruitment after winter disturbance on tidal flats by the lugworm *Arenicola marina*. Helgol Mar Res 55:161–165

Soulé ME (ed) (1987) Viable populations for conservation. Cambridge University Press, Cambridge

Stelter C, Reich M, Grimm V, Wissel C (1997) Modelling persistence in dynamic landscapes: lesson from a metapopulation of the grasshopper *Bryodema tuberculata*. J Anim Ecol 66:508–518

Strasser M, Pieloth U (2001) Recolonization pattern of the polychaete *Lanice conchilega* on an intertidal sand flat following the severe winter of 1995/96. Helgol Mar Res 55:176–181

Thomas CD (1994) Extinction, colonization, and metapopulations: environmental tracking by rare species. Conserv Biol 8:373–378