Our quantitative, predictive model for the energy budget of an individual during growth differs from phenomenological models that fit curves to data. It also differs from dynamic energy budget theory (DEB), which assumes a 2/3 power scaling of food assimilation rate during ontogeny, on the basis that energy uptake is limited by absorptive surface area, which scales like any simple geometric surface (*4*). By contrast, our model predicts that food assimilation rate cannot have a simple power-law scaling relation with body mass during ontogeny. Furthermore, DEB assumes that food assimilation rate is supply-limited, whereas our model views assimilation rate as arising from the developing organism matching food supply to metabolic energy demand. Our model provides a point of departure for addressing pathological cases of imbalance between supply and demand such as starvation or overeating. It captures the salient features of energy acquisition and allocation during ontogenetic development and quantitatively predicts universal assimilation and growth rate curves in agreement with data for mammals and birds. How well it captures the fundamental features of growth in other organisms, such as ectothermic vertebrates, insects, aquatic invertebrates, plants, and unicellular algae and protists, remains to be seen.

References and Notes

1. M. Kleiber, *The Fire of Life: An Introduction to Animal Energetics* (Wiley, New York, 1961).
2. S. Brody, *Bioenergetics and Growth* (Hafner, Darien, CT, 1964).
3. P. C. Withers, *Comparative Animal Physiology* (Saunders College/Harcourt College, Fort Worth, TX, 1992).
4. S. A. L. M. Kooijman, *Dynamic Energy and Mass Budgets in Biological Systems* (Cambridge Univ. Press, Cambridge, 2000).
5. R. E. Ricklefs, *Funct. Ecol.* **17**, 384 (2003).
6. A. M. Makarieva, V. G. Gorshkov, B. L. Li, *Ecol. Model.* **176**, 15 (2004).
7. G. B. West, J. H. Brown, B. J. Enquist, *Nature* **413**, 628 (2001).
8. M. Jobling, *J. Fish Biol.* **23**, 549 (1983).
9. M. D. McCue, *Comp. Biochem. Physiol. A* **144**, 381 (2006).
10. A. Ashworth, *Nature* **223**, 407 (1969).
11. I. Krieger, *Am. J. Clin. Nutr.* **31**, 764 (1978).
12. K. L. Blaxter, *Energy Metabolism in Animals and Man* (Cambridge Univ. Press, Cambridge, 1989).
13. K. A. Nagy, I. A. Girard, T. K. Brown, *Annu. Rev. Nutr.* **19**, 247 (1999).
14. Materials and methods are available as supporting material on *Science* Online.
15. M. E. Moses *et al.*, *Am. Nat.* **171**, 632 (2008).
16. K. W. Cummins, J. C. Wuycheck, *Mitt. Int. Ver. Theor. Angew. Limnol.* **18**, 1 (1971).
17. C. T. Robbins, *Wildlife Feeding and Nutrition* (Academic Press, New York, 1983).
18. R. E. Ricklefs, in *Avian Energetics*, R. A. Paynter Jr., Ed. (Nuttall Ornithological Club Publication Number 15, Cambridge, MA, 1974).
19. E. Evans, D. S. Miller, *Proc. Nutr. Soc.* **27**, 121 (1968).
20. J. K. Kirkwood, *J. Nutr.* **121** (suppl. 11), 29 (1991).

21. Supported by NIH grants P20 RR-018754 (for M.E.M.) and DK36263 (for W.H.W.) and by NSF grants DEB-0083422 and CCF0621900 (for J.H.B.) and PHY 0706174 and PHY 0202180 (for G.B.W.) G.B.W. also acknowledges the Thaw Charitable Trust for its support.

Supporting Online Material

www.sciencemag.org/cgi/content/full/322/5902/736/DC1
Materials and Methods
Tables S1 to S7
References and Notes

25 June 2008; accepted 19 September 2008
10.1126/science.1162302

Experimental Evidence for Spatial Self-Organization and Its Emergent Effects in Mussel Bed Ecosystems

Johan van de Koppel,[1]* Joanna C. Gascoigne,[2] Guy Theraulaz,[3] Max Rietkerk,[4] Wolf M. Mooij,[5] Peter M. J. Herman[1]

Spatial self-organization is the main theoretical explanation for the global occurrence of regular or otherwise coherent spatial patterns in ecosystems. Using mussel beds as a model ecosystem, we provide an experimental demonstration of spatial self-organization. Under homogeneous laboratory conditions, mussels developed regular patterns, similar to those in the field. An individual-based model derived from our experiments showed that interactions between individuals explained the observed patterns. Furthermore, a field study showed that pattern formation affected ecosystem-level processes in terms of improved growth and resistance to wave action. Our results imply that spatial self-organization is an important determinant of the structure and functioning of ecosystems, and it needs to be considered in their conservation.

Self-organized spatial patterns in ecological communities have been observed in arid ecosystems (*1*–*3*), peat lands (*4*), tidal wetlands (*5*), mussel beds (*6*), and rocky shores (*7*–*9*). These patterns are thought to result from local, nonlinear interactions between organisms or between organisms and the environment, developing even on completely homogeneous substrates. Models predicted that self-organized patterns can affect ecosystem-level processes, for instance, by improving resilience to perturbation, resistance to environmental change, and primary or secondary production (*3*, *6*). Most studies of self-organization in ecological systems combine observational studies with mathematical modeling (*2*, *10*) or experimentally test the mechanisms that underlie the self-organization process (*11*). Experimental demonstrations of self-organization—as have been accumulated for physical, chemical (*12*, *13*), sociobiological (*14*), and microbial systems (*15*, *16*)—are rare for ecological systems (*17*, *18*).

We investigated the origin of regular patterns in beds of the blue mussel *Mytilus edulis* (in the Menai Strait near Bangor, UK) on intertidal flats under wind-sheltered conditions (*19*). *M. edulis* is a filter-feeding animal exploiting algal plankton and detritus in the water column. Patterns consist of regularly spaced clusters of 5 to 10 cm in width that form a coherent, labyrinth-like pattern (Fig. 1A). In areas where mussel densities are lower, clusters are more isolated (Fig. 1B), whereas beds are near-homogeneous in very dense areas. Point pattern analysis based on Ripley's K (*19*) revealed clear, regularly spaced mussel clusters of ~3 to 5 cm across at ~10 cm distance from each other (fig. S1). Despite an order of magnitude difference in mussel biomass at the scale of meters, we found no significant difference in within-cluster biomass (fig. S2), suggesting that mussels self-organize to a certain local, within-cluster density, possibly to minimize predation or dislodgement losses (*20*). This concurs with a number of mathematical studies pointing at the possibility of self-organized pattern formation in mussel beds (*6*–*8*) and experimental studies in other intertidal ecosystems (*18*, *21*). Because of their small spatial scale, fast temporal development, and easy manipulation and observation of individuals, mussel beds are particularly suited for experimental testing of self-organization principles.

We tested in the laboratory the hypothesis that the observed patterns are self-organized and hence would develop spontaneously from homogeneity. Mussels that were laid out evenly in laboratory mesocosms developed coherent non-random spatial patterns within a day. These patterns were statistically similar to the patterns observed in the field (Fig. 1, C and D; movie S1; and see fig. S3, A and B, for a statistical description). When mussel densities in the laboratory were decreased, the spatial pattern became more open and clumps became more isolated (Fig. 1, E and F; movie S2; and fig. S3, C to D), as was observed under natural conditions (fig.

[1]Spatial Ecology Department, the Netherlands Institute of Ecology (NIOO-KNAW), Post Office Box 140, 4400 AC Yerseke, Netherlands. [2]School of Ocean Sciences, University of Wales Bangor, Askew Street, Menai Bridge LL59 5AB, UK. [3]Centre de Recherches sur la Cognition Animale, CNRS UMR 5169, Universite Paul Sabatier 118, Route de Narbonne, 31062 Toulouse Cedex 04, France. [4]Department of Environmental Sciences, Copernicus Institute, Utrecht University, Post Office Box 80115, 3508 TC Utrecht, Netherlands. [5]Aquatic Food Webs Department, Netherlands Institute of Ecology, Rijksstraatweg 6, 3631 AC, Nieuwersluis, Netherlands.

*To whom correspondence should be addressed. E-mail: J.vandeKoppel@nioo.knaw.nl

S1). Pattern formation in our experiment can only be caused by interactions between individual mussels, as there was no heterogeneity in substrate, suspended algal food, or initial conditions.

To elucidate how interactions between individual mussels determine spatial pattern formation, we traced the movement of individual mussels during our experiments, and we related movement characteristics to the local density of conspecifics. The resulting description of mussel movement was incorporated into an individual-based model (IBM) to test if this description is sufficient to explain the observed patterns (*22*, *23*). At first, our analysis revealed a strong negative effect on movement of mussel densities in the direct neighborhood: Mussels moved less when surrounded by conspecifics (Fig. 2A). When this relation was included in the IBM, however, no regular patterns were produced after a day of simulation time (Fig. 2B and fig. S4A), and in the long run, the model predicted the formation of a few large clusters of mussels, distinctly different from what we had observed in the field and our lab experiments. This difference implies that additional behavior prevents the formation of such large clusters and possibly that mussels decide to move when cluster size becomes too large. This idea was confirmed by a multiple generalized linear model (GLM) analysis of the relationship between movement speed and mussel density that considered a range of scales: Apart from a clear negative effect of mussel density in the neighborhood on movement at a scale of 1.87 cm, we found a strong positive effect on movement at a scale of 7.5 cm (Fig. 2, C and D). Hence, mussel movement appeared to increase again when clusters became very large. When we incorporated this new relationship in the IBM, the model correctly predicted the observed patterns (Fig. 2E and see fig. S4 for a statistical characterization).

Our laboratory observations show that a scale-dependent feedback to the processes of aggregation (Fig. 2, C and D) explains the formation of patterns: Movement decreases when mussels aggregate to form small-scale clusters, attaching themselves to each other with byssal

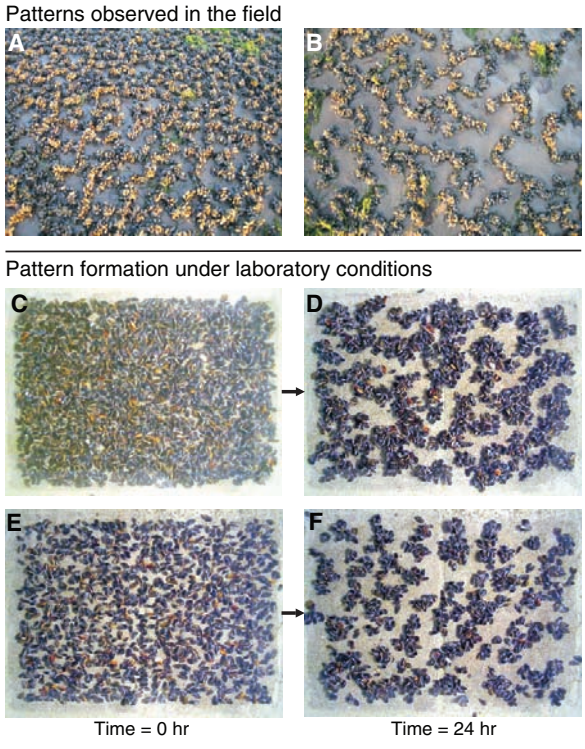

Fig. 1. Pattern formation in mussels in the field and under experimental laboratory conditions. (**A** and **B**) Small-scale, labyrinthlike spatial patterning in beds of the blue mussel *M. edulis*, as observed in the Menai Strait, near Bangor, UK. Scale is ~1.5 m wide. (**C** to **F**) Mussels that were laid out evenly under controlled conditions on a homogeneous substrate developed spatial patterns similar to those in the field within 24 hours. (C) and (D) versus (E) and (F): initial density of 6.0 and 3.8 kg/m^2, being ~1850 and ~1200 individuals, respectively. Images in (C) to (F) represent a surface of 60 × 80 cm. The development from (C) to (D) and (E) to (F) is shown in movies S1 and S2 in the supporting online material.

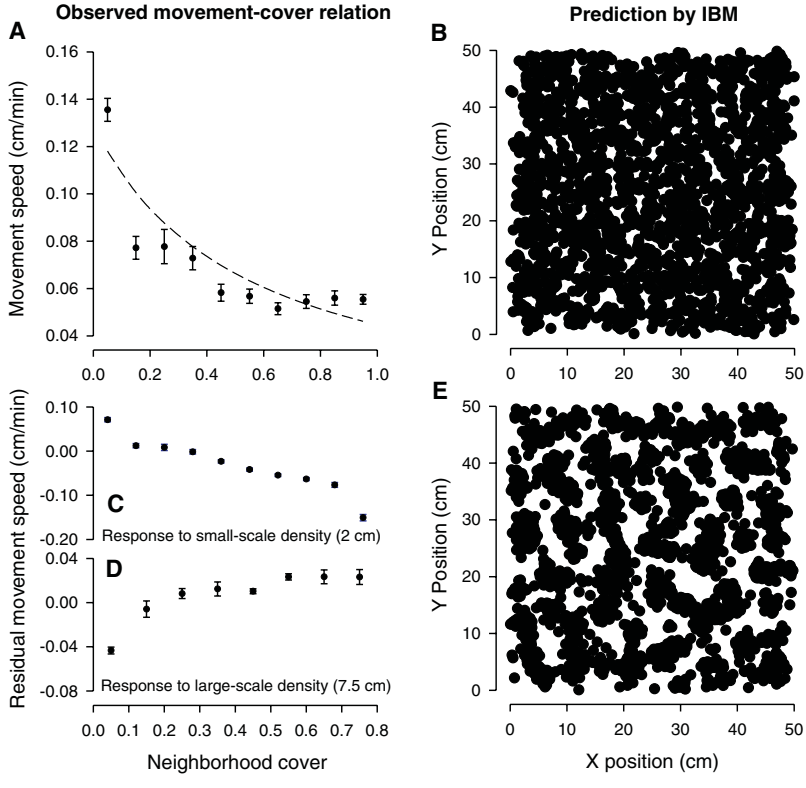

Fig. 2. Observed relationships between local mussel density and movement speed of mussels (left panels) and simulation results of IBMs that incorporate these relationships (right panels). (**A**) Relationship between movement speed of a particular tracked mussel and neighborhood cover within a 1.87-cm radius. The dashed line represents a univariate GLM fit with exponential distribution: $\beta = 1/(7.73 + 14.69\ C_{1.87})$; intercept: $z = 42.39$, $P < 0.001$; $C_{1.87}$-coefficient: $z = 22.09$, $P < 0.001$; $N = 4408$. (**C** and **D**) Residual deviance from a multiple GLM regression: $\beta = 1/(8.21 + 23.42\ C_{1.87} - 19.38\ C_{7.50})$; intercept: $z = 42.89$, $P < 0.001$; $C_{1.87}$-coefficient: $z = 23.19$, $P < 0.001$; $C_{7.50}$-coefficient: $z = -11.76$, $P < 0.001$; $N = 4408$. (C) Relationship between residual movement speed and neighborhood cover within 1.87-cm radius after removal of the effect of cover within 7.5-cm radius. (D) Relationship between residual movement speed and neighborhood cover at within 7.5-cm radius after removal of the effect of cover at 1.87-cm radius. (**B** and **E**). An IBM simulation with 2025 (45 × 45) mussels with movement characteristics based on the single-regression fit did not reproduce the patterning after a 1-day simulation run, whereas the model based on the multiple regression fit closely reproduced the patterns observed in the laboratory experiment. Error bars indicate SEM.

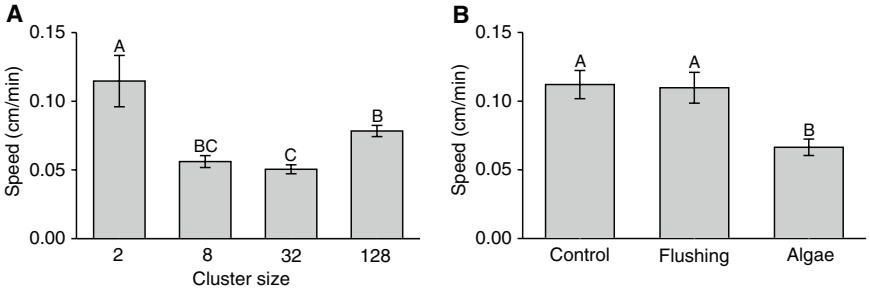

Fig. 3. Relationship between (**A**) cluster size and the movement speed of mussels and (**B**) mussel movement speed and addition of algae to large clusters of mussels. (A) Mussel movement speed initially decreases with cluster size but increases again when cluster size is increased from 32 to 128 individuals. (B) Supply of suspended algal food to clusters of 128 individuals decreases the movement speed significantly. The flushing treatment, a procedural control in which filtered seawater was supplied to mussels at the same rate as the algal supply treatment, was found to differ significantly from the algal supply treatment but not from the control treatment, indicating that the effect is caused by algal supply, not by flushing with seawater. Overall effects: (A) One-way analysis of variance (ANOVA): $F_{3,107}$ = 11.59, N = 107, $P < 0.001$; (B) one-way ANOVA: $F_{2,48}$= 7.68, N = 48, P = 0.001. Error bars represent SEM, whereas the characters on top of the bars denote significant differences based on Tukey's honest significant difference.

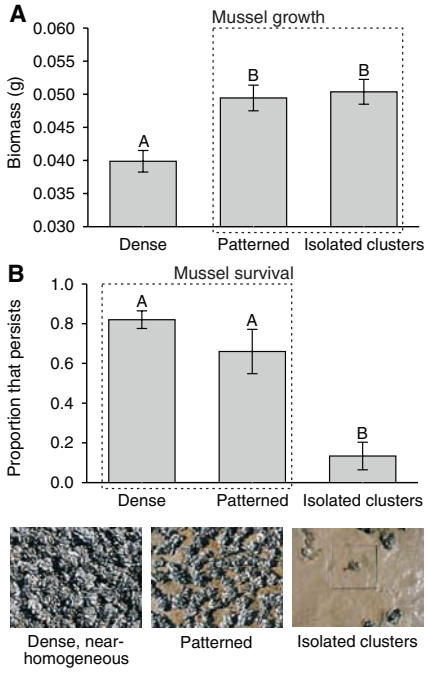

Fig. 4. Differences in (**A**) individual growth in terms of established size (Kruskal-Wallis rank sum test: χ^2 = 23.60, N = 800, $P < 0.001$) and (**B**) persistence of mussels between dense, near-homogenous beds, patterned beds of intermediate-density, and low-density beds consisting of isolated clumps (one-way ANOVA: $F_{2,30}$ = 20.05, N = 30, $P < 0.001$). Error bars represent SEM, whereas the characters on top of the bars denote significant differences between the treatments based on pairwise Mann-Witney U test for (A) and Tukey's honest significant difference post-hoc analysis of variance for (B).

threads to prevent predation or dislodgement, providing a positive feedback to the development of such small aggregates. When further aggregation leads to the formation of large-scale clusters, movement increases again, creating a negative feedback to further aggregation. This last mechanism is potentially related to competition because of the depletion of suspended algal food within the aggregates (*24*). Together, these mechanisms obey the general principle of scale-dependent activation-inhibition, which has been proposed to explain pattern formation in morphogenesis (*25*, *26*). We further investigated this hypothesis by determining the average movement speed of mussels in artificial clusters of 2, 8, 32, and 128 mussels. Our experiment revealed that mussel movement speed decreased with cluster size from 2 up to 32 mussels, but it increased again from 32 to 128 mussels per cluster (Fig. 3A), in agreement with the general principle of scale-dependent activation-inhibition. When suspended algal food was supplied to the center of large clusters of 128 individuals, movement dropped significantly, suggesting that algal depletion inhibits the formation of large clusters (Fig. 3B). This implies that mussels respond to both the local density of conspecifics within range of their foot (e.g., touch) and to the local availability of algal food. No evidence was found that other chemical signals influenced mussel movement in our experiments (*19*).

We performed a field study to investigate the emergent effects of self-organized pattern formation on the growth and survival of mussels under field conditions at the intertidal flats in the Menai Strait. At one location, fishermen seeded part of the intertidal flats with mussels of ~2 cm in size, 3 weeks before our field study. We observed strong variation in mussel density on the tidal flat, probably resulting from variation in seeding intensity. Mussel biomass on a square-meter basis was 20 to 30 kg fresh weight per square meter for dense homogeneous beds, 5- to 20-kg/m^2 for patterned beds, or <5 kg/m^2 for beds with isolated clumps. Our experiments revealed that mussels that occurred in isolated clumps had grown significantly more over these 3 weeks than those that occurred in dense, near-homogeneous beds (Fig. 4A), probably because of reduced competition. Mussel growth in patterned beds was significantly higher than in dense, near-homogeneous beds, but not significantly different from isolated mussels.

To investigate the effects of spatial patterns on persistence of mussels within the beds, we released 10 painted mussels in a group on open sediment, in patterned beds, and in dense near-homogeneous beds. After a week, >80% of the mussels were recovered from the dense bed, whereas <20% of the mussels on the open sediment remained (Fig. 4B). The local persistence of mussels released in patterned locations was significantly higher than those released as isolated clumps, but it did not differ significantly from those in dense beds. Experiments with mussel mimics (empty mussel shells filled and glued together with Blu-tac paste) yielded very similar results, indicating that most likely, physical disturbance due to water flow or wave action, rather than predation, is the cause of difference in persistence in dense or patterned mussel beds, as compared with the open areas. Hence, our experiments revealed a marked emergent effect of spatial patterns in mussel beds: It allows for high resilience of mussel beds to wave action and water flow and for high individual growth by reducing the effects of competition, properties that are incompatible in homogeneous beds.

Our results show that simple rules governing individual behavior of mussels explain the formation of spatial patterns at the population level. Spatial patterns were found to result from the interplay of positive and negative interactions between individual mussels at different spatial scales (*18*). Both growth and survival of mussels were found to be high in a patterned bed, a combination that cannot be achieved in a homogeneous bed. Hence, this is an emergent property of the spatial pattern, translating individual behavior to the functioning of mussel beds at the level of the population and ecosystem. This result has implications for our understanding of ecosystems, by showing that self-organized spatial patterns can determine their functioning, confirming the predictions of many conceptual (*27*) and theoretical studies (*3*, *6*, *28*). This is relevant to the conservation of many natural ecosystems, such arid ecosystems where human disturbance of spatial vegetation patchiness increased the loss of water from the landscape, leading to decreased productivity (*29*).

References and Notes

1. C. A. Klausmeier, *Science* **284**, 1826 (1999).
2. P. Couteron, O. Lejeune, *J. Ecol.* **89**, 616 (2001).
3. M. Rietkerk *et al.*, *Am. Nat.* **160**, 524 (2002).
4. M. Rietkerk, S. C. Dekker, M. J. Wassen, A. W. M. Verkroost, M. F. P. Bierkens, *Am. Nat.* **163**, 699 (2004).
5. J. van de Koppel, C. M. Crain, *Am. Nat.* **168**, E136 (2006).
6. J. van de Koppel, M. Rietkerk, N. Dankers, P. M. J. Herman, *Am. Nat.* **165**, E66 (2005).

7. J. T. Wootton, *Nature* **413**, 841 (2001).
8. F. Guichard, P. M. Halpin, G. W. Allison, J. Lubchenco, B. A. Menge, *Am. Nat.* **161**, 889 (2003).
9. M. Rietkerk, J. Van de Koppel, *Trends Ecol. Evol.* **23**, 169 (2008).
10. O. N. Bjørnstad, M. Peltonen, A. M. Liebhold, W. Baltensweiler, *Science* **298**, 1020 (2002).
11. J. L. Maron, S. Harrison, *Science* **278**, 1619 (1997).
12. V. Castets, E. Dulos, J. Boissonade, P. De Kepper, *Phys. Rev. Lett.* **64**, 2953 (1990).
13. G. Nicolis, I. Prigogine, *Self-Organization in Nonequilibrium Systems* (Wiley, New York, 1977).
14. G. Theraulaz *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 9645 (2002).
15. H. Wager, *Philos. Trans. R. Soc. London Ser. B* **201**, 333 (1911).
16. J. J. Tyson, J. D. Murray, *Development* **106**, 421 (1989).
17. See the supporting online material for a literature review of experimental tests of self-organization and its mechanisms.
18. M. D. Bertness, S. D. Gaines, S. M. Yeh, *Ecology* **79**, 1382 (1998).
19. Materials and methods are available as supporting material on *Science* Online.
20. M. D. Bertness, E. Grosholz, *Oecologia* **67**, 192 (1985).
21. J. C. Gascoigne, H. A. Beadman, C. Saurel, M. J. Kaiser, *Oecologia* **145**, 371 (2005).
22. D. L. DeAngelis, W. M. Mooij, *Annu. Rev. Ecol. Evol. Syst.* **36**, 147 (2005).
23. V. Grimm *et al.*, *Science* **310**, 987 (2005).
24. P. R. Jonsson, J. K. Petersen, Ö. Karlsson, L.-O. Loo, S. Nilsson, *Limnol. Oceanogr.* **50**, 1989 (2005).
25. A. Gierer, H. Meinhardt, *Kybernetics* **12**, 30 (1972).
26. A. M. Turing, *Philos. Trans. R. Soc. London Ser. B Biol. Sci.* **237**, 37 (1952).
27. S. A. Levin, *Fragile Dominion; Complexity and the Commons* (Helix Books, Cambridge, MA, 1999).
28. R. V. Solé, J. Bascompte, *Self-Organization in Complex Ecosystems* (Princeton Univ. Press, Princeton, NJ, 2006).
29. J. A. Ludwig, B. P. Wilcox, D. D. Breshears, D. J. Tongway, A. C. Imeson, *Ecology* **86**, 288 (2005).

30. We thank A. Koutstaal, B. Koutstaal, A. Matkin, and J. van Soelen for their assistance during the field work and lab experiments; K. Mould and J. Wilson for access to their mussel lots; and A. Altieri, M. Bertness, T. Bouma, F. Guichard, M. de Jager, A.-M. Neutel, P. de Ruiter, and B. Silliman for critical discussions and reading of the manuscript. The field work at Bangor was supported by a grant from the Schure-Beijerinck-Popping fund of the Royal Dutch Academy of Sciences to J.v.d.K. The research of M.R. is supported by a personal Vidi grant from the Netherlands Organization of Scientific Research/Earth and Life Sciences (NWO-ALW). J.C.G. was supported by Biotechnology and Biological Sciences Research Council contract D18866. This is publication 4410 of the Netherlands Institute of Ecology (NIOO-KNAW).

Supporting Online Material

www.sciencemag.org/cgi/content/full/322/5902/739/DC1
Materials and Methods
SOM Text
Figs. S1 to S4
References
Movies S1 and S2

29 July 2008; accepted 26 September 2008
10.1126/science.1163952

Natal Homing and Connectivity in Atlantic Bluefin Tuna Populations

Jay R. Rooker,[1]*† David H. Secor,[2]* Gregorio De Metrio,[3] Ryan Schloesser,[1] Barbara A. Block,[4] John D. Neilson[5]

Atlantic bluefin tuna populations are in steep decline, and an improved understanding of connectivity between individuals from eastern (Mediterranean Sea) and western (Gulf of Mexico) spawning areas is needed to manage remaining fisheries. Chemical signatures in the otoliths of yearlings from regional nurseries were distinct and served as natural tags to assess natal homing and mixing. Adults showed high rates of natal homing to both eastern and western spawning areas. Trans-Atlantic movement (east to west) was significant and size-dependent, with individuals of Mediterranean origin mixing with the western population in the U.S. Atlantic. The largest (oldest) bluefin tuna collected near the northern extent of their range in North American waters were almost exclusively of western origin, indicating that this region represents critical habitat for the western population.

Harvest strategies for marine fishes depend on fundamental assumptions about their complex life cycles, and management is often based on the "unit stock concept," which relies on the phenomenon of natal homing (return to spawning area) and limited or structured connectivity between populations (*1*). For Atlantic bluefin tuna, these assumptions are important because spawning populations in the western Atlantic are at 10% of the biomass prevailing when industrial fishing began, and recovery is confounded by trans-Atlantic movement across international jurisdictions (*2*). In assessments and management activities, the International Commission for the Conservation of Atlantic Tunas (ICCAT) has assumed that Atlantic bluefin tuna occur as two discrete populations that originate either in the Mediterranean Sea or the Gulf of Mexico; members of either population can undertake trans-Atlantic migrations, but adults will return to natal spawning regions; and trans-Atlantic migrations are relatively small in number, justifying the use of two broad management regions east and west of 45°W longitude. Despite four decades of regulation by ICCAT, bluefin tuna populations remain severely depressed, causing many to question the effectiveness of the current management regime (*3*, *4*). Although recent electronic tagging data demonstrated evidence for spawning site fidelity (i.e., return of adults repeatedly to the same spawning region) (*5*), the degree of natal homing in the populations and rate of exchange between eastern and western populations is unresolved. Without data on population structure and movement, there is no biological rationale for spatially explicit management, and thus rebuilding plans may be predisposed to fail.

Several approaches have been used to examine the population structure of Atlantic bluefin tuna (*2*), of which chemical traces in otoliths (ear stones) have considerable potential for quantifying natal homing and connectivity because otolith material deposited during the first year of life serves as a natural tag of the individual's place of

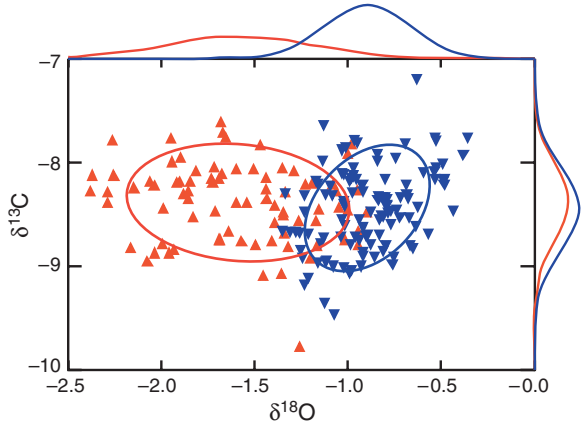

Fig. 1. Otolith $\delta^{13}C$ and $\delta^{18}O$ values for yearling Atlantic bluefin tuna collected from 1999 to 2004 in the eastern Atlantic Ocean/Mediterranean Sea (blue triangles) and western Atlantic Ocean (red triangles). Gaussian bivariate ellipses (one standard deviation of the mean) and normal distribution curves are shown. Yearlings ranged in age from 12 to 18 months. Two regions of the eastern Atlantic Ocean/Mediterranean Sea were sampled over the 6 years: the eastern Atlantic Ocean (Cantabrian Sea; 2000, 2001, and 2002) and the western/central Mediterranean Sea (Ligurian Sea to Adriatic Sea; 1999, 2000, 2002, 2003, and 2004) (n = 113). In the continental shelf waters of the U.S. Atlantic Ocean, yearlings were collected from Maryland to Massachusetts over a 6-year period (n = 81) [see S8 in (*8*)].

[1]Department of Marine Biology, Texas A&M University, 5007 Avenue U, Galveston, TX 77551, USA. [2]Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Post Office Box 38, Solomons, MD 20688, USA. [3]Department of Animal Health and Well-Being, University of Bari, 70010 Valenzano, Bari, Italy. [4]Stanford University, Hopkins Marine Station, Oceanview Boulevard, Pacific Grove, CA 93950, USA. [5]Department of Fisheries and Oceans, Population Ecology Section, St. Andrews Biological Station, St. Andrews, NB, Canada.

*These authors contributed equally to this work.
†To whom correspondence should be addressed. E-mail: rookerj@tamug.edu