Coastal-Marine Conservation:

Science and Policy

G. Carleton Ray *and* **Jerry McCormick-Ray**

Both from
Department of Environmental Sciences
University of Virginia
Charlottesville
Virginia
USA

Illustrations by Robert L. Smith

350 Main Street, Malden, MA 02148-5020, USA
108 Cowley Road, Oxford OX4 1JF, UK
550 Swanston Street, Carlton, Victoria 3053, Australia

First published 2004

Library of Congress Cataloging-in-Publication Data

Coastal-marine conservation : science and policy / [edited by] G. Carleton Ray and Jerry McCormick-Ray ; illustrations by Robert L. Smith.
p. cm.
Includes bibliographical references (p.).
ISBN 0-632-05537-5 (pbk. : alk. paper)
1. Coastal ecology. 2. Nature conservation. 3. Endangered ecosystems.
I. Ray, G. Carleton. II. McCormick-Ray, Jerry.
QH541.5.C65 C5916 2003
333.95′616—dc21
2002038282

A catalogue record for this title is available from the British Library.

Set in $9\frac{1}{2}/11\frac{1}{2}$pt Bembo
by Graphicraft Limited, Hong Kong
Printed and bound in the United Kingdom
by TJ International Ltd, Padstow, Cornwall

For further information on
Blackwell Publishing, visit our website:
http://www.blackwellpublishing.com

life-history strategies frequently co-exist in the same habitats. A species' ecological niche determines the individual's perception and the population's response to variation.

This triangular life-history continuum has a quantitative foundation. Fitness can be estimated by r, the intrinsic rate of natural increase of a population or genotype. The intrinsic rate of population increase can be approximated as

$$r \sim \ln (R_0)/T$$

where R_0 is the net replacement rate, T is the mean generation time, and

$$R_0 = \Sigma\, l_x m_x$$

In this equation l_x is age-specific survivorship and m_x is age-specific fecundity, resulting in

$$r \sim \ln (\Sigma\, l_x m_x)/T$$

Therefore, population growth rate depends directly upon fecundity, survivorship, and timing of reproduction. Averaged over many generations, the three parameters must balance, or the population eventually will decline to extinction or grow exponentially.

The three endpoint strategies result from trade-offs among age of maturation (positively correlated with mean generation time), fecundity, and survivorship. The periodic strategy corresponds to high values on the fecundity and age at maturity axes (the latter a correlate of population turnover rate) and low values on the juvenile survivorship axis. The opportunistic strategy of high r (*via* rapid maturation) corresponds to low values on all three axes. The equilibrium strategy corresponds to low values on the fecundity axis and high values on the age at maturity and juvenile survivorship axes.

Large body size in periodic strategists enhances adult survivorship during suboptimal conditions and permits storage of energy and biomass for future reproduction. The possibility of perennial reproduction represents a bet-hedging tactic whereby, sooner or later, reproduction coincides with favorable conditions that facilitate strong recruitment. Spawning tends to be periodic and synchronous, so that generations are often recognized as discrete annual cohorts that may dominate the population for many years. Correlations among parental stock densities and densities of recruits have been shown to be negligible in many of these fishes over wide ranges of parental abundances. Recruitment frequently depends on climatic conditions that influence water movement, egg/larval retention zones, and productivity, and on other environmental factors that determine early growth and survival. For periodic fishes, the variance in larval survivorship that serves as input for population projections lies well beyond our current measurement precision and accuracy. Even under pristine conditions, the fate of most larvae is an early death. Therefore, it follows that some minimum level of spawning must occur during each spawning period if strong cohorts are to develop during the unpredictable exceptional year. Management of periodic strategists requires maintenance of some minimum adult stock density so that periodic favorable conditions can be exploited, as well as protection of spawning and nursery habitats. Because recruitment is determined largely by unpredictable interannual environmental variation, this minimum density will be impossible to determine with any degree of precision.

Theoretical studies have shown that reducing mean generation time is the most effective strategy for maximizing the intrinsic rate of increase in a density-independent setting. Many opportunistic fishes are found in shallow marginal habitats, the kinds of environments that experience the largest and most unpredictable changes on small spatial and temporal scales. Tidal dynamics change water depth in shallow habitats such as tidal pools and salt marshes. In the absence of intense predation and resource limitation, opportunistic-type populations quickly rebound from localized disturbances, and these populations ought to show large variation in abundance, with infrequent strong density-dependence. Because they tend to be small and often occur in marginal habitats, opportunistic fishes usually are not exploited. Some important commercial fishes, like menhaden (*Brevoortia patronus*), are intermediate between opportunistic and periodic strategists.

The equilibrium strategy should be favored in density-dependent settings, and this may be why it is more common among coral-reef fishes than among estuarine and pelagic fishes. Compared with opportunistic and periodic strategists, equilibrium strategists tend to show moderate fluctuations in population density, and should conform better to stock–recruit models. Because equilibrium strategists produce relatively few offspring, early survivorship must be relatively high. Relatively few equilibrium fishes are commercially exploited on a large scale. Management of equilibrium fishes should stress habitat integrity and healthy adult stocks to promote surplus yields that can be harvested and replaced *via* natural compensatory mechanisms.

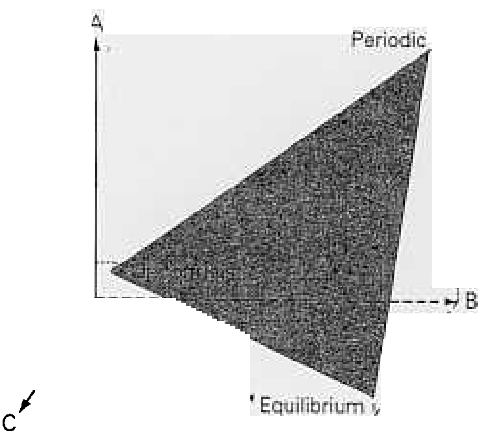
currents as if they were inorganic particles. However, evidence has accumulated that larvae possess behaviors that can, at least in part, determine their own dispersal. Blue crab (*Callinectes sapidus*) larvae depend on frontal systems and currents to enhance their dispersal from deep to nearshore estuarine water. Estuarine oysters may depend on residual currents to retain larvae in the estuary. These larvae undertake short vertical migrations or become incorporated into gyres to help direct their own dispersal. Turbulence may also act to

Box 4.2 Life-history strategies of fishes

K.O. Winemiller

A remarkable diversity of reproductive strategies is observed among the fishes. For example, certain live-bearing sharks and the coelacanth (*Latimeria chulmnae*) produce one offspring at a time, whereas the ocean sunfish (*Mola mola*) releases over 600 000 000 pelagic eggs in a single spawning bout. Life-history strategies result from trade-offs among attributes that have either direct or indirect effects on reproduction and fitness. Comparative studies have yielded a robust pattern of fish life-history syndromes, with three primary life-history strategies defining the endpoints of a triangular continuum (Fig. 1). One endpoint, the *periodic strategy*, defines species that have delayed maturation at intermediate or large sizes, produce large numbers of small eggs, and tend to have short reproductive seasons and rapid larval and first-year growth rates. Another endpoint, the *opportunistic strategy*, characterizes species that mature rapidly at small sizes, produce relatively small numbers of eggs, and have long reproductive periods with multiple spawning bouts. A third endpoint, the *equilibrium strategy*, defines species that produce relatively small cohorts of large eggs or neonates, often in association with a long reproductive season, and have well-developed parental care.

Periodic strategists enjoy two benefits from delayed maturation and large adult body size: capacity to produce large numbers of eggs, and enhanced adult survival during periods of suboptimal environmental conditions. Periodic fishes often have synchronous spawning that coincides either with migration into favorable habitats or with favorable periods within the temporal cycle of the environment. These fishes cope with large-scale spatial heterogeneity by producing great numbers of tiny offspring, at least some of which thrive once favorable locations are encountered. Normally, early larval survival is very low in the marine environment. For the few fortunate larvae that encounter areas of high resource density, growth is rapid. At higher latitudes, environmental variation is cyclic. Periodic fishes exploit seasonal variation by releasing large numbers of progeny during periods favorable for their growth and survival. In tropical pelagic habitats, large-scale variation in space may represent a periodic signal as strong as the seasonal variation at temperate latitudes. As a result of upwellings, gyres, convergence zones, and other oceanographic features, physical parameters (salinity, temperature), primary production, and zooplankton densities are unevenly distributed in the open ocean. Massive cohorts of small pelagic eggs enhance dispersal capabilities of marine fishes during early life stages. Mortality due to settlement in hostile habitats (advection) is balanced over the long term by survival benefits derived from the recruitment of a certain fraction of larval cohorts into suitable regions or habitats.



A – Fecundity ($\ln(m_x)$)
B – Maturation rate
Generation time ($\ln(T)$)
C – Parental investment/offspring
juvenile survivorship ($\ln(l_x)$)

Fig. 1 Fish species life-history strategies reflect a trade-off between reproduction and fitness.

The opportunistic strategy yields a high intrinsic rate of population increase (*r*) and is associated with high population turnover. Although the size of egg cohorts tends to be small in these small fishes, reproductive effort is actually high because they reproduce early and often. In extreme cases, serial spawning results in an annual biomass of spawned eggs that greatly exceeds female body mass. Small fishes with early maturation, high reproductive effort, and high intrinsic rates of increase are efficient colonizers. These populations can quickly compensate for high adult mortality. The opportunistic strategy is observed in anchovies (Engraulidae), silversides (Atherinidae), and killifishes (Cyprinodontidae) – species often found in dynamic habitats or faced with high predation risk.

Equilibrium fishes have large eggs and parental care that results in larger, more advanced juveniles at the onset of independent life. Marine ariid catfishes (oral brooding of a few large eggs) and sharks, rays, and other live-bearing fishes with long gestation periods and large neonates provide extreme examples of the equilibrium strategy. Parental care seems to be more common in tropical nearshore and coral-reef fishes (e.g., pipefishes, seahorses, eelpouts, some gobies) compared with tropical pelagic and temperate marine fishes.

Of course, intermediate life-history strategies occur within the triangular gradient of life histories. For example, live-bearing is usually associated with few young, but rockfishes (Scorpaenidae) and other cool-water fish often have small numbers of large eggs. Also, divergent