SHIFTED COMMUNITY STATES IN FOUR MARINE ECOSYSTEMS:
SOME POTENTIAL MECHANISMS

by

THOMAS ANTHONY OKEY

B.Sc., Saint Lawrence University, 1986
M.Sc., Moss Landing Marine Laboratories, San Jose State University, 1993

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ABSTRACT

The rigorous demonstration of truly stable alternate community states is elusive in marine ecosystems and might remain so for some time. Examples of marine community states that have shifted are nevertheless increasingly conspicuous. The growing concern over these altered community states is often related to questions of persistence and reversibility, especially when these shifted states are considered to be degraded. I used empirically-based trophic models and direct empirical field studies to explore the potential of particular hypothesized mechanisms to generate and maintain alternate community states in four marine ecosystems: a Galápagos rocky reef, Prince William Sound, Alaska, the West Florida Continental Shelf, and coral reefs of the Spermonde Archipelago or Southwest Sulawesi, Indonesia.

Construction and analysis of an *Ecopath with Ecosim* (*EwE*) model of a Galápagos rocky reef indicated that the unsustainable fishery targeting the holothurian *Stichopus fuscus* can, by itself, trigger the replacement of previously diverse reef platform communities with *Aiptasia* sp. anemone barrens.

Construction and analysis of a Prince William Sound, Alaska *EwE* model indicated that severe disturbances such as the *Exxon Valdez* oil spill can shift a marine biotic community to an alternate state that persists in a stable manner for decades, and that the character of such disturbances, in terms of their breadth and community-level life-history signatures, might strongly influence whether a community shifts to an alternate state. In addition, a search for keystone species provided a whole-system approach to identifying species or functional groups whose depletion or removal might have the most severe consequences for community structure, and the most potential for mediating shifts.

Construction and analysis of a West Florida Shelf *EwE* model indicated that increased sea floor shading by coastal phytoplankton (i.e., resulting from nutrient runoff pollution) can cause broad shifts in this continental shelf community by shading benthic primary producers, which support much of the overall shelf community.

An empirical field study of monsoons and runoff in Southwest Sulawesi, Indonesia indicates some of the mechanisms involved in shifting tropical reefs from coral-dominated to algae-dominated systems.

These contributions feature some newly emerging approaches for gaining insights into marine communities and for developing hypotheses that can be more rigorously evaluated in the future. None of these examples, however, are comprehensive or strictly falsificationist by themselves. The continued integration of these emerging community/ecosystem modeling approaches with direct empirical studies should vastly increase the potential for distinguishing the relative roles of natural and anthropogenic forces in shaping marine communities. The goal of the first steps described here was to identify particular mechanisms in each example that have the potential to generate or maintain community shifts.

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PREFACE

This dissertation work was conducted and documented as individual manuscripts written for submittal to peer-reviewed scientific journals. Chapter 2 was reprinted from Ecological Modelling 172(2-4), T.A. Okey, S. Banks, A.F. Born, R.H. Bustamante, M. Calvopiña, G.J. Edgar, E. Espinoza, J.M. Fariña, L.E. Garske, G.K. Reck, S. Salazar, S. Shepherd, V. Toral-Granda, P. Wallem, A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies, Pages 383-401, Copyright (2004), with permission from Elsevier. Chapter 6 was reprinted from Ecological Modelling 172(2-4), T.A. Okey, G.A. Vargo, S. Mackinson, M. Vasconcellos, B. Mahmoudi, C.A. Meyer, Simulating community effects of sea floor shading by plankton blooms over the West Florida shelf, Pages 339-359, Copyright (2004), also with permission from Elsevier. In some cases, the text from these manuscripts is updated in content and adapted to thesis formatting. For example, *Ecopath with Ecosim* modeling methodology descriptions—the main analytical method used herein—were removed from individual chapters and summarized at the end of Chapter 1. In other cases, certain paragraphs that I did not write or initiate were deleted for the present format. The cited literature is listed at the end of each chapter and the reference formats differ among chapters according to target journal. I generally approached each chapter with the goal of journal submittal in order to streamline the research communication process.

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Chapter 4

Chapter 5

Chapter 6

Chapter 7

for

Molly Rose McNulty-Finn

Clara Riley McNulty-Finn

and

Maura Joan McNulty-Finn

for the oceans

CHAPTER 1. Overview and Summary

The notion that biological communities are regulated at a balanced state (i.e., an equilibrium state) persists throughout society and modern ecology. The western roots of this equilibrium paradigm include Calvin's transcendental notion of divine order (Green 1995) and strict mechanistic determinism as construed by Laplace (1819). These ideas continue to permeate modern scientific inquiry (Botkin 1990) despite their metaphysical rather than empirical foundations (Dupré 1993). Classical ecological thought embraced the culturally engrained presumption of a 'balance of nature' (see Egerton 1973), or a nature that is self-regulating (sensu Hutchinson 1948, Margalef 1968), or one that tends towards 'maturity' through succession (Elton 1930, Odum 1969, 1971, Christensen 1995). However, natural variability and scale constraints makes the rigorous demonstration of community *stability* or 'balance' very challenging (Connell and Sousa 1983, Pickett et al. 1992, Dodd et al. 1995). Even defining ecological stability has been so challenging that some authors have proposed new vocabularies (Grimm and Wissel 1997).

Despite a paucity of direct empirical evidence of stability *per se*, the existence of stabilizing feedback mechanisms in ecosystems (Hutchinson 1948, Margalef 1968) continues to tempt ecologists with the notion that biological communities are attracted to 'equilibria' on some scale, even if 'dynamic' (Huston 1979, O'Neill 2001). Ecological stability is, arguably, an entirely scale-dependent concept (Connell and Sousa 1983, Levin 1992, O'Neill 2001). From one year to the next, the world around us remains largely self-similar. Such experiential observations explain the origins of the stability idea and lend credence to the notion that stability is not a delusion. Such evidence cannot, however, transcend context and scale dependency. Although the reluctance to surrender a comforting world view might be a principle reason for the attraction of ecologists to the idea of stability, some find practical convenience in the equilibrium notion when applied to appropriately-useful scales and inference (Pauly and Christensen 1995, Walters et al. 1997, Pauly et al. 2000).

The alternative notion that change, chance, or chaos pervades nature is also traditional and persistent (Karma-glin-pa 14th century, Milton 16th century, Hesiod 800 bc, Engels 1882, Poincaré 1914, Lorenz 1963, Kirthisinghe 1984, Prigogine and Stengers 1984, Laszlo 1991, Waldrop 1992). Thus, the maturing of ecological thought has proceeded from simple conceptual models of a neatly balanced nature (e.g., Odum 1953) to conceptual models in which disturbance and stochasticity, i.e., indeterminacy on the scale of an organism's experience (sensu Botkin 1990), dominate the shaping of biological communities (O'Neill et al. 1982, Sousa 1984, Pickett et al. 1992, Levin 1999). The burgeoning integration of these two realms of thought, i.e., balance versus chaos, or equilibrium versus stochastic variability and change, represents a conceptual threshold for understanding the basic rules of community organization.

Notions of self-regulation of biological communities on one hand and external regulation of biological communities (e.g., via physical forces) are both given credence by theory and empirical evidence, but debates over particular ecological dilemmas still organize according to camps that advocate

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either one view or the other (see Wilson 1998). The intellectual tribalism and isolationism underlying such polarization of discourse perpetuates false dichotomies, as in some debates over the primacy of biotic and physical forces as organizers of communities. Those that continue splitting non-equilibrium mechanisms from equilibrium mechanisms in an attempt to understand community regulation risk continued perpetuation of such false dichotomies (Beisner et al. 2003). In reality, biotic communities are regulated and organized by mixtures of biological and physical forces that vary continually in both time and space (e.g., Okey 2003).

A corollary to the notion of equilibrium, stability, or 'balance' is the idea that a given biological community has *global stability* (Lewontin 1969); that is to say, a single 'stable' state to which the community is attracted. This 'global attractor' is illustrated by a marble at the bottom of a bowl (Hurd and Wolf 1974), or valley. A disturbance can push the marble from the global basin of attraction, but the marble always returns to the previous state after some period of fluctuations. A strictly deterministic 'equilibrium' system, in which the biotic community possesses a single-unique-stable-state, will presumably always return to this initial 'global attractor' position when a disturbance or stressor is removed, even when the community is perturbed beyond historical levels of fluctuation.

Another view is that biological communities have multiple stable states, or more than one *local attractor*. This is envisioned as valleys in a dynamical landscape wherein a strong disturbance can push a marble from one local basin of attraction to another (Lewontin 1969, Holling 1973, Sutherland 1974, May 1977). In a system containing stochasticity, historical accidents (sensu Sutherland 1974) can direct a natural community to one of many possible attractors on the broader dynamical landscape. The effects of shape, height, and steepness of the bowl on the marble represent both a community's resistance to being changed by external forces (Boesch 1974) and the community's *resilience*, which is how much disturbance (e.g., magnitude, frequency, severity) a community can endure and still return to its previous state (definition based on Holling and Clark 1975). Resilience is also thought to incorporate the speed of return to the equilibrium state (Boesch 1974, Pimm 1991).

Any system equilibria, whether global or local, develops within the context of natural environmental variability and disturbance regimes in addition to the ever-changing biotic forces within a community. Anthropogenic or exotic disturbances modify the conditions in which these supposed equilibria developed, especially when new disturbances are exotic in the sense that they differ in magnitude and quality from natural regimes of disturbance or sources of variability (Sousa 1984). Such new disturbances can thus push communities away from normal community attractors. Thus, populations in a system with multiple community states will shift to new levels and persist there after a perturbation of adequate severity, or exotic enough character. The salient point is that if multiple persistent states exist, communities might not recover to a previous state after stressors are alleviated, but rather remain in an alternative basin of attraction (e.g., Krebs 2001, p. 509).

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The detection of multiple persistent states has been constrained by inherent difficulties in conducting ecological studies at appropriate, i.e., broad enough, scales in time or space (Connell and Sousa 1983, Petraitis and Latham 1999). Nevertheless, some indications of multiple community states have recently emerged. Examples from non-marine systems include lakes (Blindow et al. 1993, Scheffer et al. 1993, Moss et al. 1996, Romo et al. 1996, Scheffer et al. 1997, Weisner et al. 1997, Bachmann et al. 1999), streams (Strange et al. 1993), rangelands (Walker et al. 1981, Laycock 1991, Perrings and Walker 1997), deer and forest systems (Stromayer and Warren 1997), savannah woodlands (Dublin et al. 1990), sand dunes (Adema et al. 2002), laboratory mesocosms of phytoplanktors and aquatic crustaceans (Drake et al. 1993), and yeast cultures (Zamamiri et al. 2001). Furthermore, empirically-based models indicate the potential for multiple stable states in settings that include Everglade swamps (Dong et al. 2002), rangelands (Noy-Meir 1975, Westoby et al. 1989, Laycock 1991, Lockwood and Lockwood 1993), island systems (Sinclair et al. 1998, Ward and Thornton 1998), a butterfly metapopulation (Boughton 1999), and grasslands/woodlands (Fuhlendorf et al. 1996).

Evidence of multiple persistent states has likewise emerged from marine settings such as the temperate rocky intertidal (Barkai and McQuaid 1988, Petraitis and Dudgeon 1999, Dudgeon and Petraitis 2001), the sub-tropical rocky intertidal (Barry 1989), temperate hard bottoms (Elner and Vadas 1990), coral reefs (Hatcher 1984, Knowlton 1992, McManus et al. 2000), and marine soft bottoms (Herman et al. 2001, van de Koppel et al. 2001). Several notable reviews address multiple stable states (Connell and Sousa 1983, Done 1992, Knowlton 1992, Carpenter 2000, Muradian 2001, Scheffer et al. 2001).

Sutherland (1974) concluded that, "…multiple stable points are an undeniable reality in space and time…," because history (timing of disturbance) could determine alternate communities of marine fouling invertebrates, which then persist. He also pointed out that in addition to different stable points for an intact community, alternate community states can take the form of 'non-trivial boundary points' in which one or some species are removed or missing from the system. That is to say, the removal of a strongly interacting species can lead to a system that becomes 'stuck' at a 'boundary point' away from the previous 'equilibrium point' or 'attractor' as illustrated in the following description.

The alternation of kelp forest and urchin barren communities along rocky coastlines of the northeast Pacific Ocean is a classic marine example of alternative states that are persistent (Estes and Palmisano 1974, Dayton 1975, Estes et al. 1978, Simenstad et al. 1978, Estes and Duggins 1995, Konar and Estes 2003). Removal of sea otters (*Enhydra lutris*) leads to replacement of kelp forests with urchin barrens because otters normally control these voracious grazers of canopy-forming macrophytes. Effects cascade throughout the system because kelp canopies and understories provide production and biogenic habitat structure for a broad suite of organisms. This shift occurs in kelp forests where the otter-mediated trophic cascade is not naturally dampened by persistent wave disturbance or other factors (Foster 1990, Kvitek et al. 1998, Konar 2000). Rather than being an *alternative stable point* for an intact community, however,

the urchin barrens presumably represent a *non-trivial boundary point* of the system's global equilibrium (Sutherland 1974); i.e., the system is stable and very different from a kelp forest at this boundary point because one or more strongly interacting species is missing. By definition then, non-trivial boundary points are achieved whenever *keystone* species (Paine 1969, Power et al. 1996) are removed. In this classic example, we have two alternative states that are stable, but only because of extrinsic forces that occasionally remove the keystone predator. Thus, the system exhibits *alternative persistent states*, but does not intrinsically manifest the maintenance of *alternative stable states*. Similar examples in other kelp forests are described by Steneck et al. (2002).

Evidence of (intrinsic) alternative stable states must consist of the testable or observable attributes of *hysteresis*, which is a disparity between the levels of stressors that cause sudden (catastrophic) forward and backwards shifts of an observed state, or state variable (Figure 1-1). In hysteretic systems, the alleviation of a given stressor will fail to restore the community to the previous state until the stressor is reduced to somewhat lower levels than those that caused the catastrophic shift to the degraded state, and sometimes much lower levels. The observation of non-linear or catastrophic shifts indicates resistance (or persistence) of the alternative community states. Such resistance implies reinforcing feedbacks of a given community state and thus some degree of stability. Related attributes can be examined in terms of space or time rather than level of stressor(s). Thus, observations of spatially distinct boundaries of community types along smooth environmental gradients, or observations of sudden changes, indicates the potential for hysteresis, or alternative stable states.

Catastrophe theory, initiated by Thom (1972) and also described by Zeeman (1976) and Saunders (1980) for both biological and social systems, goes parallel to the theory of alternative community states in the sense that catastrophes are the sudden shifts to a radically different community state. A catastrophic state-and-threshold model developed for rangeland dynamics (Laycock 1991) led Lockwood and Lockwood (1993) to suggest that catastrophe theory could unify competing theoretical frameworks (i.e., continuous change versus discontinuous change models) for understanding rangeland dynamics. The first four of these authors' five essential symptoms of catastrophe systems match our conceptual model of multiple stable states (Figure 1-1):

1. "Modality (distinct conditions or states of existence);
2. Inaccessibility (conditions which are very unstable);
3. Sudden changes (relatively rapid movement between states);
4. Hysteresis (processes associated with degradation or recovery are not readily reversible by simply inverting the sequence of events); and
5. Divergence (relatively small changes in initial conditions can result in dramatically different outcomes with time)."

Their fifth symptom is best illustrated by imagining a third axis on Figure 1-1 projecting out the back of the page. We can also imagine that differing environmental conditions along this hypothetical third

axis changes the response curve to a more linear shape. The result is a *cusp* in the dynamical landscape (Zeeman 1976). A resulting property of this cusp landscape is that very slight changes on such a landscape can cause dramatically different outcomes, as when a hiker misses a switchback while descending a steep trail.
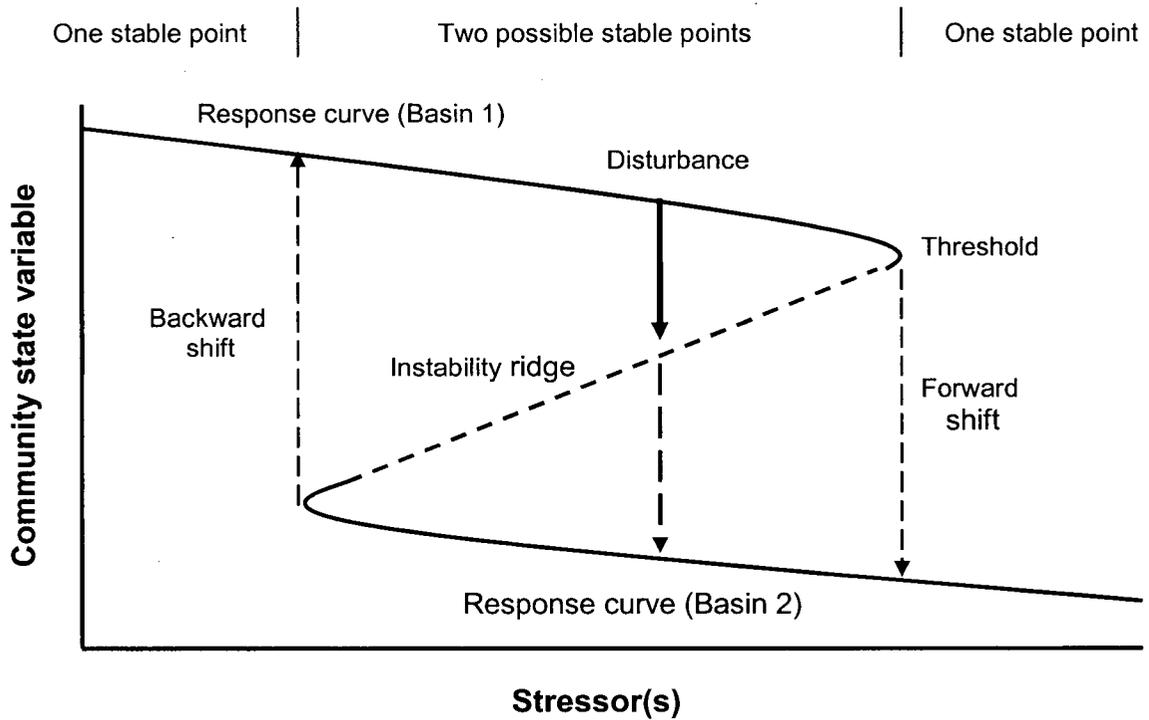
Figure 1-1. Response curve of a community that exhibits hysteresis. Theory suggests that response curves of community state variables sometimes fold back underneath themselves to form two possible equilibrium points at levels of stress within a certain range. A community's resilience, or 'stability,' keeps it within a basin of attraction (Basin 1) until a threshold of stress is reached and a catastrophic shift occurs, or until a disturbance of adequate severity or character can force the system beyond the boundary of instability to an alternative basin of attraction (Basin 2). A considerable reduction of the stressor might be required to restore the system to the previous realm (Basin 1). Real systems contain multiple stressors with different shapes of response curves. Thus, multiple basins of attraction on a far more complex dynamical landscape are possible in real systems.

Rigorous criteria for evaluating claims of multiple stable states were developed by Connell and Sousa (1983), who found no compelling evidence of the phenomenon in a number of empirical studies of the time. They found three classes of shortcomings: (1) differing physical environments in the different alternate states, (2) persistence of alternate states only when artificial controls are maintained, and (3) inadequate evidence of stability due, e.g., to inappropriate scales. However, Peterson (1984) argued that differences in physical environments between alternate stable states could be biogenic, and thus intrinsic to the community, and that such modifications were reinforcing feedbacks and would be a likely mechanism for the maintenance of multiple stable states. He also argued that their criteria for stability were too strict because persistence and self-replication of patches indicates stability. Sousa and Connell

(1985) agreed with "Peterson's feedback mechanism," but they disagreed that their criteria for stability were too strict.

Scheffer et al. (2001) seemed to echo these debates when they concluded, "...case studies [can] suggest shifts between alternative stable states...[but] proof of multiplicity of stable states is usually far from trivial." They suggest that observations of non-linear shifts and demonstrations of positive feedback mechanisms are, by themselves, insufficient evidence to demonstrate the existence of alternate stable states. They conclude that, "...the strongest cases for the existence of alternate stable states are based on combinations of approaches." The present study was guided by this 'broad evidence' principle.

Six types of evidence were chosen for evaluating apparent shifts to alternative persistent states (no order of evidence priority is implied):

1. Dynamic simulations showing plausibility of shifts;
2. Reinforcing feedback mechanisms that are intrinsic to a given community state;
3. Abrupt interfaces or shifts between alternative community states (in time or space);
4. Repeated shifts;
5. Persistence of a given state beyond one complete population turnover;
6. Discontinuity between forward and backwards shifts along an axis of stress (hysteresis).

All these types of evidence require some degree of empirical information. The present study was focused on the first type of evidence, but the existence of other evidence became apparent to varying extents as the case studies unfolded. Some information was collected directly and some was distilled from available literature. I examined four apparent marine community shifts that were indicated from exploratory-level observations and analyses. These continental shelf examples range from tropical to sub-polar settings.

1. The appearance of 'anemone barrens' on previously diverse shallow reefs in the Galápagos;
2. A possible alternative community state following the catastrophic *Exxon Valdez* Oil Spill;
3. A possible benthic to pelagic shift in West Florida Shelf community organization;
4. A shift from corals to ephemeral algae on polluted Indonesian reefs.

After assembling the types of evidence needed to evaluate the apparent shifts, and the possibility of alternative stable states, my general approach was to evaluate the four examples using different combinations of whole-system trophic modeling, field sampling, and observation to address as many of the types of evidence as feasible within the scope of the current study. Different combinations of evidence were evaluated according to the unique constraints of each system. A related objective was to explore potential explanations (i.e., mechanisms) for the existence of alternative persistent states in these marine communities. An underlying pre-supposition of this investigation was that explanations for the existence of alternative community states are likely to emerge from the marriage of equilibrium and non-equilibrium theoretical views of community organization (e.g., Okey 2003).

Scheffer et al. (2001) suggested that physical forces are the primary the cause of hysteresis in ocean ecosystems, while both physical and biotic factors explain hysteresis in coral reef systems. The present study indicates that combinations of physical and biotic forces cause the apparent community shifts in *at least* three of the four marine communities examined herein: The replacement of a diverse reef community by 'anemone barrens' could have been initiated by recent strengthening of El Niño events, but the resulting alternative community state appears to be maintained by positive biological feedbacks (Chapters 2 and 3); A search for keystones in Prince William Sound provides a general approach that provides insights into how communities can shift (Chapter 4); Simulated alternate community states in Prince William Sound, Alaska indicate that the *trophic character* of disturbances may rival their magnitude and severity as shapers of communities, and that strictly biotic forces can maintain a radically changed system (Chapter 5); Simulations of seafloor shading by plankton blooms over the West Florida Shelf indicate the potential for shading to cause broad shifts of continental shelf biological communities due to benthic to pelagic shifts in energy flow patterns (Chapter 6); Finally, sedimentation or other types of pollution appear to have influenced shifts in the spatial and temporal patterns of coral reef flora and fauna in South Sulawesi, Indonesia, although modifications of fish communities might have shaped those apparent community shifts as well (Chapter 7).

Mounting evidence that marine ecological systems are degraded and continuing to lose their biotic integrity has caused growing concern throughout the world (Vitousek et al. 1997, Jackson et al. 2001). This concern is particularly focused on continental shelf systems in which primary and secondary production is very high (Smith 1981, Duggins et al. 1989, Vetter 1995), and from which large quantities of food are collected by humans. A variety of human activities influence the organization of biological communities on, and overlying, continental shelves. Fisheries and various types of pollution are two conspicuous agents of change, or disturbance, in these systems (Goni 1998, Pauly et al. 1998a, Cloern 2001), but climatic (i.e., oceanographic) changes on various scales are also known to have profound effects on continental shelf biota, and marine biota in general (e.g., Glynn 1990, Anderson and Piatt 1999, Smith et al. 1999).

The general goal of this dissertation is to scrutinize mechanisms by which human activities might fundamentally alter the natural biological communities of some continental shelves, and whether these changed states might persist within in local basins of attraction. Each of the case study examples include predicted or observed shifts in community organization and some preliminary attempts to scrutinize the natural and anthropogenic variables in order to explain the indicated shifts.

A final introductory caveat must be understood when undertaking a study that fundamentally involves the notion of stability: it is unlikely that strict criteria for evaluating stability itself can be satisfied or even evaluated well in marine ecological settings. Indeed, natural populations or communities are variable at most, if not all, scales. The implications of finding compelling evidence of *alternate stable states* in natural communities would be far reaching because of the implications of irreversibility, as would the

implications of demonstrating *alternate persistent states*. Thus, my approach is to gather various types of evidence that might indicate alternative stable states, and otherwise to explore the possible reasons that some alternate community states appear persistent but are not indicated to be intrinsically and strictly stable.

Demonstrating persistence of a community within stable limit cycles, or as Connell and Sousa (1983) put it, "stochastic boundedness without equilibria," would also imply similar cautions for human interactions with ecosystems. Indeed, the *initial* management implications would be similar with degraded communities that have no stability, persistence, or boundedness whatsoever. Restoring community or ecosystem services in degraded ecosystems usually requires the reduction of anthropogenic stressors or disturbance, whether or not the systems exhibit alternate domains of attraction or stability. Those systems that do exhibit hysteresis and *alternate stable (or persistent) states* will ultimately require special attention in terms of policy and management attention, and in terms of basic research. The present research was conceived to help avert ecological and economic catastrophes that are, by definition, characteristic of systems that exhibit hysteresis. The work was undertaken because it is likely that such precautionary investments will prove crucial in averting catastrophes that will be difficult and expensive, if not impossible, to reverse.

Modeling and direct empirical studies

The power and usefulness of analytical tools for characterizing biological communities and exploring ecological mechanisms has increased tremendously in recent years. Network analysis of food webs and dynamic simulation capabilities, such as those used in the mass-balanced trophic modeling approach *Ecopath with Ecosim,* exemplify this advancement (Christensen and Pauly 1992, Walters et al. 1997, Walters et al. 1999, Pauly et al. 2000, Walters et al. 2000). Such whole system modeling approaches are built on empirically based characterizations of food webs, and sometimes represent knowledge distilled from major scientific programs, or from many decades of empirical research. These new approaches to ecosystem synthesis and analysis can help provide unprecedented insights into how nature works and how humans influence nature. Such insights can, nevertheless, be critically limited without comparisons to independent empirical studies. My general approach, thus, is to compare the predictions and mechanisms indicated by trophic modeling and simulation with independently derived empirical evidence to gauge whether the models and simulations are acceptable for their intended uses (sensu Rykiel 1996) and to judge the overall usefulness of resulting predictions and insights.

Ecopath with Ecosim methodology

Ecopath trophic models describe the state of energy flows in a food web. They are designed to include all biotic components of an ecosystem, and the most typical currency is biomass wet-weight (used here). Polovina (1984) developed *Ecopath* to study coral reefs at French Frigate Shoals. A variety of

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dynamic capabilities have since been added (e.g., Christensen and Pauly 1992, Walters et al. 1997, Walters et al. 1999, Christensen et al. 2000, Pauly et al. 2000). Scores of applications of *Ecopath with Ecosim* can be found at: http://www.ecopath.org/, along with the freely distributed software and documentation. Although the formulations and basic concepts are accessible in these venues, the general approach is summarized here.

The master equation (Equation 1-1) expresses the law of conservation of mass or energy and it indicates the basic input parameters. This equation balances a group's net production (terms to the left of the equal sign) with all sources of mortality, migration, or change for that group (terms to the right). More specifically, it says that the net production of a functional group equals the sum of (1) the total mass (or energy) removed by predators and fisheries, (2) the net biomass accumulation of the group, (3) the net migration of the group's biomass, and (4) the mass flowing to detritus.

Equation 1-1. $\qquad B_i \cdot (P/B)_i \cdot EE_i = Y_i + \Sigma\, B_j \cdot (Q/B)_j \cdot DC_{ji} + BA_i + NM_i$

B_i and B_j are biomasses of prey ($_i$) and predators ($_j$) respectively;

P/B_i is the production/biomass ratio, equivalent to total mortality (Z) in most circumstances (Allen 1971);

EE_i is the ecotrophic efficiency; the fraction of the total production of a group utilized in the system;

Y_i is the fisheries catch per unit area and time (i.e., $Y = F*B$);

Q/B_j is the food consumption per unit biomass of j;

DC_{ji} is the contribution of i to the diet of j;

BA_i is the biomass accumulation of i (positive or negative); and

NM_i is the net migration of I (emigration less immigration).

The implied thermodynamic constraints of this equation underscore the power of *Ecopath* models as a focal point for refinement of ecosystem information. The need to reconcile energy production and demand among components of the food web narrows the possible ranges of parameter estimates for particular groups. Inclusion of a biomass accumulation factor and migration factor in the general *Ecopath* equation distinguishes *Ecopath* modeling as an 'energy continuity' approach rather than a strictly 'steady state' approach. Conservation of energy (*continuity*) is assumed for every identified component of the ecosystem, and the whole system. This basic constraint enables representation of changes in populations (i.e., functional groups) when expressed in dynamic form.

Ecopath was considerably refined with the dynamic simulation routines *Ecosim* and *Ecospace* (see Walters et al. 1997, Walters et al. 1999, Pauly et al. 2000, Walters et al. 2000). In *Ecosim*, information in the static *Ecopath* file is re-expressed in a dynamic formulation (Equation 1-2).

Equation 1-2. $\qquad \dfrac{dB_i}{dt} = f(B_i) - M \cdot B_i - F_i \cdot B_i - \displaystyle\sum_{j=1}^{n} c_{ij}(B_i \cdot B_j)$

f (B_i) is a function of B_i if (i) is a primary producer, or f (B_i) = $g_i\Sigma\ c_{ji}$ (B_i, B_j) if (i) is a consumer;

g_i is the net growth efficiency;

$c_{ij}(B_i.B_j)$ is the function used to predict consumption rates from B_i to B_j.

Ecosim uses a function for c_{ij} derived from assuming possible spatial/behavioral limitations in predation rates (Equation 1-3):

Equation 1-3.
$$C_{ij} = \frac{v_{ij}a_{ij}B_iB_j}{v_{ij} + v'_{ij} + a_{ij}B_j}$$

C_{ij} is the trophic flow of biomass per time, between prey (i) and predator (j) pools;

B_i and B_j are the biomasses of prey and predators, respectively;

a_{ij} is the rate of effective search for prey i by predator j; and

v_{ij} and v'_{ij} are prey vulnerability parameters, with default setting $v_{ij} = v'_{ij}$.

Parameters v_{ij} and v'_{ij} represent prey vulnerabilities, or the rate of exchange of biomass between two prey behavioral states: a state in which all predators have full access to prey and a state in which prey have full refuge from predators. Prey use refugia in real ecosystems. Thus, not all prey biomass is vulnerable to predation at any given time, and predator-prey relationships are limited by behavioral and physical mechanisms. *Ecosim* is designed so that the user can specify the type of trophic control (Lotka-Volterra type vs. donor control) that mediates any interaction in the food web. Maximum consumption rates are hypothesized, and thus the rate of exchange of biomass (v_{ij}) that a predator normally exerts. For low predator biomass or high prey vulnerability (v_{ij}) the functional relationship approximates a mass-action flow, or Lotka-Volterra type interaction (c = aB_iB_j) implying a strong 'top-down' effect. For high predator biomass or low prey vulnerabilities the functional relationship approaches a donor-controlled (bottom-up) flow rate (c = $v_{ij}B_i$), so v_{ij} is the maximum possible instantaneous mortality rate that j can cause on i (see Walters et al. 1997).

Prey vulnerabilities can be specified by adjusting the proportion of prey in vulnerable and invulnerable states (pools) via adjustment of the v values, which are scaled such that pure Lotka-Volterra type control = 1 and pure donor control = 0. In the real world, this mixture of trophic control is mediated by temporal or spatial refugia, or by the relative primacy of physical and biotic forces in regulating communities, i.e., predator-prey interactions.

Although examples of biological communities with alternate stable states seem to be accumulating rapidly in the general ecological literature, compelling examples of truly alternate stable states in marine biological communities (wherein intrinsic mechanisms reinforce alternate states) are very rare (e.g., Barkai and McQuaid 1988). This is either because alternate stable states are truly rare in marine communities, or because the evidence required for demonstrating the existence of alternate stable states is

difficult to obtain from marine communities due to the unique constraints related to studying them. This dissertation is an examination of four marine communities, using empirically-based whole food web modelling approaches and empirical field studies, to explore the potential ability of particular mechanisms in shifting and maintaining alternate stable states. The results of these explorations are intended to be considered hypotheses that can be evaluated with iterations of experimentation (manipulative or "natural") and further simulations.

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CHAPTER 2. Trophic model of a Galápagos rocky reef with simulations of fishing impacts

ABSTRACT

A balanced trophic model of a Galápagos rocky reef system was constructed using *Ecopath* and *Ecosim*. The *Ecopath* approach allowed characterization of food web structure through integration of disparate ecosystem information derived from many years of study of Galápagos shallow-water rocky reefs. *Ecosim* and *Ecospace* routines enabled us to explore various hypotheses about system dynamics as well as potential solutions to conservation concerns about overfishing. A full series of functional group removal simulations resulted in estimations of trophic interaction strengths and 'keystone' potentials for the all the living functional groups in the 43-box model (the detritus group is non-living). Relative interaction strengths in a pristine unfished system are likely to be quite different from interaction strengths indicated by this present-day model. At present, humans extract food from very low trophic levels (mean trophic level = 2.3) in Galápagos rocky reef systems because sea cucumbers and detritivorous mullets comprised 71% and 15% respectively of the total fisheries catch. Catch rates of sea cucumbers (*Stichopus fuscus;* referred to here as '*pepinos*') are shown to be unsustainable, and the population should be declining rapidly. The exclusion of fishing from 23% of the total reef area, representing a hypothetical non-extractive zone, prevented the functional extinction of *pepinos* that the present analysis predicted to occur with no areas protected (given 1999-2000 capture rates). Even with 23% of the hypothetical area protected, *pepinos* were predicted to decline overall to a stable 36% of their current estimated biomass. *Pepino* biomass was predicted to increase to 8 times that of current levels if *pepino* fishing were stopped altogether.

INTRODUCTION

The Galápagos Archipelago lies in the equatorial eastern sector of the Pacific Ocean, about 1000 km west of the coast of Ecuador, South America (between 01°40′N-01°25′S and 89°15′W-92°00′W) (Figure 2-1). The archipelago consists of 13 large and 6 small islands, 42 islets, and numerous exposed rocks (Snell et al., 1995). These current islands represent the tops of relatively young volcanoes that rose from the sea between 1 and 3 million years ago, though submerged islands in the archipelago have been dated at 9 million years old, and islands might have been produced over this mantle hotspot for much longer (Christie et al., 1992). The islands rise from a relatively shallow (<200m) Galápagos Platform surrounded by deep waters (>1000 m).

The location of the Galápagos Archipelago, at the confluence of warm currents (26-29°C) from the north, cool waters (20-22 °C) from the southwest, and nutrient-rich upwelling waters from the west propagating eastward, has led to complex and poorly understood marine and coastal ecosystems (Houvenaghel, 1984; Wellington, 1984; James, 1991). Between three and five major biogeographic units

have been proposed for the archipelago; however, the number of units and their boundaries still require clarification (Abbott, 1966; Harris, 1969; Jennings et al., 1994; Banks, 1999; Wellington et al., 2001). The largest regional mix of marine species occurs on the central Galápagos shelf, including the study area located around the island of Floreana (Figure 2-2). This area is characterized by a particularly diverse combination of warm- and cool-water biota (Witman and Smith, 2003).

Figure 2-1. Map of the Galápagos Islands showing the coastal use zoning scheme that has been in effect since 2000. Floreana Island is shown in the lower central part of the map. Wolf and Darwin Islands are not pictured; they are smaller and they lie to the NNW of the main islands.

The shallow water ecosystems around Floreana Island consist primarily of sloping lava fields interspersed with sandy pocket beaches, as do most of the coastal shores of the Galápagos. These beaches are composed of both biogenic material (white and brown sand mainly from corals and echinoid tests) and pulverized lava (black sand), while sporadic mangrove forests occur in sheltered inlets. Subtidal lava reefs surround all the Galápagos Islands, and they can be subdivided into categories that include bedrock, boulders, cobbles, and sand (Figure 2-2).

Figure 2-2. A map of Floreana Island and the waypoint areas used to estimate proportions of habitat types around the island. The accompanying chart in the lower panel shows the estimated proportions of habitat types at each waypoint reference area. These relative proportions were used to estimating biomasses of various functional groups in the modeled area.

Cool nutrient-rich waters on the Galápagos platform support high biomasses of small pelagic fishes such as sardines, thread-herrings, anchovies, mackerel, scads, halfbeaks and lantern fishes, which in turn feed substantial populations of top predators such as sharks, tuna, wahoo, billfishes, jacks, barracuda, dolphinfish, seabirds and toothed cetaceans (Feldman, 1985, 1986), many of which visit and feed actively on Galápagos rocky reef habitats.

This productive pelagic system surrounds and interfaces with the benthic rocky reef habitats fringing each island of the Galápagos Archipelago, and plankton carried by oceanic currents is a major source of primary production on the reefs. Planktivorous reef fishes inhabit the boulder-strewn reef and feed in the water column. They include *gringo* (*Paranthias colonus*)—the most abundant Galápagos reef-dwelling fish species. In addition to sustaining large numbers of pelagic and reef-associated fishes and seabirds, plankton supports a high biomass of suspension and filter feeding invertebrates. These include the barnacle *Megabalanus peninsularis,* the sessile mollusc *Hipponix* sp., brittle stars, and the black and stony corals *Antipathes* spp. and *Pavona* spp.

Benthic primary production is the other major source of primary production in this system. Galápagos rocky reefs in some areas include an algal turf and foliose macroalgae that, along with diatoms and other microphytobenthos, provides a large bulk of the energy supporting high biomasses of whole suites of invertebrates, fishes, and other vertebrates, including the marine iguana (*Amblyrhynchus cristatus*)—a unique sea-going lizard and active marine grazer that symbolizes the system's strong dependence on benthic primary production.

Three highly abundant species of sea urchins (*Tripneustes depressus, Eucidaris thouarsii,* and *Lytechinus semituberculatus*) exert intense grazing pressure on benthic primary producers (and corals), often forming extensive urchin barrens (Breen and Mann, 1976; Ayling, 1981; Himmelman and Lavergne, 1985). Herbivorous fish species include damselfish, surgeonfish and parrotfish. Herbivorous green sea turtles (*Chelonia mydas*) are also present, sometimes in relatively high numbers. Several species of sea cucumbers (holothurians, Spanish *pepino del mar*), which are traditionally categorized as 'detritivores' but likely consume meio-fauna and flora, are also very widespread and abundant, notably the slow growing *Stichopus fuscus,* hereafter *pepino*.

Omnivorous reef fishes, including chubs, butterflyfish, and damselfish, consume algae and small benthic invertebrates. Small benthic invertebrate-eating fishes include grunts, small wrasses, and an angelfish. Predatory invertebrates include whelks, conch, spiny lobsters, and crabs. Upper trophic levels feature many species of piscivorous reef fishes such as groupers and snappers. Large benthic invertebrates are consumed by large wrasses and triggerfish. Other high-level predators include octopus, the Galápagos sea lion (*Zalophus wollebaeki*), and unique seabirds such as the Galápagos penguin (*Spheniscus mendiculus*) and the flightless cormorant (*Nannopterum harrisi*). A variety of shark species is present including the Galápagos shark (*Carcharhinus galapagensis*), the white-tipped reefshark (*Triaenodon obesus*), other reef sharks, and species that interface with pelagic systems.

Small-scale fisheries feed tourists and residents, but most of the catches in the archipelago (high-value sea cucumbers and lobsters) are exported to lucrative foreign markets (e.g., Japan, Taiwan, U.S.). As an example, in 1999 and 2000, local fishers were paid about US$ 0.90 for every landed *pepino* (*Stichopus fuscus*), although the price fell to $0.55 in 2001 (PIMPP, Programa de Investigación y Monitoreo Pesquero Participativo, 2001).

The international fisheries markets drive the growing population of local fishers to deplete exploitable marine invertebrates (as well as illegally captured sharks), potentially shifting the structure of these ecosystems directly and indirectly, and undermining their sustainability (Constant, 1993; Camhi, 1995; Merlen, 1995). In addition, water quality is jeopardized around urban areas, and overflows from rudimentary septic tanks increase nutrient levels near the expanding population centers. Large and small spills occur occasionally when fuel is brought to the islands for delivery to tourist vessels, and visitors directly stress coastal biota. A Special Law of Galápagos was enacted in 1998 to improve marine reserve management and enforcement, but these stresses nevertheless continue. Finally, oceanographic and climatic changes, including the El Niño/La Niña oscillations and the potential for global climate change can profoundly influence the structure of Galápagos marine communities (e.g., Colinvaux, 1972; Houvenaghel, 1984; Glynn, 1988; Bost and Le Maho, 1993).

A provisional coastal use-zoning plan has been in place in the archipelago since 2000 (Bustamante et al., 2002; see Figure 2-1). In this scheme, fully-protected 'no-take' areas, i.e., areas where no entry or human uses other than scientific research are allowed, protect 8% of the island's coastlines (zones shaded in black in Figure 2-1); non-extractive use areas, i.e., areas where tourism, recreation and education are allowed, cover 10% of coastlines (zones shaded in dark grey in Figure1); regulated extractive uses, i.e., recreational and fisheries uses, are allowed along 77% of the coastlines (zones shaded in light grey in Figure 2-1); and special zones nearby the inhabited port areas, i.e., areas where the local stakeholders will define their status through a participatory process, cover the remaining 5% of the island's coastline (zones shaded in thickened light grey in Figure1). This zoning plan provides an opportunity to protect small and replicated portions of Galápagos coastlines, and to evaluate the potential consequences and benefits of small and large marine protected areas (Branch et al., 2002).

Although some violations of this scheme occur, fishing in the 'fisheries exclusion' zones (about one fifth of the total coastlines) is lower than in the zones open to fishing. The Charles Darwin Research Station has an ongoing marine ecological monitoring program designed to gather baseline information about these unique marine systems and to reveal any biological changes that might be related to the zoning and associated changes in human use patterns throughout the islands. The rocky reefs around Floreana Island are divided among fisheries, tourism, and fully protected zones.

The present modelling exercise complements this monitoring program in a way that allows refinement of knowledge and management through an iterative approach to learning and an adaptive (or experimental) approach to conservation and fisheries management. The purpose of the model is to

provide accessible 'views' of the whole system and to predict how it might respond to changes in human actions or other stresses. The model may also provide insights into the underlying ecological mechanisms operating in the system and explore possible solutions to conservation problems. In particular, this continually updated ecological synthesis can be used to generate hypotheses about the dynamics of this special system and to address questions such as:

- Which functional groups currently exert large effects on the system?

- What are the potential ecosystem consequences of removing particular species from the system?

- Are any species in this system currently being fished at unsustainable levels?

- To what extent will fisheries exclusion zones alleviate declines of overfished species or restore previous abundances?

METHODS

Modelling tools: *Ecopath with Ecosim*

Ecopath trophic models are mass-balance models, or more accurately mass-continuity models, that account for the energy flows in a food web. The *Ecosim* routine expresses the mass balance constraint in a dynamic context to explore the direct and indirect ecological effects of fisheries, perturbations, and even physical forces. For example, the relative strengths of trophic interactions among species can be estimated, and the effects of changes in a particular fishery on various biotic components can be simulated. These models are continually refined and evaluated in an iterative process. See Chapter 1 for a summary of the formulation and basic approach of *Ecopath* and *Ecosim* (also see Polovina, 1984; Christensen and Pauly, 1992; Walters et al., 1997; Walters et al., 1999; Christensen et al., 2000; Pauly et al., 2000; Walters et al., 2000; Oritz and Wolff, 2002; Froese and Pauly 2003 [http://www.fishbase.org]; Christensen and Walters, 2004).

In *Ecospace*, the simulated interactions among organisms occur in a spatially explicit, and habitat-based, context rather than in a single 'reaction vat' (Walters et al., 1999). *Ecosim*, because of simulated refugia from predation, also does not work as a simple vat. The area of interest is represented by a spatial mosaic of cells that can be designated as land and a variable number of marine habitats. For each functional group, these habitats are specified as preferred or not preferred. The dynamic redistribution of organisms in the system is based on user-specified base dispersal rates, relative movement rates in bad habitat, relative feeding rates in bad habitat, and the constantly changing densities of predator and prey groups with which a given functional group interacts. The instantaneous dispersal rates across cell boundaries are determined by the specified base dispersal rate, the habitat type in the source cell, and the responses of functional groups to predation risk and feeding conditions in the source cell (Walters et al., 1999). Spatial variations in primary production and current advection fields can be specified, as can spatially relative fishing costs (i.e., effort) and the spatial distribution of marine

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protected areas (i.e., fisheries exclusion zones). Grid number and sizes can be adjusted or scaled appropriately.

Delineating Floreana rocky reefs

The region characterized in this balanced trophic model includes reefs shallower than 20-m depth along the eastern, northern and western coasts of the Floreana Island – a relatively homogeneous area that is also representative of the central Galápagos shelf region, which includes the large islands of Santiago, Santa Cruz, Santa Fé, San Cristóbal and northern Española, and the eastern coast of Isabela—the largest of the islands (Figure 2-1). Because the southern coast of Floreana is much more exposed and influenced by cooler waters associated with the southern equatorial current and equatorial undercurrent, and has been little studied, that region was excluded from the model described here. Spatially, the exclusion represents an estimated 42% of the 20-m isobath (all strata) and 64% of the total rocky reef model area for the island. Reefs in water depths >20 m, and soft-sediment habitat types, were also excluded from the current model. Exclusion of soft-sediment habitats from this model might have unrealistically simplified the model because potentially important trophic interactions between soft bottoms and overlying or adjacent reefs would be ignored.

A combination of site aerial photography and chart bathymetric data, geo-referenced within an ArcView GIS system, was used to estimate the spatial extent of the 20-m isobath from the coast. Spatial estimations were further weighted against a modifier for estimated habitat coverage (see Figure 2-2). A series of 67 observations of substrate composition was taken around the coastal perimeter of the island at approximately 500-m intervals. The spatial localization of each observation was taken as a polygonal area roughly equidistant between adjacent sampling points extending from the coast to the reported 20-m isobath. Rocky and bedrock strata estimations were grouped as representative of the model space and weighted by localized area to give a final estimation of the entire model space (Table 2-1).

Table 2-1. Model space estimations within the 0-20 m isobath

Area	Total area (km^2)	Weighted habitat modifier (%)	Corrected area (km^2)
0-20 m isobath	28.38	62.2	17.65
Southerly exclusion	11.91	94.2	11.22
Modelled rocky reef	16.47	39.1	6.44

Defining functional groups

The 43 functional groups in the Floreana Island rocky reef model were the product of a collaborative process that defined the system. A number of experts, including the present authors, participated in several iterations of the list of functional groups. All the species in the system were aggregated into these functional groups based on similarity of ecological role, defined by similarities in diet, production and

consumption rates, life history, and habitat associations, but also sometimes on value-driven criteria such as commercial status or importance for tourism.

In the final iteration, benthic invertebrates were represented by 19 functional groups; others were fishes, 13; primary producers, 3; zooplankton, 2; marine mammals, 2; marine reptiles, 2; birds, 1; and detritus, 1. Because of the nature of the Galápagos archipelago, i.e., a relatively small and narrow rocky platform surrounded by deep open-ocean waters, the model includes discrete, but interconnected, benthic-based and pelagic-based subsystems.

Estimating Ecopath input parameters

Biomass estimates were derived using methods specific to each functional group. Production/biomass (P/B), consumption/biomass (Q/B), and diet compositions for each species were derived mostly from the scientific literature and with the help of FishBase (Froese and Pauly 2003 [http://www.fishbase.org]). P/B was usually estimated by assuming that it equals total mortality (Z) under the assumption of population equilibrium (Allen, 1971). Q/B was most commonly estimated from the empirical relationship proposed by Palomares and Pauly (1999), and setting mean water temperatures at 22-25°C. Representative values for aggregated groups were derived as averages of species-specific estimates weighted by relative biomass (B) or consumption (Q) as appropriate.

Input biomass estimates of benthic and demersal fish groups and large invertebrates (> 20 mm) were obtained directly from site-specific surveys of Floreana rocky reefs. These middle trophic level groups represent the strong core of the model, and confidence in these estimates is expected to increase further as the ecological monitoring program progresses. Site-specific data were also available for pelagic fish groups, birds, turtles, sharks, and marine mammals, but resulting biomass estimates (or estimates of dietary proportions originating from the rocky reef) are more uncertain for these more mobile groups because of the haphazard nature of the existing sightings data, or knowledge of foraging patterns. Biomasses of macro-invertebrates (0.5 to 20 mm) and lower trophic level groups were estimated by the model, but empirically-based estimates of primary production of benthic macroalgae and phytoplankton were used to structure the base of the food web.

Missing input parameters were taken from the literature (e.g., production/biomass and consumption/biomass ratios, and diet composition) and adjusted proportionally as weighted estimates for all species in a functional group whenever possible (e.g., most of the fish groups). Diet compositions were the least certain type of input parameter because of the paucity of site-specific dietary data. Examination of the knowledge gaps revealed during model construction enabled adaptive refinements to strategies for the continuing monitoring program.

Primary producers

Mean phytoplankton standing stock was estimated using multispectral image analysis software to extract SeaWiFS chlorophyll concentration estimates from geo-referenced 1.1 km^2-resolution localities over the eight target sites group averaged to the surrounding 10 km^2 at each point, accounting for coastal overlap and cloud cover. Data were collated over the year 2000 as available from local area coverage from the NASA-PODAAC distributed data archive. Time series plots at target sites were constructed to examine seasonal and geographic variability within the model area, and averages compared against *in situ* samples collected during trips on 26 May 2001 and 18 June 2001. An averaged value of 12 t·km^{-2} was derived from an estimation of 0.64 mgChl m^{-3} following conversion factors for phytoplankton standing stock from Durbin and Durbin (1998), Arreguín-Sánchez et al. (1993), and Pauly et al. (1993a). Macroalgal biomass on the rocky reef at Floreana Island was estimated based on measured standing wet biomass at two sites on Santa Cruz Island, and based on subtidal observations. Microphytobenthos biomass was left to be estimated by the *Ecopath* routine. SeaWiFS data estimate only chlorophyll concentration within a few centimeters of the surface, and macroalgal estimates were very rough in terms of extrapolation to broader reef areas.

Invertebrate groups

Biomass estimates for 10 of the 15 mega-invertebrate (>20 mm) groups in the model were derived from visual line transect surveys at 9 Floreana rocky reef sites sampled during 2000 and again in 2001. Twenty-five species were aggregated into these 10 sampled functional groups. At each site, a 50-m transect line was laid down along two selected depth contours, and the number of large invertebrates within one meter of each side of the line recorded as the diver moved along one side and then back along the other side of the transect. The wet masses of individuals of most mega-invertebrate species from Floreana were also measured to estimate mean wet mass. In a few cases, the maximum length (e.g., arm radius for seastars, shell for gastropods, or body for sea cucumbers) or diameters (for sea urchins) of up to 30 individuals of each invertebrate species were recorded *in situ* using a measuring tape for later estimation of mass using length-weight relationships. Mean densities were multiplied by mean weights to obtain biomass density estimations, and skeletal carbonate weights were subtracted as appropriate.

Fish groups

Biomass estimates for the 13 fish groups were derived from visual line transect surveys at 9 rocky reef sites around the Floreana coastline during 2000 and 2001. At each site, divers swam at a constant speed on each side of 50-m transect lines placed along the 6- and 15-m isobaths, while recording the numbers and sizes of fish species observed within a 500 m^2 area (10 m total swathe) and 5 m above the transect line. The density of each size class for each species was transformed into biomass/area, using length-weight relationships in FishBase (www.fishbase.org). Conversion factors for related proxy species were

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used when no conversion factor was available for a species. The biomass/area values of the size classes were summed for a total species biomass and these were summed for total functional group biomass estimates.

Higher vertebrates (sea lions, sharks, turtles, iguanas)

Biomass estimates for sharks and turtles were the products of the number of diver sightings and average mass of individuals divided by the approximate area surveyed per dive. A sightings correction factor based on the discrepancy between diver-observed sea lion biomass and sea lion biomass based on counts on rookeries was then applied to the shark and turtle visual estimates to calculate rough error-corrected biomass estimates. A corrected biomass estimate for sea lions that feed on reefs was derived by multiplying the haul-out survey biomass estimate by the proportion of the diet from reefs. The biomass estimate for marine iguanas was based on surveys on Floreana Island, and is likely an underestimate for most of the north side of the island. However, a correction factor for such a density discrepancy is not yet developed, and the density presently used is likely more representative of the archipelago in general than it is of the north side of the island.

Fisheries information

Fisheries catch and effort data for the Galápagos Archipelago have been collected since 1997 through a daily monitoring program that includes recordings of the landed catch, effort, and distributions of finfish, sea cucumbers and lobsters. Data are collected at the three main ports in Galápagos at the islands Santa Cruz, San Cristóbal, Isabela, and occasionally in Floreana. For the calculation of the average annual catch rate for these species we divided the catches that are extracted from the Floreana area by an estimate of the modelled area. Catches were calculated for the monitored species with use of conversion factors that describe the relation between the state of the product at landing (dried, salted, gutted, etc.) and its actual fresh weight. *Pepino* catch data in numbers of individuals were converted into fresh weight with the assumption that the average length is 21.3 cm in the population around Floreana (Anon., 2001). Given the length-weight relationship for *pepino* estimated in 1999 (n = 4363, R^2 = 0.355) this length corresponds to a 333 g fresh weight. The fresh weights were summed per functional group and an average was calculated for the period under investigation. The average monitored finfish landings were multiplied with a raising factor to convert the monitored landings into an estimate of the total landings. This conversion factor (1.66) expresses the 34% effectiveness of the monitoring program and was derived from Espinoza et al. (2001). Even with this conversion factor, some illegal fishing removals might have been missed. No conversion factor was used for invertebrate catches because these are fully covered (100% monitored) through a system of export certificates. Landings per km^2 were calculated with a fixed area of 16.47 km^2 because fishing activities around the total coast of Floreana were taken into account. The resulting estimates of fishing density are applicable to the more limited area that was modelled.

The majority of the missing parameters left to be estimated by the *Ecopath* software were ecotrophic efficiency (EE) values, as empirically based estimates were available for most basic parameters in the system. However, *Ecopath* estimated 10 missing biomass values by specifying a reasonable EE value and solving the *Ecopath* master equation. One missing P/B value was estimated by additionally specifying a reasonable rate of production to consumption (P/Q). Trophic levels were calculated as the biomass weighted average of food items plus 1, and the omnivory index was the variance of the trophic levels of the prey groups (Pauly et al., 1993b). The basic flows in the system and other indices were also summarized while characterizing the system (see Christensen and Pauly, 1992; Christensen et al., 2000).

Using *Ecosim,* a full series of 'removal' simulations was conducted to evaluate the relative interaction strength of each species in the Floreana rocky reef food web. Additional mortality was imposed on one *pepino* group so that it declined to zero by year 10 of the 30-year simulation. System-wide changes in biomasses resulting from the removal of a species were recorded. Mortality rates were then reset to initial levels before the next removal simulation. An interaction strength index (ISI), defined as the sum of all resulting relative changes in the system (the total absolute relative changes in all but the removed group), was used to derive a 'keystone' index, which is the ISI divided by the relative biomass of the respective affecting groups (see Power et al., 1996, for definition of keystone species).

Fisheries were analyzed in terms of the proportion of the total catch in the system contributed by each functional group as well as the proportion of each group's total mortality accounted for by fisheries. An analysis of the directed *pepino* fishery was conducted because it stood out as unsustainable. Biomasses and catches were plotted as a function of capture rate (annual catch/biomass) as predicted by surplus production models in hypothetical equilibrium conditions.

A simple *Ecospace* simulation was used to explore the potential effects of fishery exclusion zones on *pepinos* in the Galápagos Islands. The Floreana rocky reef model was re-expressed spatially using a mosaic of cells scaled to simulate Floreana Island, but the simulation was set up as a hypothetical island within the Galápagos archipelago. The area of rocky reef was exaggerated on the *Ecospace* base map for diagrammatic purposes (the reefs in the spatial simulation are made much wider than the actual narrow band around most Galápagos Islands; Figure 2-2). The hypothetical no-fishing zone covers approximately 23% of the coastline in the *Ecospace* base map reflecting the current proportion of protected coastline in the Galápagos Archipelago (18%) plus the special port areas (5%) in which local communities specify uses (Figure 2-5). This would tend to provide overly optimistic predictions of population responses to protection since local communities choose fishing. This hypothetical zone takes the form of a single no-fishing zone at one island. The simulation assumes a base dispersal rate of 5 km year^{-1} for the *pepino* group, corresponding to 14 m per day. Additional simulations were performed to account for higher dispersal rates of *pepino* larvae.

RESULTS

The Floreana rocky reef food web model is characterized by very high biomasses of fishes and invertebrates (Table 2-2). The model is unique among *Ecopath* mass-balanced models in that the primary and secondary production needed to support such high biomasses are specified as a net 'immigration' of phytoplankton and zooplankton delivered to these reefs by oceanic currents, assuming that oceanic islands are plankton sinks. This results in a strong system heterotrophy, as indicated in the descriptive statistics (Table 2-3) and visible when examining a summary of system flows (Table 2-4). The diet composition matrix for the Floreana rocky reef model is presented in Appendix A.

The 10 groups with the highest estimated trophic interaction strengths (Table 2-2; see also Chapter 4 for index formulation) were (in decreasing order): pelagic predators, large benthic invertebrate-eating fishes, shrimps and small crabs, omnivorous reef fishes, benthic algae, microphytobenthos, small benthic invertebrate eaters, other herbivorous fishes, noncommercial reef predators, and herbivorous zooplankton. Sea lions and sharks ranked 12th and 15th, respectively. The 10 groups with the highest indicated 'keystone index' values (Table 2-2) were (in decreasing order): toothed cetaceans, birds, sharks, sea lions, octopus, *Hexaplex* gastropods, spiny lobsters, noncommercial reef predators, pelagic predators, and large benthic invertebrate eating fishes. Omnivorous reef fishes ranked 11th.

Specific results of the first of 43 functional group removal simulations are shown in Figure 2-3. Toothed cetaceans, sea lions, and noncommercial reef predators are predicted to increase when sharks are removed, thus causing decreases in *bacalao,* i.e., the grouper *Mycteroperca olfax*, other commercial reef fishes, and small benthic invertebrate-eating fishes through increased predation or competition, or both. Sea turtles, marine iguanas, large benthic invertebrate-eating fishes, and parrotfish are also predicted to increase when sharks are removed. Some small benthic invertebrates are predicted to increase, while large benthic invertebrates are predicted to decrease, and other trophic cascades are apparent.

The model also shows the mean trophic level of the fisheries catch to be particularly low (2.3; see Table 2-3). Humans fill an unusually low trophic position in the Galápagos because, for example, *pepinos* comprised 71% of the fisheries catch from Floreana Island during the late 1990s and detritivorous fishes (Mugilidae) comprised 15% (Table 2-5).

Pepinos declined in every simulation that included *status quo* fishing rates, because estimated overall mortalities from fisheries, predators, and senescence exceeded this group's estimated production for the entire range of input parameters reasonable for this species. The *pepino* fishery, as executed at 1999-2000 levels, accounted for 88% of the total mortality of this species.

The current capture rate far exceeds the optimum sustainable capture rate estimated by *Ecosim* (Figure 2-4) indicating highly unsustainable fishing pressure. On the other hand, six to eight-fold increases in *pepino* biomass were predicted when total fishing moratoriums were simulated.

Table 2-2. Basic parameters of the Ecopath model of the Floreana rocky reef, Galápagos

Group name	Trophic level	OI	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	ISI	% of biomass	Keystone Index
Sharks	4.4	**0.40**	0.75	0.24	4.90	**0.030**	8.6	0.03	286.7
Toothed cetaceans	4.4	**0.50**	0.02	0.08	14.60	**0.000**	1.6	0.001	1600.0
Bacalao grouper	4.2	**0.34**	7.14	0.35	4.50	**0.649**	1.0	0.27	3.6
Birds	4.1	**0.32**	0.01	5.40	80.00	**0.340**	0.2	0.0004	575.0
Sea lions	4.0	**1.27**	5.68	0.07	25.55	**0.864**	9.4	0.22	42.8
Pelagic predators	3.9	**1.19**	30.00	0.42	4.35	**0.282**	22.4	1.14	19.6
Non-commercial reef predators	3.8	**0.23**	14.86	1.03	11.07	**0.877**	11.5	0.57	20.2
Octopus	3.5	**0.10**	0.79	1.10	7.30	**0.511**	0.9	0.03	30.0
Pelagic planktivores	3.4	**0.15**	5.50	0.98	32.10	**0.353**	1.6	0.21	7.6
Other commercial reef predators	3.3	**0.16**	9.30	0.62	7.11	**0.557**	1.7	0.35	4.9
Large benthic invertebrate eaters	3.3	**0.06**	32.71	0.65	9.82	**0.658**	18.7	1.25	15.0
Planktivorous reef fish	3.3	**0.31**	281.13	1.50	45.07	**0.260**	7.0	10.73	0.7
Hexaplex gastropod	3.0	**0.02**	3.61	2.80	14.00	**0.667**	3.7	0.14	26.4
Small benthic invertebrate eaters	3.0	**0.31**	100.99	1.39	13.73	**0.569**	13.4	3.85	3.5
Carnivorous zooplankton	2.8	**0.52**	3.58	8.70	29.00	**0.475**	8.8	n/a [b]	n/a
Spiny lobsters	2.8	**0.26**	3.00	0.45	7.40	**0.650**	2.6	0.11	23.6
Slipper lobster	2.7	**0.39**	4.00	0.45	7.40	**0.722**	0.7	0.15	4.7
Omnivorous reef fishes	2.7	**0.29**	41.52	1.02	21.85	**0.896**	17.7	1.58	11.2
Shrimps and small crabs	2.6	**0.33**	**55.13**	3.60	20.45	0.950	18.0	2.10	8.6
Asteroids	2.5	**0.36**	10.49	0.49	3.24	**0.105**	0.4	0.40	1.0
Other herbivorous fish	2.4	**0.42**	200.60	0.88	25.83	**0.265**	13.4	7.66	1.7
Eucidaris urchin	2.2	**0.23**	104.43	1.40	2.81	**0.830**	8.4	3.99	2.1
Anemones	2.2	**0.26**	**79.24**	2.00	4.00	0.900	3.1	3.02	1.0
Worms and ophiuroids	2.2	**0.25**	**84.67**	4.14	61.60	0.950	10.3	3.23	3.2
Stony corals	2.2	**0.22**	**91.16**	1.09	15.00	0.900	2.6	3.48	0.7
Chitons	2.2	**0.29**	**2.85**	0.34	11.70	0.900	0.1	0.11	0.9
Detritivorous fish	2.1	**0.12**	**39.95**	**1.37**	13.70	0.095	0.6	1.52	0.4
Small gastropods	2.1	**0.11**	**188.05**	2.50	14.00	0.950	6.4	7.18	0.9
Sea turtles	2.1	**0.15**	3.02	0.15	3.50	**0.162**	0.2	0.12	1.7
Pepino sea cucumber	2.1	**0.07**	3.90	0.60	3.36	**0.972**	0.0 [b]	0.15	0.0 [b]
Other urchins	2.0	**0.01**	4.65	1.40	2.81	**0.755**	0.1	0.18	0.6
Parrotfishes	2.0	**0.00**	21.50	0.50	16.60	**0.627**	1.7	0.82	2.1
Marine iguana	2.0	**0.00**	0.80	0.11	15.00	**0.376**	0.1	0.03	3.3
Other sea cucumbers	2.0	**0.00**	3.55	0.60	3.36	**0.166**	0.1	0.14	0.7
Tripneustes urchin	2.0	**0.00**	48.74	1.40	9.71	**0.350**	3.9	1.86	2.1
Lytechinus urchin	2.0	**0.00**	8.72	1.40	2.81	**0.903**	0.5	0.33	1.5
Small crustaceans	2.0	**0.03**	**91.41**	9.00	125.50	0.950	0.5	3.49	0.1
Filter + suspension feeders	2.0	**0.08**	**367.39**	2.00	16.50	0.900	9.0	14.02	0.6
Herbivorous zooplankton	2.0	**0.08**	3.19	17.30	57.70	**0.656**	10.9	n/a [a]	n/a
Phytoplankton	1.0	**0.00**	12.00	70.00	-	**0.946**	3.7	n/a [a]	n/a
Microphytobenthos	1.0	**0.00**	**393.59**	23.70	-	0.990	16.1	15.02	1.1
Benthic algae	1.0	**0.00**	256.80	12.00	-	0.986	16.5	9.80	1.7
Detritus	1.0	**0.29**	500	-	-	0.499	n/a	n/a	n/a

Notes: Values in bold have been calculated by the *Ecopath* software; other values are empirically based inputs, or values that were adjusted from empirically based values during balancing. The omnivory index (OI) indicates dietary breadth; ecotrophic efficiency (EE) is the proportion of production not consumed or exported; P/B and Q/B are the ratios of production and consumption to biomass; ISI is the trophic interaction strength index, which is the sum of the predicted relative biomass change (of all affected groups) after removal of the indicated affecting group at the beginning of 30-year dynamic simulations. The keystone index is the ratio of the interaction strength index and the percent of the system's overall biomass that is represented by the group. See Chapter 4 for equations describing both of these indices.

a. Keystone indices were not estimated for the three plankton groups in the system because of high specified immigration rates.

b. *Pepino* almost entirely disappear during 30-year simulations due to unsustainable catch rates, so 'removing them' is redundant.

Table 2-3. Basic flows and indices in the Floreana rocky reef Ecopath model

Flows	$(t \cdot km^{-2} \cdot year^{-1})$
Calculated total net primary production	13,250
Net system production	-14,388
Sum of all production	17,337
Sum of all consumption	51,600
Sum of all exports	-5,412
Sum of all respiratory flows	27,638
Sum of all flows into detritus	21,024
Total system throughput	94,850
Total catches	4.15

Biomass	$(t \cdot km^{-2})$
Total living biomass	2,620

Indices	
Total primary production/total biomass	5.06 $year^{-1}$
Total biomass/total throughput	0.03 $year^{-1}$
Total primary production/total respiration	0.48
Proportion of flows originating from detritus	0.62
Connectance index	0.16
Mean trophic level of the catch	2.27
System omnivory index	0.25 TL units

Notes: Flows and biomass are expressed in wet weight. Minus signs indicate net imports of production

The biomass of *pepinos* was predicted to increase inside a hypothetical no-fishing zone (Figure 2-5), but the overall biomass of *pepinos* is predicted to decline and stabilize at 36% of the 2000-2001 levels by the end of the 10 year simulation. Although the fisheries exclusion zone does not prevent overall *pepino* biomass from declining, it does prevent these intense fisheries from completely eliminating this slow-growing species. Dispersal rates higher than 14 m day^{-1} result in a larger 'spillover' effect (catchable emigration), but a lower buildup (protection) of biomass in the no-fishing zone.

Table 2-4. Flows from primary production and detritus

TL	From primary production					From detritus				
	Consumed	Export	To detritus	Respiration	Throughput	Consumed	Export	To detritus	Respiration	Throughput
VI	0	0	0	1	1	0	0	0	1	1
V	1	0	5	15	20	1	0	4	12	16
IV	16	0	224	381	621	13	0	210	337	561
III	1099	-927	2125	3237	5533	1048	-927	1050	1684	2855
II	10276	-8843	9956	13058	24448	5086	-3648	7195	8912	17544
I	14668	-1600	155	0	13223	10490	10534	0	0	21124
Sum	26059	-11370	12465	16692	43846	16639	5959	8459	10946	42102

Note: Flows are expressed in $(t \cdot km^{-2} \cdot year^{-1})$. System imports and exports are not shown. Some flows reach trophic level VI because some organisms within some functional groups are supported by energy that has traversed five links from primary producers.

Table 2-5. Percentage of total annual catch comprised by the 10 functional groups targeted in Floreana reef fisheries

Functional group	TL	Catch $(t \cdot km^{-2} \cdot year^{-1})$	% of total catch	% of total mortality
Bacalao grouper	4.2	0.031	0.8	1.4
Pelagic predators	3.9	0.221	5.4	1.9
Non-commercial reef predators	3.8	0.067	1.6	0.5
Pelagic planktivores	3.4	0.004	0.1	0.1
Other commercial reef predators	3.3	0.037	0.9	0.6
Large benthic invertebrate eaters	3.3	0.006	0.1	0.9
Spiny lobster	2.8	0.178	4.3	13.1
Slipper lobster	2.7	0.011	0.3	0.7
Detritivorous fishes	2.1	0.621	15.2	1.2
Pepino (S. fuscus sea cucumber)	2.1	2.922	71.3	87.5

Notes: Analysis based on data from 1997 to 2000. A great majority of the catch comprised pepinos and detritivorous fishes. TL is trophic level, and the final column is the percent of each group's total mortality that is directly caused by fisheries.

Figure 2-3. Predicted changes resulting from the complete removal of sharks from the present day Floreana rocky reef trophic model. Results shown are the predicted relative change in biomasses at the end of a 30-year simulation in which sharks were removed by year 10 (V = 0.4).

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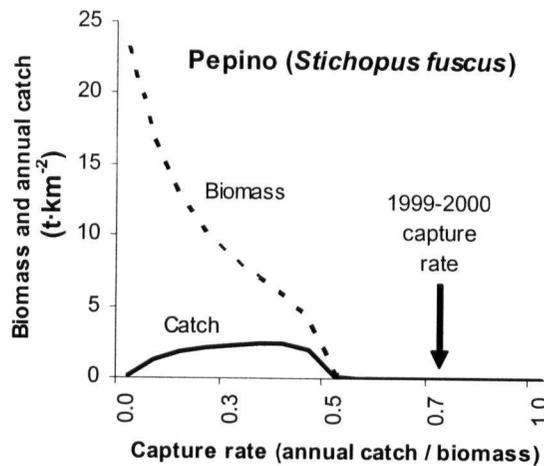
Figure 2-4. Predicted catch and biomass curves for pepino sea cucumbers (Stichopus fuscus) on the rocky reefs at Floreana Island, Galápagos. The 1999-2000 capture rate (annual catch/biomass) of this species was essentially twice that of sustainable levels. This figure represents the predicted states of the biomass and annual catch after the system reaches 'equilibrium' based on the specified biomass and production rate (P/B) of *pepino* and the combined effect of all sources of mortality in the system. It is possible for the actual capture rate to greatly exceed sustainable capture rates, but only if the population is rapidly collapsing.
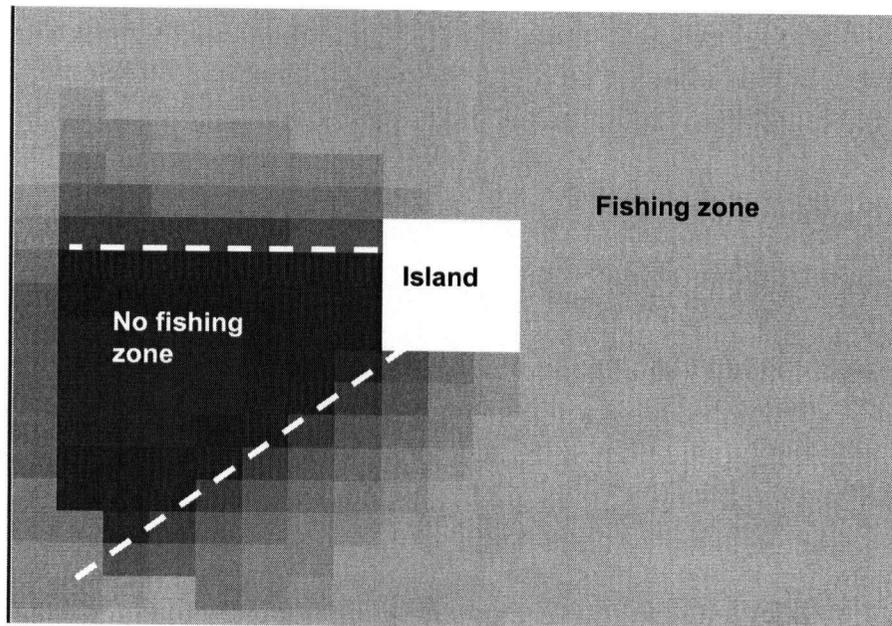
Figure 2-5. A simple diagrammatic representation of the potential effects of a fisheries exclusion zone on pepino (S. fuscus) biomass at the end of a 10-year *Ecospace* simulation at a hypothetical Galápagos island. Darker areas represent high biomasses and lighter areas represent low biomasses. Catchable emigration of *pepinos* can be seen as dark shading outside the dotted lines that demarcate the boundaries of the hypothetical fisheries exclusion zone. *Pepinos* still decline to a biomass lower than present, but the no-fishing zone prevents the intense fishery from extirpating them.

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DISCUSSION

It seems obvious after construction of the Floreana rocky reef model that the remarkably high biomasses of fishes, invertebrates, and other organisms on Galápagos rocky reefs is made possible not only by high *in situ* production of macroalgae and microphytobenthos, but also because these reefs are sinks for oceanic plankton. Stated another way, it is imported food (energy) that allows the high biomass observed on Galápagos reefs. The reefs must capture the primary and secondary production of large oceanic areas as currents continually flow past and around the islands. These large quantities of plankton are captured by high biomasses of filter- and suspension-feeding invertebrates and planktivorous reef fishes creating unusually rapid turnover of diversity and biomass, particularly in areas of continual upwelling (Witman and Smith, 2003). This might seem odd to terrestrial ecologists who are used to communities that are almost entirely supported by *in situ* primary production, but there are now many examples of marine or coastal communities that are strongly shaped by allochthonous subsidies (Okey, 1993; Vetter, 1994; Bustamante et al., 1995; Vetter, 1995; Polis and Hurd, 1996; Okey, 1997; Polis et al., 1997; Vetter and Dayton, 1999; Okey, 2003).

The importation of large quantities of carbon to rocky reefs through this planktonic-benthic linkage is discussed by Bray et al. (1981) and Bray (1981). The necessity for such importation (to support the existing high biomasses on reefs) is, however, made clear only through construction of mass-balance trophic models. One implication of this import is that secondary production and tertiary production are strongly coupled and magnified by oceanographic conditions, as discussed by Menge et al. (1997). Although trophic connections, linkages, and cascades in nearshore rocky subtidal systems can be dampened by physical oceanographic forces (e.g., Kvitek et al., 1998), there is some evidence that biological oceanographic conditions (food inputs) can strengthen trophic connections along rocky shorelines (Polis and Hurd, 1996; Menge et al., 1997; also see Oksanen et al., 1981), just as kelp subsidies can increase competition and secondary production in the rocky intertidal zone (e.g., Bustamante et al., 1995).

The changes predicted by the shark removal simulation (Figure 2-3) have presumably already taken place to a much larger extent than the present day simulation predicts. Sharks might be considerably reduced over Galápagos reefs due to unaccounted shark fisheries since the 1950s and which continue illegally today (Constant 1993, Camhi 1995). Indeed, the commercial reef predator groups (including groupers) make up only 1.8% of the present day Galápagos fisheries catch (present analysis), whereas these fishes were the main target in the past (Reck, 1984; Ruttenberg, 2001). The implication is that recovery of sharks could lead to increases in other reef predators by decreasing the biomass of their respective predators.

Several functional groups in the system are likely to have lower than normal interaction strength than in the present day system because their biomasses or size distributions (or diets) have been

considerably reduced or modified. These now depleted functional groups with reduced biomass potentially include sharks, sea lions (*Z. wollebaeki*), birds, 'bacalao' grouper (*Mycteroperca olfax*), large benthic invertebrate eating fishes (e.g., *Bodianus diplotaenia, Semicossyphys darwini*), *pepinos*, spiny lobster (*Panulirus gracilis* and *P. penicillatum*), slipper lobster (*Scyllarides astori*) and stony and black corals. The situation of formerly important commercial large groupers (i.e., *Epinephelus mystacinus* and *Epinephelus cifuentesi;* Reck, 1986) is unclear, as they are confined to deeper waters, and their fishery has not been given much attention during the last decade.

Such reductions of species and functional groups can severely modify marine ecosystems (Dayton et al., 1995; Dayton et al., 1998), especially because many of the groups removed are from upper trophic levels and have high 'keystone' values (Table 2-2). Local fisheries are now supported by lower trophic-level species instead of the upper trophic-level species that were preferred in the past (Table 2-5). Still other species may have become more abundant in response to reductions in biomasses of predators that structure the system. These species with net gain might include planktivorous reef fish (i.e., *gringo, P. colonus*), sea urchins (e.g., *Eucidaris thouarsii, Tripneustes depressus, Lytechinus semituberculatus*) and in some cases anemones (i.e., *Aiptasia* sp.). The central Galápagos rocky reefs appear to be a local example of the global pattern of 'fishing down marine food webs' (Pauly et al., 1998). Even if increases in *pepino* fishing pressure in the Galápagos is driven more by global increases in demand than local depletion of fishes like *bacalao* (M. olfax), the lucrative financial incentives for catching *pepinos* are arguably driven by global changes in coastal species composition (i.e., fishing down the food web) that have lead to increasing markets for holothurians and other low trophic level organisms. The fishing down effect is however reinforced by the fact that the *bacalao* grouper, a top predator, was in the past the main target for the local and mainland salt-dried market (Reck, 1984); today, two species of planktivorous mullets (*Mugil spp.*) dominate the salt-dried landings (Espinoza et al., 2001).

Many of the changes might be exacerbated indirectly through trophic cascades. For example, Ayling (1981) suggested that the removal of large benthic invertebrate-eating fishes might have led to increases in sea urchin biomass in New Zealand. In the Galápagos, any such increase in densities of the urchin *Eucidaris thouarsii* could have contributed to the decline of stony corals and caused other changes in this benthic rocky reef system (Glynn et al., 1979). Wellington (1975) noted that a conspicuous urchin predator, the Mexican hogfish *Bodianus diplotaenia*, has declined locally. Recent data have suggested an increase in urchins and herbivorous fish resulting from the removal of such large predatory fishes during the 1970s (Ruttenberg, 2001). These ecological cascades are indicated even in the present day shark removal simulation shown in Figure 2-3.

Indeed, modifications to the Galápagos marine ecosystem have shaped a present-day marine system that is probably more removed from its pristine state than we tend to think. This puts modelling exercises at a disadvantage when the working model is based on the present-day system, because organisms that might have played a strong structuring role in the past might now have only negligible

effects on the system. In the context of modified ecosystems, therefore, the only fair way to evaluate the potential role of organisms using whole trophic modeling is to construct a past system model (*sensu* Pitcher and Pauly, 1998; Pitcher, 2001; Pitcher et al., in press). This can be accomplished in relatively short order by using the present day Floreana rocky reef model as a template, but only if good information about the chosen past system is available. Luckily, some information is available on past abundances of some of the organisms in question throughout the Galápagos Archipelago.

Heavy grazing by sea urchins is known to be the immediate cause of extensive 'barren grounds' where the bottom is dominated by crustose coralline algae and high abundances of urchins (Mann and Breen, 1972). Such an ecological phenomenon resembles a shift to an alternate stability domain (*sensu* Scheffer et al. 2001), though it is perhaps more accurately described as a shift to a non-trivial boundary point (Sutherland 1974) where one or more species in the system (i.e., predators of sea urchins) are removed. Regardless of how they are categorized, such shifts generally have negative implications for diversity and ecosystem integrity. Similar shifts that are linked to removal of urchin predators are documented worldwide (Estes and Palmisano, 1974; Elner, 1990; Levitan, 1992; Estes and Duggins, 1995; McClanahan et al., 1996; Sala, 1998; Sala et al., 1998). These barren grounds are now a common feature of the seascape of Galápagos reefs (Glynn et al., 1979; Ruttenberg, 2001). In some areas, 'anemone barrens' have begun to appear, in which a single species of anemone (*Aiptasia* sp.) has replaced previously diverse shallow reef habitats (Chapter 3; Okey et al., 2003).

Questions surrounding the genesis of this Galápagos seascape can be explored using a model that features more pristine levels of urchin predators; i.e., lobsters and groupers. For example, why is the *bacalao* grouper indicated to have such low interaction strengths *and* such a low keystone index in the present day model, particularly when groupers are thought to be strong shapers of reef ecosystems (Hixon and Beets, 1993)? One hypothesis is that their biomass has been considerably reduced. Another is that their size class distribution shifted to smaller individuals and they simply do not interact like the big grouper predators they once were. Both trends might be true (Ruttenberg, 2001), but explicit specification of past information (e.g., from Reck, 1984) could provide insights into this group's past role in shaping the system relative to their current role. It is tempting to suggest that *large bacalao* groupers are size-overfished (Coello and Grimm, 1993) and functionally negligible in the Galápagos Archipelago, but more information is needed to evaluate that question.

A 'past system' model will allow assessments of the roles of such strong interacting species, but moreover, it can be used to postulate and explore the trophic cascades and other mechanisms that changed a pristine system to a degraded system. Moreover, this approach can be used to provide potential 'roadmaps' to restoration (Pitcher, 2001), as well as helping to guide the continuing ecological monitoring of the Galápagos Marine Reserve.

Unavoidable uncertainty in the predictions of *pepino* equilibrium catch and biomass in relation to capture rate is a function of the paucity of information on stock-recruitment relationships for *pepinos*,

which is probably nonlinear. Theoretically, stock recruitment relationships are implicit in the specified *pepino* production rate (P/B) of 0.6 year^{-1}, which is based on information in Pauly et al. (1993a). These authors assumed that total mortality (Z; and thus P/B) of holothurians is approximately twice that of natural mortality (M), like fishes targeted by a fishery. Opitz (1986) used a P/B of 0.29 year^{-1} as equivalent to the natural mortality of unfished Caribbean holothurians. One option for pursuing shortcomings in this analysis would be to specify split, but linked, pools for different life stages of *pepinos*. This can be done using *Ecopath with Ecosim* when enough information becomes available on the early life stages of this species.

The simulation of the effects of a fishery exclusion zone on *pepino* is a simplistic representation of the real dynamics of the system. For example, the exaggeration of the width of the fringing reefs was necessary due to the resolution constraints of the *Ecospace* grid (e.g., a proportionally narrow band of reef around Galápagos islands could not be simulated with the current version of *Ecospace*). In the context of the spatial characteristics of these fringing reefs, there is considerable uncertainty with respect to dispersal and effort response effects, as implied above (also see Mangel, 2000). We expect that the resulting exaggerated area of the reef would overestimate the beneficial effects of the fishery exclusion zone (Figure 2-5), if anything. Size does matter when it comes to protected areas, *pepinos* or no *pepinos* (Walters et al., 1999; Martel et al. 2000; but see Halpern, 2003). Nevertheless, since overall distances across the cell matrix are scaled properly (with reference to Floreana Island), the simulation has at least made it clear that protecting small portions of reef areas (23%) is likely inadequate to prevent further overall declines of *pepino* biomass in the Galápagos Islands without considerable reductions in *pepino* capture rates. At the same time, the simulation indicated that *pepino* biomass increased in the hypothetical fishery exclusion zone, thus preventing extirpation of *pepinos*. This indicates a positive effect of the exclusion zone on the fishery —related to emigration (Walters et al., 1999) and consistent with empirical findings of Roberts et al. (2001)—despite the prediction of an overall catch decline even when implementing fishery exclusion zones. In spite of its simplicity and inherent uncertainties, these simulation results are remarkably similar to a recent empirical evaluation of the effects of a fishery and marine reserves on a closely related sea cucumber (*Parastichopus parvimensis*) in California's Channel Islands (Schroeter et al., 2001).

This *Ecospace* simulation is also fully consistent with the conclusions of Allison et al. (1998) that marine reserves are necessary but not sufficient for marine conservation, and especially their conclusion that well-intentioned networks of marine reserves must be complemented with strong conservation efforts in the areas *outside* the reserves (also see Murray et al., 1999). A fisheries free-for-all justified by the establishment of a network of reserves is reasonable to expect, and would quite likely prevent achievement of conservation goals.

Finally, we must stress that the present model does not represent some major areas of the archipelago. For example, the biotic communities of the central Galápagos shelf are markedly different

from the communities of the more northern Wolf and Darwin Islands and the western side of Isabela and Fernandina Islands (see Figure 2-1). Evidence is mounting that these latter two areas comprise discrete biogeographic zones, though separated by very short geographical distances (Abbott, 1966; Harris, 1969; Glynn and Wellington, 1984; Reck, 1986; Jennings et al., 1994; Bustamante et al., 2000; Wellington et al., 2001; Bustamante et al., 2002). This situation gives rise to several new questions: Should these differences be integrated into one model or should models of each biogeographic zone be constructed? What are the roles oceanographic forces in shaping these biotic communities relative to trophic forces? Such questions will inform the development of the present ecosystem research; the results presented here constitute a first step to explore and understand the nature and dynamics of the broader Galápagos marine ecosystems.

My continuing strategy is to evaluate and refine the Floreana Island rocky reef ecosystem model iteratively in parallel with the ongoing baseline monitoring program. Only by combining such analytical approaches with ongoing empirical field investigations can the usefulness of ecological models be truly evaluated. This adaptive approach will help evaluate the potential effects of human activities and management policies such as the effectiveness of zone-based fisheries and conservation management in the Galápagos Marine Reserve. Examination of the knowledge gaps revealed during model construction has already enabled adaptive refinements to strategies for the continuing monitoring program in the sense that the focus of this program is shifting to less certain aspects of the Galápagos subtidal rocky reef.

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CHAPTER 3. Discovery of anemone barrens in the Galápagos and potential explanations

ABSTRACT

Mono-specific carpets of the anemone *Aiptasia* sp. were observed for the first time after the 1997/98 El Niño event on shallow horizontal reef platforms at Fernandina and Isabela Islands in the Western Galápagos Archipelago, Ecuador. Detailed transects in this area during the middle 1970s (Wellington 1975), including a transect across one of these reef platforms, indicated that these recently observed 'anemone barrens' have replaced previous algal and invertebrate assemblages. Observations during the last 10 years also support the notion that these barrens emerged recently. Community surveys and whole community trophic modeling was conducted during the present study to evaluate the community impacts of the anemone barrens and the possible mechanisms for their emergence and maintenance. Surveyed sites at these two anemone barrens were found to have significantly fewer fish species than 11 other sites in the western portion of the archipelago. Declines in marine iguana (*Amblyrhynchus cristatus*) populations might be explained by the emergence of the anemones, which can preempt the subtidal reef areas that normally produce the marine algae food of adult marine iguanas. These anemone barrens might have emerged as the result of recent severe El Niño-Southern Oscillation events, but preliminary whole community trophic modeling indicates that depletion of predators by unsustainable fisheries might be sufficient, in itself, to trigger the emergence of anemone barrens. Anemone barrens might be a true alternate stable state because of their potential ability to resist invasion by any other species.

INTRODUCTION

Pre-emption of space is one mechanism that can lead to the domination of particular habitats (Sousa 1979b, a) and alternate stable states (Sutherland 1974), or at least alternate persistent states (Connell and Sousa 1983, but see discussion by Peterson 1984, Sousa and Connell 1985, Sutherland 1990). Such dominance by a single species that is competitively superior can result from the removal of predators (Paine 1966, Paine 1969, Knowlton 1992), or by changes to the natural disturbance regime (Dayton 1971, Sousa 1979b, a, 1984, Petraitis and Latham 1999, Dudgeon and Petraitis 2001), or both.

Anemone barrens have recently appeared on some shallow horizontal reef platforms in the Western Galápagos Archipelago (Okey et al. 2003). I define *anemone barrens* as areas of reduced diversity of species or biogenic habitat structure caused by the unchecked spread of competitively dominant anemones. These carpets of *Aiptasia* sp. anemones (genus identified by D. Fautin; University of Kansas) were surveyed and quantified in the two locations at which they were observed in great abundance during the present study. Several lines of evidence indicate that this is a new phenomenon. For example, Wellington (1975) found a somewhat diverse assemblage of algae, invertebrate, and fish species at a transect location where Scoresby Shepherd (South Australian Research and Development Institute)

and I found 95% cover of *Aiptasia* anemones in 2000. One conservation concern relating to this phenomenon is that the anemones have invaded much of the space that was previously used for grazing on algae by the largest remaining population of marine iguanas (*Amblyrhynchus cristatus*) in the Galápagos.

There are other examples of anemones and other Hexacorallia spreading over intertidal and subtidal areas and persisting for some time. *Rhodactis rhodostoma,* a corallimorpharian, invaded large areas of the inner reef flat at Eilat in the northern Red Sea (up to 69% of the area) after an unusually extreme low tide event in 1970, effectively replacing corals there (Chadwick-Furman and Spiegel 2000). *Heteractis magnifica* dominated the reef at Moorea, Society Islands, until cyclones disrupted the anemone fields (D. Fautin, pers. comm. with S. Shepherd). *Anthopleura elegantissima* can dominate large areas in sheltered intertidal habitat along North America's west coast (Dayton 1971, Ayre and Grosberg 1995, present author's pers. obs.). *Metridium senile* grows over large areas in the shallow subtidal of Europe and western North America (Purcell and Kitting 1982, Anthony and Svane 1995, present author's pers. obs.). A mechanism for the persistence of extensive anemone colonies was suggested by Dayton (1971): colonial anemones can successfully resist invasion and effectively pre-empt space by consuming any propagules of competitors that would otherwise settle. There is evidence that similar settlement interference by polychaetes plays a prominent role in shaping soft bottom benthic communities as well (Woodin 1974b, a, Peterson 1979).

Two general classes of potential explanations for the appearance of the anemone barrens on the horizontal reef platforms in the Galápagos are (1) exotic magnitudes (*sensu* Sousa 1984) of physical oceanographic forces and (2) exotic changes in the trophic interactions shape these reef communities, or both. The 1997-1998 El Niño was a particularly extreme oceanographic event that heated the surface waters of this region to unusual levels for an unusual duration. It was barely second in magnitude to the strongest recorded El Niño event (1983-1984), but the 1997-1998 event had two maximum peaks rather than one (e.g., Wolter and Timlin 1998) thus causing widespread ecological changes throughout the tropical Pacific (Jimenez et al. 2001, Aronson et al. 2002) perhaps by causing longer-lasting maximum effects [still, the 1983-1984 El Niño event is known to have caused widespread ecological changes (Glynn 1990)]. As a whole, these increasing impacts might portend considerable changes to tropical reefs in the future (Wilkinson 1996, McClanahan 2002). Observations during benthic surveys in the western archipelago conducted during 1998-99 showed that this El Niño event caused considerable mortalities of cold-water sessile species on the shallow reef platforms along Eastern Fernandina Island (R. Bustamante, pers. comm.). Elevated regional water temperatures associated with El Niño likely combined with normally intense solar exposure of these shallow reef platforms. This might have opened space for the opportunistic and fast-spreading *Aiptasia* sp. anemones. Alternatively, the rapid serial depletion of reef predators in the Galápagos Archipelago, including the very intensely-fished '*pepino*' sea cucumber (*Stichopus fuscus*) (Chapter 2, Okey et al. 2004a), might have released this competitively dominant sessile

reef cnidarian from its last constraining predation force and given it free reign on these reef platforms. Preliminary evidence from Bermeo-Sarmiento (1995) indicates that *S. fuscus* consume small cnidarian polyps in Galápagos, and this predation could be incidental small post-settlement or juvenile anemones as these holothurians use feeding tentacles with adhesive papillae to remove 'particles' from the sea floor (Barnes 1987). It is also plausible that both classes of changes have worked in concert. For example, the shift might have been initiated by a physical force (the El Niño event), but maintained by a biotic force (the depletion of predators) (see Petraitis and Latham 1999).

The purpose of the present chapter is to document the sudden appearance, existence, and characteristics of the recently discovered anemone barrens in the Galápagos archipelago, and to begin exploring the possible explanations for their emergence and maintenance. The main operational question is, 'What caused the appearance of the anemone barrens?' To begin addressing this question, I conducted dynamic simulations using the trophic model of a Galápagos rocky reef, described in Chapter 2, in an attempt to recreate the initiation of the anemone barrens with strictly fishing/trophic derived forces (predation hypothesis) and no change in oceanographic conditions.
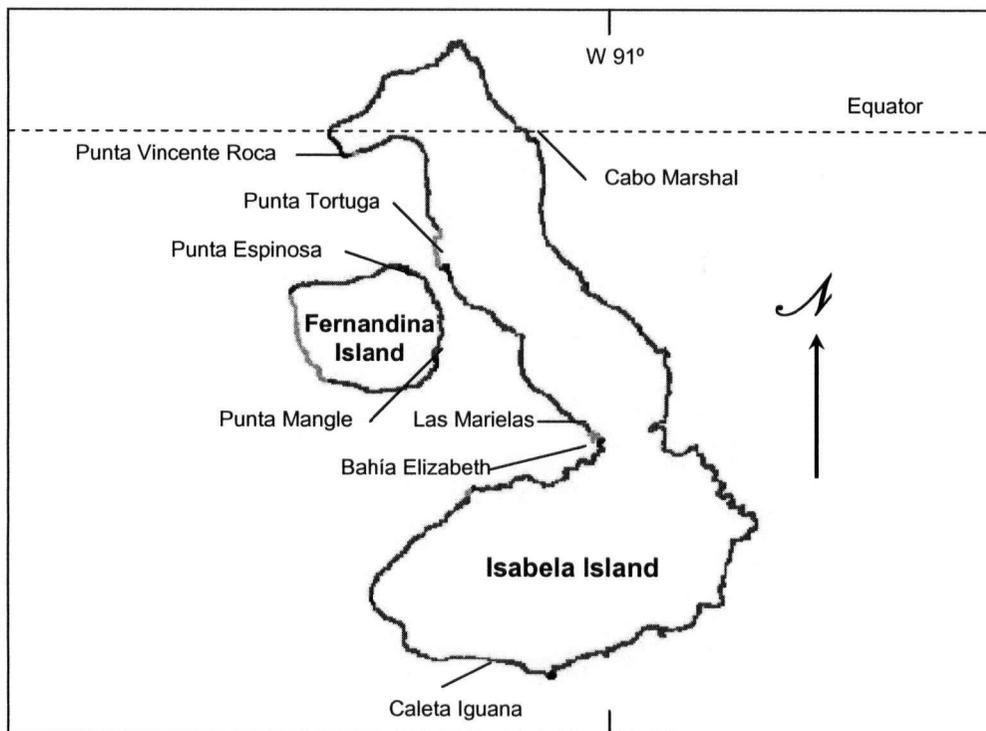
Figure 3-1. Isabela Island and Fernandina Island, Galápagos, Ecuador, with locations of Punta Espinosa and Punta Mangle, where the anemone barrens were observed, and indicating the locations of other areas that were surveyed between 3 and 16 December 2000 (see Table 3-1 for exact locations of 13 transects). Green coasts are fully protected (P), blue coasts are protected zones with tourist access (T), and red coastlines are zones in which extractive uses are allowed (E), though these new designations have no effect on any of the results presented here.

METHODS

Study location

The first confirmed observations of the anemone barrens were made in 1998 at Punta Espinosa and Punta Mangle during research expeditions to Fernandina Island in the western portion of the Galápagos Archipelago (R. Bustamante, pers. comm., Figure 3-1).

Sampling and observations

A research expedition on the *R/V Beagle* was conducted between 3 and 16 December 2000 as part of the Galapagos Marine Reserve biodiversity baseline ecological monitoring program (Danulat and Edgar 2002), which commenced that year at the Charles Darwin Research Station, Puerto Ayora, Galápagos. For this survey, fish community transect sampling was conducted using standard visual reef census techniques (specific to each group), in which divers recorded species occurrences, abundances, and sizes along a single 100 m-long weighted transect line deployed along the 6 m depth contour at each sampling location (Figure 3-1, Table 3-1).

Table 3-1. Coordinates and 'use zoning' of visual fish transects.

Site	Latitude	Longitude	Use zone
Caleta Iguana	S 00° 58.748'	W 91° 26.833'	Extractive
Punta Mangle Norte	S 00° 21.881'	W 91° 22.807'	Tourist
Punta Mangle Sur	S 00° 26.472'	W 91° 23.314'	Extractive
Bahía Elizabeth	S 00° 38.547'	W 91° 06.181'	Tourist
Las Marielas	S 00° 35.989'	W 91° 05.477'	Protected fully
Punta Espinosa Sur	S 00° 16.349'	W 91° 26.276'	Tourist
Punta Espinosa Norte	S 00° 15.775'	W 91° 26.523'	Tourist
Punta Tortuga	S 00° 15.336'	W 91° 23.415'	Protected fully
Punta Vincente Roca	S 00° 03.129'	W 91° 34.076'	Extractive
Punta Vincente Roca	S 00° 03.134'	W 91° 33.106'	Tourist
Punta Vincente Roca	S 00° 03.117'	W 91° 56.833'	Protected fully
Cabo Marshal	S 00° 00.529'	W 91° 12.986'	Extractive
Cabo Marshal	S 00° 01.087'	W 91° 12.419'	Tourist

Note: Coordinates were plotted with a hand-held Global Positioning System just prior to deployment of transects.

For the fish surveys, Scoresby Shepherd and I swam a 5 m-wide swathe on each side of the transect lines for a total combined swathe width of 10 m (each transect covered an area of 1,000 m²) including all fish to 5 m above the substratum. This information was recorded separately for each 10 meter increment on underwater paper. The transect length differs from that reported in Chapter 2 because of design changes made after this survey. Recorded fish identifications were verified by referring to Humann (1993), usually within an hour after each transect was completed. Data were computerized from the raw data sheets using a two-person verification technique. A one-tailed Mann-Whitney test with tied ranks was conducted on number of fish species data to test the hypothesis that there were fewer fish species at the sites with anemone barrens than there were at sites without anemone barrens. A total of

15,206 individual fish from 57 species and 27 families were identified and enumerated from 26 benthic line transects, each covering an area of 1,000 m², for a total sampled area of 26,000 m² along the coasts of Isabela and Fernandina Islands, Galápagos during this pilot study (see also Okey and Shepherd 2001). The list of fish species from these transects is shown in Appendix B.

Bathymetry and habitat varied among locations; some transects were located along 25° to 40° boulder slopes, some on horizontal reef platforms, and some over sand or gravel. Visibility and habitat characteristics at each site were noted. *Aiptasia* sp. anemones were removed from two 10 m² circular clearings at the Punta Espinosa anemone barren using marine rust scrapers, other types of scrapers, and wire brushes with the hopes of using these clearings to evaluate the resilience of the carpet. The Punta Espinosa anemone barren was also surveyed using a diver's benthic sled (a board attached to a rope towed behind a boat such that the pitch of the board can be controlled by a diver to adjust survey depth). The purpose of this diver's benthic sled survey was to evaluate the areal extent of this anemone barren.

The modeling approach

A whole community trophic model of a Galápagos rocky reef (Chapter 2, Okey et al. 2004a) was used to explore the plausibility of the predator limitation explanation for the *Aiptasia* sp. anemone barrens' emergence on shallow reef platforms at Punta Espinosa and Punta Mangle. This whole food web model was constructed using the *Ecopath* approach (Polovina 1984, Christensen and Pauly 1992, Pauly et al. 2000) through the coordination of a broad collaboration of scientists who helped design the model structure and who contributed the best available parameter estimates from the scientific literature on Galápagos marine biota and from the latest empirical information from the Galapagos Marine Reserve biodiversity baseline ecological monitoring program (Danulat and Edgar 2002). My main approach was to conduct a series of simulated predator removals using *Ecosim* (Walters et al. 1997) to try to reveal the combinations of predator removals that would generate and maintain anemone barrens. After finding a plausible trophic scenario, I repeated this simulation under a series of different assumptions for prey vulnerability settings for the purpose of testing the sensitivity and 'dynamic reliability' of the explanatory simulation.

The thermodynamic continuity of the model (its mass-balanced starting point) cannot be achieved for the '*pepino*' *(S. fuscus)* functional group, or for the Galápagos rocky reef model as a whole, without specifying a biomass accumulation value of negative one tonne·km^{-2}·year^{-1}, thereby specifying a declining biomass of *S. fuscus* as part of the baseline model. This is due to the enormous extraction rate of *S. fuscus* from this reef model (2.922 tonnes·km^{-2}·year^{-1}). Any simulation, then, would automatically include an intense *pepino (S. fuscus)* fishery from the beginning. For the purpose of simulating the onset of an *S. fuscus* fishery, therefore, the catch and the biomass accumulation for this group was set to zero at first, and then increased. In addition, because of the preliminary evidence that *S. fuscus* consume small cnidarian polyps (Bermeo-Sarmiento 1995) and because of the manner in which they forage, I split the

anemone group into an early juvenile stage (younger than 2 months) and an older stage using a multi-stanza modeling function in Ecosim, which employs a von Bertalanffy growth function to calculate reasonably consistent biomasses and rates for lesser-known stages.

RESULTS

Anemone barrens observations

The *Aptasia* sp. anemone covered greater than 90% of the reef platform deeper than 4 m (and not beyond 12 m) on the shallow reef platform at Punta Mangle Sur, which slopes gently from the intertidal within a sheltered bay. The substratum between 0 m and 2 m was 30-40% covered with *Ulva* sp. and 10-20% covered with other algal species. At 3-4 m depth, cover of the fleshy brown alga *Padina* sp. was 40-50% with most of the other space occupied by the colonial *Aptasia* sp. anemone (a shallow, perpendicular transect was deployed here in December 2000 in addition to the 6 m isobath transect). The echinoid *Eucidaris* was common only at depths less than 2 m.

The *Aiptasia* sp. anemone barrens covered 95% of the bottom between 5 and 13 m depths on the reef platform at Punta Espinosa Norte (Table 3.1). Here the anemones were interrupted by occasional clumps of *Padina*, which were partially covered with the anemones. This platform is also shallow and gradual. This area was described by Wellington (1975) by his 'Transect B' (which was perpendicular to the shore and extended from a depth of 4 m to beyond 8 m). We found an algal mat covering 100% of the area between 0 and 5 m depths (90% *Ulva* spp.), and a sharp transition to the anemone barrens. The benthic sled surveys indicated that this anemone barren was very large, but that it was restricted to open horizontal and non-structured reef flats (away from boulder habitats) on the protected east side of Punta Espinosa within sight of Mangroves. The removal of the *Aiptasia* sp. anemones from the two 10 m^2 circular clearings at Punta Espinosa proved extremely difficult. Each clearing took two divers over an hour of very hard work.

Scoresby Shepherd and I observed *Aiptasia* anemones under rocks at Playa Mansa, Tortuga Bay and Academy Bay, both on Santa Cruz Island, in January 2001. We also observed large patches of *Aiptasia* anemones near mangroves along the west coast of Isabela Island in March 2001.

Fishes

Significantly fewer fish species (62% fewer) were found at the two sampling locations with anemone barrens than at the other 11 sampling locations (those without anemone barrens) (one-tailed Mann-Whitney test with tied ranks; $p < 0.05$). The mean number of species at the anemone barrens location ($\pm$ 1 SE) was 5 $\pm$ 1.0 species, whereas the locations without anemone barrens had 13 $\pm$ 1.7 species. The two locations that had the lowest number of demersal fish species out of 13 locations/transects were the same two locations that were almost entirely covered by *Aiptasa* sp.

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anemones—Punta Mangle Sur and Punta Espinosa Norte (Figure 3-2). The number of demersal fish species was also relatively low at Las Marielas and Punta Vincente Roca sites, perhaps because these were the only two sites sampled in failing daylight (between 1700 and 1800 hours). At least 10 species per transect were found at all other sites.
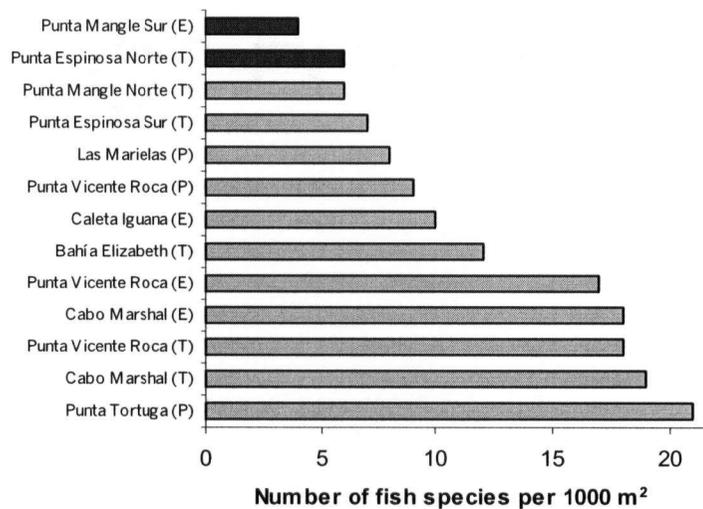
Figure 3-2. Number of fish species observed in the December 2000 baseline monitoring program pilot study. Two sampling stations with the lowest number of species (black bars) were the two stations at which the colonial anemone *Aiptasia* sp. had covered 90-95 percent of the substratum. Anemone barrens were not present at stations with grey bars. (P) denotes fully protected zones; (T) denotes protected zones with tourist access; (E) denotes zones in which extractive uses (e.g., fishing) are allowed. These zones were being established at the time of the surveys and thus would have no effect on the data presented.

Anemone barrens simulations

Predicted changes in the biomass of anemones could be triggered in the model by specified changes in only two functional groups—*pepinos (S. fuscus)* and omnivorous reef fish. The omnivorous reef fish functional group is made up of damselfishes, including the territorial *Stegastes leucorus beebei* and *S. arcifrons*, which both consume and actively remove anemones and other invading biota from their territories and gardens (Branch et al. 1992). Hereafter, the omnivorous reef fish group will be referred to as *Stegastes*. Changes resulting from these removals are described here in sequence because of their informative trajectories.

The biomass of juvenile anemones increased with the simulated removal of *pepinos*. This recruitment was followed by an increase of adult anemones, which then inhibited juvenile anemones (Figure 3-3). The increase in adult anemones was subsequently controlled by *Stegastes* in the Ecosim manifestation of the model, which has no explicit spatial structure. Subsequent specified removal of *Stegastes* lead to predicted dramatic increases in adult anemones. Juvenile anemones also began increasing with the onset of the *Stegastes* decline, but it then began declining after adult anemones had increased sufficiently to impose a detrimental competitive effect.

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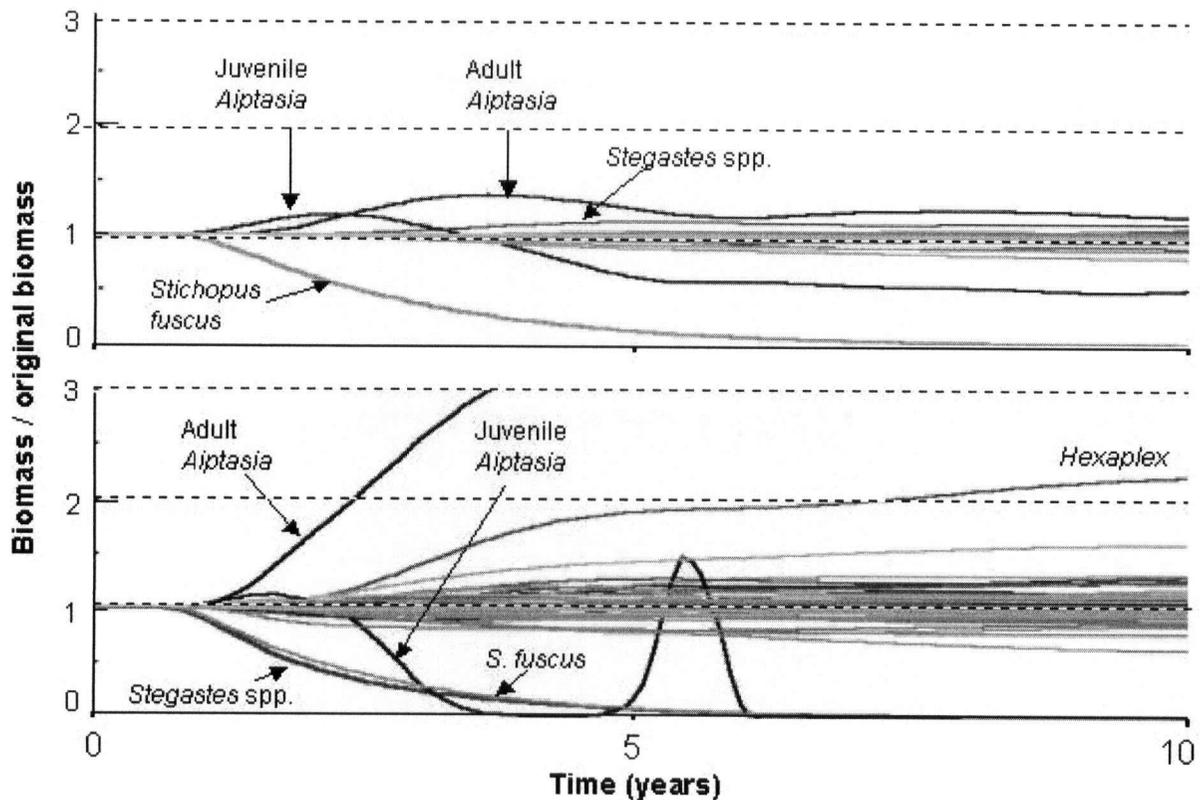
Figure 3-3. Predicted changes in biomass resulting from the removal of Stichopus fuscus (upper panel) and omnivorous reef fish (Stegastes) and S. fuscus (lower panel). *Aiptasia* anemones were predicted to increase by a factor of five when both groups were removed. Results include all the groups in the 44 compartment Galápagos rocky reef model. Overall prey vulnerability (*v*) was set at 0.4, which represents a mixture of bottom-up and top-down forces structuring the system.

DISCUSSION

The emergence of the Aiptasia anemone barrens

The first confirmed observations of the *Aiptasia* anemone barrens occurred in late 1998 and late 1999 at Punta Espinosa and Punta Mangle on the east coast of Fernandina Island (R. Bustamante, pers. comm.). Unconfirmed observations of Anemone 'patches' were made by Jimmy Penaherrera at Punta Espinosa in 1995. The anemone barrens were first described by Okey and colleagues (2003, 2004a). These are called 'anemone barrens' because of the virtual absence of other megafauna and flora where these carpets of *Aiptasia* occur. A number of observations and recollections provide further insights into the timing and character of the emergence of these anemone barrens (Table 3-2).

Mr. Penaherrera's observations of smaller anemone patches in 1995 would be consistent with the notion that El Niño conditions, or reductions in predators such as *S. fuscus*, or both, can lead to the emergence of anemone barrens. El Niño conditions indeed predominated from 1991 to 1995 (though water temperatures did not reach the record levels of 1982/1983 and 1997/98). Also, the *pepino (S. fuscus)* fishery apparently arrived in the Galápagos from mainland Ecuador beginning in 1991 (Jenkins

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and Mulliken 1999). This fishery generally increased in intensity through 1996, and probably beyond. The subsequent confirmed observations of the anemone barrens in 1998 and 1999 point to the strong 1997/1998 El Niño as the initiator of the broader-scale shift (Table 3-2), but reduction of predators cannot be ruled out as a contributor even to this conspicuous shift (or at least to its persistence).

Table 3-2. Observations pertinent to the appearance of anemone barrens in the Galápagos Archipelago

Year	Observation	Location	Observer
1975	No anemones seen	Punta Espinosa	G.M. Wellington
1993	Does not recall seeing any anemones	Punta Espinosa	J. Penaherrera
1994	No anemones seen	Punta Espinoza, Punta Mangle	R. H. Bustamante
1993-1996	*Ulva* spp. and foliose red algae dominate	Punta Espinosa & Mangle	P.C. Martinez
1995	Recollections of anemone patches seen	Punta Espinosa	J. Penaherrera
Aug 1997	Bleached coralline algae dominate; ophiuroids reduced	Punta Espinosa & Mangle	P.C. Martinez, R.H. Bustamante
June 1998	Large and discrete patches of anemones found	Punta Mangle	F. Rivera, R.H. Bustamante
Feb 1999	Extensive anemone barrens found	Espinosa, Mangle, Priscilla	F. Rivera, R.H. Bustamante
Nov 1999	Barrens covered much of bottom; 1.5 – 10m	Espinosa, Mangle, Priscilla	P.C. Martinez
June 1999	Anemones found in great abundances	Punta Espinosa	C. Hickman
Dec 2000	Anemone barrens observed	Punta Espinosa & Mangle	Okey et al. (2003)
Jan 2001	*Aiptasia* anemones observed under rocks	Playa Mansa, Tortuga Bay	S.A. Shepherd
Jan 2001	Observed only under rocks; *Stegastes* present	Academy Bay, Santa Cruz Isl	S.A. Shepherd
Feb 2001	Anemones observed in abundance	Cabo Douglas, Fernandina	K. Fujiwara
Mar 2001	*Aiptasia* patches observed near mangroves	West coast of Isabela Island	TAO & SAS

Notes: Observations summarized from Okey et al. (2003) and further refined.

Wellington (1975) found that *Ulva, Amphiroa,* and *Codium* covered almost 100% of the reef platform to 10 m depth at his transect B, which was located about 300 m south of Punta Espinosa. Scoresby Shepherd and I observed this same area of his transect B to be entirely carpeted with the anemones in December of 2000. Occasional surviving specimens of the alga *Padina* were somewhat smothered by anemones on this reef platform. At least the lower surfaces of the plants were covered by anemones and many upper surfaces had anemones as well.

The ecological effect of Aiptasia anemone barrens

The finding of significantly lower numbers of demersal fish species at the sampling locations at the *Aiptasia* anemone barrens, despite the low sample sizes and the unequal comparative design, indicates that the effect these barrens have on the ecology of Galápagos reefs is significant. The almost complete replacement of the diverse assemblage at Punta Espinosa described by Wellington (1975) by *Aiptasia* anemones indicates a dramatic and fundamental shift in the structure of this marine community, and its potential for supporting fish and invertebrate communities. Most of the apparent ecological effects of

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these barrens have not been quantitatively evaluated, but one conspicuous conservation concern with global significance is that the largest remaining marine iguana (*A. cristatus*) colony in the world is located adjacent to the *Aiptasia* barren at Punta Espinosa (Laurie 1983, Snell and Marquez 2002). The adults of this herbivorous iguana species rely largely on the normally lush green macroalgae mats on tops of these reefs (juveniles feed in the intertidal and shallower subtidal). The anemone barrens have apparently reduced adult marine iguana foraging areas. The iguana population has experienced considerable famine mortalities, apparently related to recent El Niño-Southern Oscillation events (Romero and Wikelski 2001).

An alternate explanation for the significantly lower number of demersal fish species is that reef topography influenced fish assemblages and the presence of anemones. That is to say, open reefs support few fish species due to a lack of topographic features rather than because of the assemblage of sessile fauna. Indeed, the anemones might owe part of their success on these open reefs to the preference of omnivorous reef fishes (i.e., *Stegastes*) to boulder habitat that provides refuge. Still, replacement of the sessile benthos that provides biogenic fish habitat from the open reefs likely has adverse effects on many fish and mega invertebrates. The overall community is shaped by a combination of biotic and abiotic habitat.

Simulations of the emergence of Aiptasia anemone barrens

The results of the *pepino (S. fuscus)* and *Stegastes* removal simulations are consistent with observed anemone distribution patterns. First, the *Stegastes* damselfishes stand out as the strongest existing predatory controllers of *Aiptasia* anemones in the present model, as indicated by the strong response of anemones to *Stegastes* removal (Figure 3-3). These fishes, however, are found only around boulder habitat, which they use as refuge from their predators. Anemone barrens are found only on exposed platform reefs, where *Stegastes* spp. was not observed to venture. In cobble habitat near boulders, *Stegastes arcifrons* quickly attacked anemones that Scoresby Shepherd and I exposed by turning rocks.

In contrast to *Stegastes*, the sea cucumber *S. fuscus* inhabit exposed or moderately exposed platforms presumably because of its evolved defenses against predators (Francour 1997). *S. fuscus* is a suspected predator of *Aiptasia* because Bermeo-Sarmiento (1995) found 'cnidarian polyps' in *S. fuscus* stomachs that were collected from this same sub-region of the Galápagos. Being the only other predator of these anemones known to recently exist at functional levels (according to the specification of the Galápagos rocky reef model), it is quite possible that a recently emerged sea cucumber fishery has indirectly triggered the emergence of these anemone barrens by considerably reducing *S. fuscus* (Okey et al. 2004a)—which was perhaps the last remaining check on the anemone population on the open reef flats. This more spatially explicit hypothesis can be pursued further when Ecosim capabilities are combined in the future with the Ecospace routine, which is a habitat-based, spatially explicit routine.

Aiptasia is a well known aquarium pest that can take over all aquarium surfaces rapidly and harm preferred display species. Aquarists commonly use natural predators of *Aiptasia,* such as the hyppolytid shrimp *Lysmata wurdemanni* to control this anemone (Rhyne et al. 2001). Butterfly fish and nudibranchs (both discussed above) are less reliable for this purpose due to handling difficulties. *Lysmata* spp. are common in tropical areas of the eastern Pacific (Wicksten 1990) and at least three species in this genus are found in the Galápagos: *L. argentopunctata, L. galapagensis,* and *L. chica* (Hickman and Zimmerman 2000). Some species of *Lysmata* do not appear to prey on *Aiptasia* and, to my knowledge; it is not known whether these three do. Some members of the prawn genus *Rhynchocinetes* are also thought to feed on *Aiptasia,* and one species, *Rhynchocinetes typus,* occurs in the Galápagos (Hickman and Zimmerman 2000), but again it is not known to the present author whether this particular species feeds on *Aiptasia.* If any of these crustacean species do prey on, and help control, *Aiptasia* on Galápagos rocky reefs, their populations were likely reduced by the 1997/1998 El Niño event, at least on shallow reefs like much of the attached flora and fauna, thus enabling the anemone invasion. Established adult anemones might benefit from size or colonial refuge from such crustacean predators. Furthermore, most of these crustaceans are cryptic during the day when they can be found under boulders and active foragers at night. Thus, like *Stegastes*, these crustaceans seem more likely to have effects near boulder refuge habitats than on open reef flats where the anemone barrens are found. Notwithstanding these possibilities, crustaceans were not specified to consume anemones in the current model iteration because specific information on such feeding interactions was not available for the Galápagos reefs.

It is possible that lobsters, whelks, and conch normally exert some predatory control over *Aiptasia* as well. All are regularly removed as "byproducts" during *pepino (S. fuscus)* diving by fishers. These casual non-target removals are very effective in removing this biota (R. Bustamante, pers. comm.). Mega-invertebrates such as sea urchins might also graze on anemones, either incidentally or intentionally. There is no information on the feeding of *Aiptasia* anemones by any of these organisms, however, so these are not considered here as main candidates for *Aiptasia* emergence.

Many vertebrate species prey on anemones (Actinaria) and other orders in the anthozoan subclass Hexacorallia (Table 3-3). Some of these predators, or related species, were formerly more abundant in the Galápagos Archipelago than they are now. *Chaetodon auriga* can be seen only at the northern Darwin and Wolf Islands (Humann 1993), but it is rare, and *C. unimaculatus* has not been recorded, but two other *Chaetodon* species (Appendix B) are present in some locations. *A. meleagris* is uncommon, but has been recorded (Anon 2001). Hawksbill turtles were considerably more abundant in the past (NRC 1990, Bjorndal et al. 1993), and they might have shaped shallow reef ecosystems strongly (Jackson 1997, Bjorndal et al. 2000, Jackson 2001).

The few predators that remain in the vicinity of these anemone barrens have been ineffective in controlling the spread of *Aiptasia* on these platform reefs.

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The results of both predator removal simulations indicated competition for food between adult and juvenile (e.g., budding or settling) anemones, thus implying food limitation in the absence of predators. Although this is an expected result of using a mass-continuity *Ecopath* model, as a population will reach food limitation when all sources of mortality are removed, it indicates a reasonable result if these two predators are indeed the only remaining anemone predators in the system—an unresolved question. Nevertheless, these results are consistent with the pattern that anemone barrens, to the best of my knowledge, have appeared only on reef platforms that are protected from swell and that have minimal vertical profile or complexity that might offer shelter to cryptic predators. In addition, the Anemone barrens are often adjacent to mangroves, which are sources of considerable organic detritus to local marine ecosystems (Jennerjahn and Ittekkot 2002). Other anthozoans are known to get large proportions of their nutrition from such terrigenous sources (Risk et al. 1994). Manipulative field experiments should be conducted to explore these dynamics further, and to refine conceptual and quantitative models.

Table 3-3. Some predators of Aiptasia sp. or other Hexacorallia

Predator	Common name	Prey	Location	Source
Stegastes arcifrons	Yellow-tail damselfish	*Aiptasia* sp.	Galápagos	Grove & Lavenberg (1997)[a]
S. leucorus beebei	White-tail damselfish	*Aiptasia* sp.	Galápagos	Grove & Lavenberg (1997)[a]
Stichopus fuscus	*Pepino* sea cucumber	Cnidarian polyps	Galápagos	Bermeo-Sarmiento (1995)
Lysmata wurdemanni	Pepperment shrimp	*Aiptasia pallida*	Caribbean/Gulf	Rhyne et al. (2001)
Berghia verrucicornis	Aeolid nudibranch	*A. pallida*	Caribbean, etc.	Kempf (1991)
B. major	Aeolid nudibranch	*Aiptasia pulchella*	Hawaii	Muller-Parker (1984)
Arothron meleagris	Guineafowl puffer	*A. pulchella*	Hawaii	Muller-Parker (1984)
Chaetodon fasciatus	Butterflyfish	Anemones	The Red Sea	Fricke (1975)
Chaetodon auriga	Threadfin butterflyfish	*A. pulchella*	Hawaii	Muller-Parker (1984)
C. unimaculatus	Teardrop butterflyfish	*A. pulchella*	Hawaii	Muller-Parker (1984)
Clinocottus globiceps	Mosshead sculpin	*Anthopleura* spp.	Washington, USA	Hand (1996)
Aeolidia papillosa	Aeolid nudibranch	*Anthopleura* spp.	Washington, USA	Waters (1973)
Dermasterias imbricata	Leather star	*Anthopleura* spp.	Washington, USA	Sebens (1977)
>50 fish species	Fish	Anemones	The world	Ates (1989)
Eretmochelys imbricata	Hawksbill sea turtle	Anemones		Den Hartog (1980)
E. imbricata	Hawksbill sea turtle	*Zoanthus sociatus*	St. Croix, USVI	Mayor et al. (1998)
E. imbricata	Hawksbill sea turtle	corallimorpharian	Dom. Republic	Leon (2000)
Caretta caretta	Loggerhead sea turtle	Anemones	Gulf of Mexico	Plotkin et al. (1993)
Erignathus barbatus	Bearded seal	Anemones	Can. high arctic	Finley and Evans (1983)
Many bird species	Birds	Anemones	The world	Ates (1991)

Notes: Some of these anemone predators, or closely related groups, are less common in the Galápagos now than they were in the past, and this depletion of predators might partially explain the emergence of Anemone barrens (see text). (a) and personal observations.

In addition to the benefits these *Aiptasia* anemones might receive from adjacent mangroves, their gastrodermal cells contain the photosynthetic symbiont zooxanthellae (a dinoflagellate), thus enhancing their growth and vigor in times of food scarcity (Clayton and Lasker 1985). The occurrence of *Aiptasia* on

these shallow reef platforms suggests that their distribution is influenced by this symbiosis. Anemones can reproduce sexually and asexually by cloning through longitudinal fission, inverse budding or marginal budding, but pedal laceration is the method used by *Aiptasia* (G. Muller-Parker, pers. comm.) This method of asexual reproduction entails very low reproductive effort (Hunter 1984), and it is considered a good strategy for colonizing space because clones inherit high site-specific fitness (Schick 1991, Ayre and Grosberg 1995) and because budded clones can colonize space rapidly (G. Muller-Parker pers. comm.). Cloning can thus result in extensive patches on reef bottoms. Pedal laceration also ensures the transfer of zooxanthellae (Muller-Parker and D'Elia 1997). The advantages of exploiting carbon subsidies from both mangroves and zooxanthellae, as well as the low reproductive effort required for cloning, are compatible with patterns observed in the field and in the present simulations. These characteristics are likely contributors to the recent emergence of *Aiptasia* anemone barrens.

An explanation for the recent spread of the *Aiptasia* anemone in the Galápagos, other than the depletion of predators, is that the biological assemblages on the shallow reef flats of Fernandina were severely impacted by unusually high temperatures and other characteristics associated with the El Niño-Southern Oscillation events of the 1990s. Benthic surveys conducted during the 1997/98 ENSO event, have showed that nearly all fleshy macro algae and encrusting corallines were killed or bleached and up to 98% of the bed-forming sessile gastropods *Hipponix grayanus* and the giant barnacle *Balanus* spp. were dead by mid 1998 (R. Bustamante, unpubl. data). This mass mortality of the existing assemblage led to the availability of space for colonization by the opportunistic ("weedy") anemone species *Aiptasia* sp. The resulting physical pre-emptive presence of the anemone invaders, their consumption of settling propagules, and their nematocyst defenses all constitute reinforcing feedbacks that might stabilize the alternative community state of these anemone barrens as long as no successful predators or severe physical limiting mechanisms intervene. The reinforcing feedbacks related to the preemptive presence of these anemones is reasonable evidence that these anemone barrens constitute a true alternate stable state (Sutherland 1974, Connell and Sousa 1983, Carpenter 2000, Scheffer et al. 2001), but further scrutiny of this system will be required to evaluate this possibility.

Several studies (Schick 1991, Anthony and Svane 1995, Chadwick-Furman and Spiegel 2000) lend support to the general hypothesis that catastrophic disturbances can lead to barrens dominated by anemones. The extreme low tide in the northern Red Sea (discussed in the Introduction) was presumably a natural, albeit rare, event. In this Red Sea example, it is possible that the anemone-coral assemblages have adapted to that rare disturbance, albeit on a broad temporal scale. Similarly, did the Galápagos fauna on these shallow reef platforms ever adapt to the apparent deleterious effects of El Niño events that are as severe as those recently observed? Observed increases in the frequency and intensity of El Niño events corresponding with sudden shifts in community states would lend weight to the notion that exotic disturbances or natural disturbances with exotic (new) characteristics may have led to an alternative community state that has persisted for several years. It would not be surprising if the severe 1997/98 El

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Niño event was the proximate cause of the expansion of an anemone, probably already present in low abundance in the archipelago, but this would not rule out the possibility that a depletion of predators, by both ENSO-related disturbance and fishing, was a key reason for the spread of *Aiptasia*. Indeed, the simulations described here using a whole food web model of a Galápagos rocky reef indicates that anemones can spread over these reefs through trophic forces alone (i.e., the release from predator control), which could include the effects of unsustainable fisheries in the Galápagos Archipelago. Distinguishing the relative roles of these two general explanations is the task of the continuing investigation of the anemone barrens phenomenon. An iterative combination of manipulative experimentation (*sensu* Petraitis and Dudgeon 1999, Petraitis and Latham 1999) and continually refined whole food web dynamic simulations would be useful to this end.

The emergence and persistence of these sessile benthic cnidarians resembles recent observations of increases in planktonic cnidarians (jellyfish) in various oceans (e.g., Mills 2001). Both seem to be alternative energy pathways in marine ecosystems that we can reasonably assume to have intrinsically-reinforced persistence. This similarity is especially worrisome when considering the notion that both types of cnidarian increases might be partially caused by fisheries (Pauly et al. 2002, the present chapter). Such observations beg the question of whether it is possible that further anthropogenic degradation of marine ecosystems could lead to an 'age of cnidarians,' like the Cambrian Period.

CONCLUSIONS

Extensive carpets of *Aiptasia* anemones were discovered at Punta Espinosa and Punta Mangle on the east coast of Fernandina Island, Galápagos, Ecuador. They appear to have emerged at these locations and in the vicinity during the 1990s, but particularly in 1998-1999. Fish community surveys indicated that these *Aiptasia* carpets were negatively associated with number of fish species, thereby helping to justify the term 'anemone barrens.' Although the increasing intensity and frequency of El Niño-Southern Oscillation events might have initiated the emergence of these anemone barrens, preliminary simulations using a whole community trophic model indicates that the depletion of predators, e.g., through unsustainable fisheries or environmental disturbance, is an adequate causal mechanism for their emergence. It is possible that predator removals and direct El Niño forces worked in concert. These anemone barrens might be a true alternate stable state because of their potential ability to resist invasion by any other species through preemptive mechanisms that reinforce their own state, but this possibility awaits further evaluation.

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CHAPTER 4. A search for keystones in Prince William Sound, Alaska using a mass-continuity trophic model

ABSTRACT

Keystone species play a central role in shaping at least some marine communities in the sense that system-wide phase shifts can be mediated by the presence, absence, or the relative abundance of these key interactors. Identifying keystones is considered crucial for understanding the resilience of ecosystems to exogenous forces because non-linear, or catastrophic, community changes might hinge on the populations of one or a few species. Removal experiments are traditionally the most reliable approach for identifying keystone species, but such experiments can be accomplished only on small scales and with only a few types of species in any given system. An alternate field approach to identifying keystones is the tracking of 'natural experiments', but this places scientists at the whim of chance and carries the intrinsic problem of confounding. Intensive study of a few famous keystone species has improved understanding of particular marine ecosystems and led to the development of keystone theory, but a comprehensive analytical approach to identifying and ranking keystones has not been proposed until now. I describe the results of a series of simulated (functional group) removal experiments using a whole-system food web model of Prince William Sound, Alaska for the period 1994-1996. Four indices were used to rank functional groups, based on the results of these simulated removal experiments: *community importance, community longevity support, interaction strength index,* and a *keystone index.* Here, *interaction strength index* (ISI) refers to trophic, not per capita, interaction strength, and the *keystone index* is a functional group's ISI relative to the percent of the system's biomass represented by the group. Transient orcas produced the highest *keystone index* followed by avian raptors.

INTRODUCTION

The notion that one or a small number of species can dominate a biological community (Strong 1977, Paine 1980, Dayton 1985) implies that large changes in the populations of dominant species (e.g., trees, mussels, kelp) would fundamentally alter the communities in which they dominate. Protection of dominants from too much degradation by exotic forces, while preserving natural disturbance regimes, is thus necessary for enabling the maintenance of such communities within 'natural' bounds of variation. In contrast, the realization that, in at least some ecosystems, one or a small number of species influence biological communities to an extent that is disproportionately large relative to their abundance (or biomass) (Dayton 1972, 1984) implies that small changes in certain populations can cause large, or catastrophic, shifts in the state of communities.

This concept has fueled considerable interest since Paine (1966) described the phenomenon and used the term *keystone species* (1969) when referring to the asteroid predator *Pisaster ochraceus* that apparently structures a particular rocky intertidal community very strongly by preying mainly on

barnacles (*Balanus glandula*) and mussels (*Mytilus californianus*) thus preventing the competitively-dominant mussels from monopolizing a limiting resource; i.e., the open space in the intertidal zone at Mukkaw Bay, Washington, USA. Continued study has supported the notion that this intertidal community type is shaped strongly by keystone species, that interaction strengths vary greatly among species, and that indirect effects are common in marine rocky intertidal communities (e.g., Paine 1974, Menge et al. 1994, Menge 1995, Navarrete and Menge 1996). Paine's usage of the term *keystone species*—a species that maintains a community's structure, integrity, and stability by preventing a competitive dominant from monopolizing a resource—appeared to also fit sea otters (*Enhydra lutris*), which, when living in hard-bottom ecosystems, usually succeed in controlling herbivores that would otherwise control habitat-forming kelp canopies (Estes and Palmisano 1974, Estes and Duggins 1995, Estes et al. 1998). It also fit a number of other examples to which the term *keystone species* appears to have stuck (e.g., see Table 1 in Power et al. 1996).

Because of the dramatic community shifts implied by, and inherent in, the loss of *keystone species*, Power and her colleagues (1996) suggested that searching for and identifying them is essential for understanding how biological communities will be affected by species losses or reductions. Their suggestion appears even more urgent in light of recent revelations about the remarkable rates of recent reductions of higher trophic level species in marine ecosystems (Pauly et al. 1998a, Myers and Worm 2003, Springer et al. 2003). Based on musings by Mills, Soulé, and Doak (1993), Power et al. (1996) provided an operational definition for identifying and ranking *keystone species* that included an index called *community importance*; i.e., "…the change in a community or ecosystem trait per unit change in the abundance of the species', thus clarifying the *keystone* concept in terms very similar to Dayton's (1972) original discussion of *foundation species*. Finally, after presenting helpful approaches to revealing keystones of species in communities, they challenged ecologists to begin the important task of identifying keystones by measuring the relative effects of species or guilds in communities.

An important aspect of the notion of *keystone, or foundation,* species is the observation that changes in the abundance or biomass of most species in a system have imperceptible effects on populations of other species or the overall community, while one or a few species (generally with low abundances or biomass) have large, or a very large, effects (Dayton 1984, Paine 1992, Power et al. 1996). Removal of these species from the system might well cause strong cascading effects (e.g., Carpenter and Kitchell 1993, Shiomoto et al. 1997) or the loss of natural cascades (Pace et al. 1999) that structure the system. The salient point is that catastrophic, or at least non-linear, community changes can occur if and when such ecologically special species are reduced or removed.

Differences in relative interaction strengths, or the identity of keystone species, have been revealed in the past either through manipulative field experiments (e.g., Fowler 1981, Menge and Farrell 1989, Paine 1992) or by tracking 'natural experiments' (e.g., Estes and Duggins 1995, Estes et al. 1998) and the intensive study of such famous keystone examples has improved understanding of those particular

marine ecosystems. However, such approaches are inherently limited to either small scales or fortuitous opportunities to glimpse the roles of small subsets of species. In contrast, computer models of marine food webs are limited in the sense of their simplicity relative to the complexities of real systems, the uncertainties in their input parameters, and difficulties in verification and interpretation, but they do provide a framework in which all existing ecological information about a system can be integrated into dynamic simulations that can be designed to address particular questions. Computer modeling, in the present case, is an economical way to gain insights into such ecological questions as, 'which species are keystones?' and 'how *keystony* are they?' The results of such dynamic simulations are especially useful when they are considered as testable hypotheses, rather than presented as reality. The present search for keystones in Prince William Sound, Alaska featured a full series of simulated removal experiments from a dynamic trophic model in which all direct and indirect trophic effects can be tracked, and the predicted effects of each of these removals on all other functional groups in the system were quantified and examined with four indices, including an index of *community importance* (Mills et al. 1993, Power et al. 1996) and three others described in the Methods: *community longevity support, interaction strength index*, and a *keystone index*.

Paine (1992) suggested that, "Significantly, none of this information [for quantifying interaction strength] can be obtained without experimental manipulation..." Yodzis (2001) concluded that the only way to begin understanding such complex ecosystem dynamics is through multi-species models. Both authors are correct. The present chapter is an example of how empirically-based whole-system dynamic food web models can be used to identify and rank keystone species from the perspective of trophic interaction strength [the attribute preferred by Power et al. (1996) over per capita interaction strength as used by Paine (1992)]. As we shall see, the results of the present quantitative modeling approach match the theoretical model outlined by Power et al. (1996), which was inspired by per capita results from field manipulations (Paine 1992, Fagan and Hurd 1994). The present approach, because of its whole-system scope and its emergent properties that are keystone-like, addresses the criticism of Hurlbert (1997) that keystone-type patterns are, "..artifacts resulting from small sample sizes and the plotting of frequency distributions on arithmetic rather than logarithmic scales." With analytical approaches such as that presented here, combined with continued empirical refinement, the keystone species metaphor might no longer have such a, "...stultifying effect on ecological thought and argument."

As implied by Paine (1966, 1969) the abundance (or biomass) of keystone species might influence the diversity and the stability of ecosystems strongly. He found that almost half the megafaunal species vanished from the plot from which *Pisaster* was removed. Although there has been some healthy debate about the effects of overall species diversity from this manipulation (e.g., Lohse 1993), several other *keystone* examples corroborate the positive effect of keystones on diversity (Bond 1993). Paine (1969) inferred, based on his results and other examples, that the effect of removing certain *keystone species* on stability or ecosystem structure might be much stronger than any effect that complexity might

have on stability. This is a difficult question, as complexity and interaction strengths are interrelated. May (1973) developed models and analyses to evaluate the relationship of complexity and stability, not to evaluate relative interaction strengths in the sense of any search for strong interactors or keystones in a particular system. His basic analyses indicated that stability is inversely related to complexity, thereby spawning a decades-long debate. It now appears that the complexity of interaction-webs generally adds to stability because of the dynamical attributes of real systems such as adaptive foraging (e.g., Fowler and Lindstrom 2002, Kondoh 2003) as well as stabilizing aspects of metapopulation structure (Caswell 1982, Hastings 2003, 2004), refugia (Sih 1987, Gonzalez-Olivares and Ramos-Jiliberto 2003), and density dependence (Murdoch 1994). Such attributes likely have great bearing on the interaction strengths of species or groups, and they can probably either increase or decrease community effects of keystones, depending on the specific context (e.g., Power et al. 1996, Estes et al. 1998, Konar 2000, Piraino et al. 2002, Springer et al. 2003). Wooton's (1994) combination of experiments and path analysis to predict direct and indirect effects was a step toward an approach that could rank interaction strengths without having to conduct separate manipulative experiments for each potential interaction. Berlow et al. (1999) made additional progress during their testing of the interaction strength indices provided by Paine (1992) and Power et al. (1996).

The present chapter is presented as a next step toward identifying keystones and other strong interactors in biological communities, in this case by employing the mass continuity modeling approach *Ecopath with Ecosim* to examine trophic interaction strength and other indices on the scale of the whole system, thus applying whole system biological models to the problem, as advocated by Osenberg et al. (1997). Kitchell et al. (2002) performed functional group reduction simulations using an *Ecopath* model of the Central North Pacific, and their simulations allowed them to evaluate the keystone role of sharks, but their study was designed primarily to evaluate the community-wide effects of pelagic longline fisheries rather than as a systematic investigation of keystones and interaction strengths. Link (2002) expressed his uncertainty in the application of food web theory (e.g., connectivity and stability proxies) to marine ecosystems when presenting a 'topological food web' of the Northeast US Shelf. The present chapter is an example of the potential usefulness of food web theory when applied to a well refined and adequately complex mass-continuity model of a marine food web (see also Chapters 2 and 6, Okey et al. 2004b, Okey et al. 2004c) and when applied to a well-suited question. Nevertheless, inherent uncertainties in the model input parameters that characterize the Prince William Sound system inevitably lead to some uncertainty in the estimates and rankings in such keystone searches.
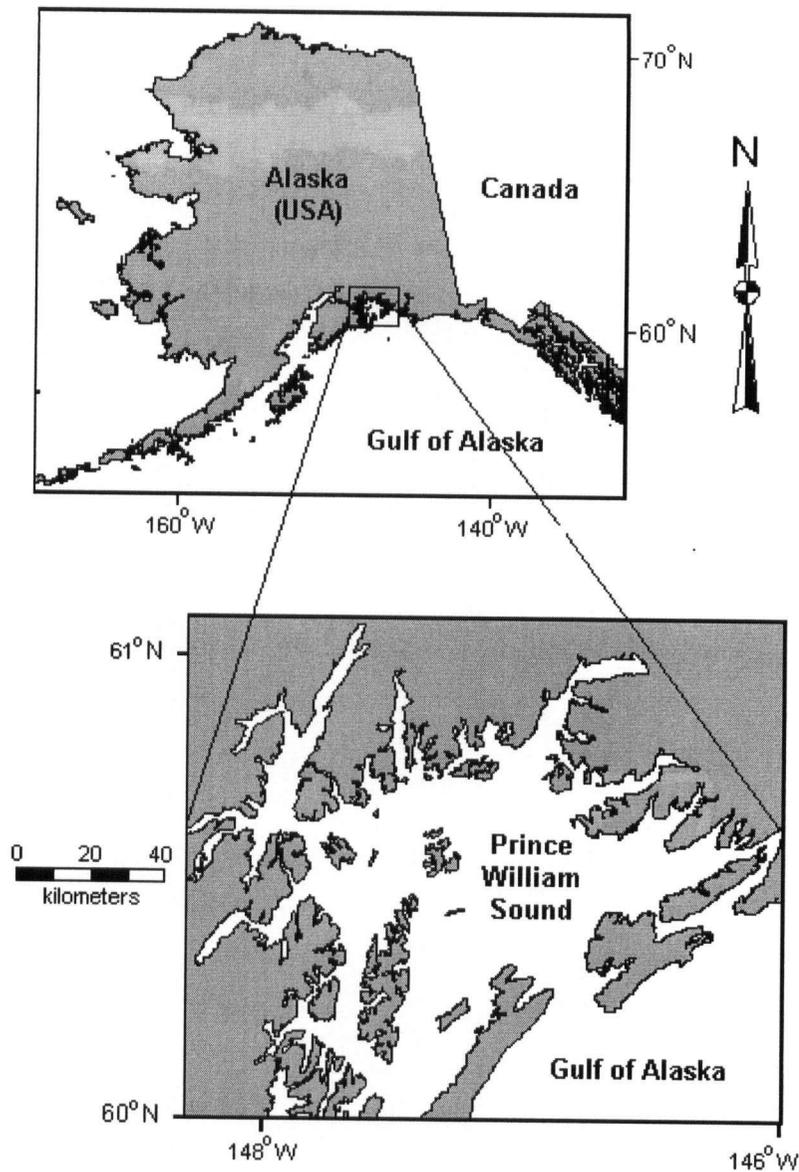
Figure 4-1. Map of Prince William Sound, Alaska, located at the northern apex of the Gulf of Alaska (North Pacific Ocean). Prince William Sound covers approximately 9,000 km^2, and it contains both shallow and deep habitats (to almost 800 m depth).

METHODS

Study location

Prince William Sound, Alaska (PWS) is a 9,000 km^2 protected sub-polar embayment located at the northern apex of the Gulf of Alaska (Figure 4-1). It is 15 times the size of San Francisco Bay, and has a highly articulated coastline and a variety of rocky, cobbley, and sedimentary habitats. It is well defined geographically by islands that separate it from the Gulf of Alaska, but there are two major channels through which flow strong tidal and coastal currents. The sound is a submerged portion of the highest coastal mountain range in the world, thus partially explaining its variety of depths, which approach 800

m. This topography and coastal oceanography condenses the moisture from the saturated air that is pushed from the Gulf of Alaska via southerly winds to produce the world's highest rates of precipitation. Runoff from this precipitation and from the many glaciers surrounding the sound, in addition to an incoming freshwater lens atop the Alaska coastal current, and the steep terrain contributes to a productive and unique ecology. In terms of salmon, the sound naturally produces mostly pinks (*Oncorhynchus gorbuscha*) due to the steep terrain and short cobbly spawning reaches.

The Prince William Sound model

The present search for keystones in Prince William Sound's biological community was made possible by the existence of a trophic model of the system's whole food web (Okey and Pauly 1999a, b) that was constructed using the *Ecopath with Ecosim* modelling approach (Christensen and Pauly 1992, Walters et al. 1997, Christensen et al. 2000). I coordinated a broad collaboration of experts on the biological community of the Sound to construct this model, which characterizes the state biomass flows throughout the PWS food web between 1994 and 1996. This chosen time period was five to seven years after the catastrophic *Exxon Valdez* oil spill occurred in PWS, which in turn lead to a rich array of ecological information about the Sound mostly from projects funded by the *Exxon Valdez* Oil Spill Restoration Program. The resulting *Ecopath* model of PWS included a total of 48 functional groups, but this was increased to 51 groups for the present exercise by dis-aggregating the shark group into its 3 species and by adding an 'octopods' group. These changes were an attempt to ensure representation of apex predators to increase the usefulness of a search for keystones.

The PWS model, at the time of the present analysis, included 6 marine mammal groups, 3 bird groups, 21 fish groups (including 6 'forage fish' groups), 9 benthic invertebrate groups, 1 squid group, 5 zooplankton groups (including gelatinous forms), 2 phytoplankton groups, 1 macrophyte group, and 3 detritus groups. Additional structural characteristics included the splitting of several lower trophic level groups, i.e., two zooplankton groups, phytoplankton, and one detritus group, into spatially defined sub-webs delineating nearshore and offshore habitats and the splitting of each of four fish species into two ontogenetic stages (resulting in 8 separate groups). Estimated mean fishery removals for that time period, including landings data, discard estimates, and other inputs, were also specified. The PWS model has been used to explore ecosystem-based policy alternatives with the goal of balancing disparate ecosystem objectives while restoring populations of concern (Okey and Wright in press). The collaborative approach to construction and the derivations of parameters is documented in accessible formats (Okey and Pauly 1999a, b). The shark and octopod group updates and the newly refined diet composition are presented in Appendices C and D, respectively. The updated basic input parameters are shown in Table 4-1, and summary statistics characterizing the PWS model are presented in subsequent tables. The detailed modelling methodologies for both the static *Ecopath* approach and the dynamic *Ecosim* approach are described in Chapter 1.

Simulated removal experiments

As in Chapter 3 (also published as Okey et al. 2004b), the basic approach used here to search for keystones was a full series of functional group removal simulations and a quantitative analysis of the results. This approach is developed further in the present chapter, as the search for keystones is the central focus here. *Ecosim's* basic gaming interface (Walters et al. 1997), which is included in *Ecopath with Ecosim* (Christensen et al. 2000, Pauly et al. 2000, Christensen and Walters 2004) (see Chapter 1 for detailed methods), was used to simulate the complete removal of functional groups from the food web, and repeat these removal experiments for all functional groups.

Enough mortality was imposed on a functional group to eliminate it from the system by the tenth year of 30-year simulations (increased mortality was imposed at year 2). Resulting system-wide changes in biomasses were recorded at year 30. The four indices described below were then applied to the estimated changes that each and all affected living functional groups experienced (i.e., the differences between the starting baseline biomasses specified for each functional group and the predicted ending biomasses [of all but the manipulated functional group]). Mortality rates were then reset to initial baseline levels before the next simulated removal. This was repeated for all 48 living functional groups (the three detritus groups were excluded from the analyses). All simulations were conducted using a universal prey vulnerability setting of v = 0.4, which represents a mix of top-down and bottom-up forces. This setting was shown to be a reliable and conservative overall setting in sensitivity tests with the PWS model (Okey and Wright in press) for purposes of scenario comparison. This setting also makes resulting analyses comparable to other analyses (Kitchell et al. 2002, Okey et al. 2004b). The 30-year time period for simulations was chosen simply because it was considered to be of adequate duration to examine emergent changes. In many cases functional groups appeared to reach equilibrium by 30 years, while in other cases the dynamics of some functional groups appeared to maintain some transient dynamics.

Indices for identifying and ranking keystones

Four indices were employed for evaluating the role of each functional group in the model: *community importance, community longevity support, interaction strength index,* and a *keystone index. Community importance* was proposed and operationalized by Mills et al. (1993) and Power et al. (1996), respectively, to provide an index of the impact of a species relative to its biomass. It is expressed here in a form suited to the present analysis (Equation 4-1).

Equation 4-1
$$CI_i = \frac{-\left[\sum_{a=1}^{47}\left(\left(\frac{B_a^{end}}{B_a^{start}}\right)-1\right)\right]}{\%B_i^{start}}$$

Where B_a is the biomass of one of the 47 affected living groups and $\%B_{i\,start}$ is the percent of the overall system biomass made up by the one affecting group before it was removed.

Community longevity support (CLS) is also an index of relative impact, but it is quite different from community importance in that the changes in affected groups are weighted by the estimated *longevity* of each affected group before being summed (Equation 4-2).

Equation 4-2

$$CLS_i = -\left[\sum_{a=1}^{47}\left(\left(\left(\frac{B_a^{end}}{B_a^{start}}\right)-1\right)\cdot\left(\frac{1}{P/B}\right)_a^{start}\right)\right]$$

Where $1/(P/B)_{a\,start}$ is the longevity of each affected group. Longevity is the inverse of the ratio of production to biomass (P/B), which is a basic (production rate) input parameter for each group. The use of longevity as an 'ecological weighting factor' is discussed by Okey and Wright (in press), but here it is used in the CLS index as a measure of the degree to which a species or functional group supports long-lived biomass in the overall system. The underlying assumption of this index is that long-lived biomass in a system is an integrative representor of ecosystem integrity because these organisms tend to be apex predators (with the arguable exception of baleen whales) that require the production and biomass of the underlying biotic components. That is to say, long-lived organisms require some *intactness* of community structure, whereas short-lived organisms do not. Long-lived organisms also tend to be the most charasmatic organisms in the general view of society, thus having the highest social value. From this perspective, maximizing overall system longevity arguably maximizes both ecological and social values, whereas a degradation of system longevity means that these values are degraded. The *Community Longevity Support* index is used to indicate the degree to which a species (or functional group) in the system *supports* overall community longevity in a given circumstance. This index provides a very different view than *community importance, [trophic] interaction strength index*, and the *keystone index*.

The *interaction strength index* (ISI) used here is a trophic formulation of the per capita function envisioned and used by Paine (1966, 1969, 1992). The ISI measure is similar also to 'functional importance' as discussed by Hurlbert (1997). Here it really indicates the estimated 'trophic interaction strength' of the manipulated group; it is equivalent to 'absolute value of a community impact' mentioned by Power et al. (1996) (Equation 4-3). Summing the *absolute value* of the resulting biomass changes prevents potential underestimations of system impacts, which can occur when using the CI.

Equation 4-3

$$ISI_i = \sum_{a=1}^{47}\left|\frac{B_a^{end}}{B_a^{start}}\right|$$

Table 4-1. Basic parameters of the 51 compartment Ecopath model of the 1994-1996 Prince William Sound food web arranged by trophic level and presented with 'community role' indices generated from a full series of functional-group removal simulations. See text for index formulations and notes below for descriptions.

Group name	Trophic level	Biomass (t·km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	CI [a]	CLS [b]	ISI [c]	Keystone index [d]
Transient orca	5.41	0.001	0.05	6.04	0.00	-317.83	-46.2	14.6	66330.8
Salmon shark	5.10	0.221	0.10	7.30	0.14	-1.02	-31.9	7.9	161.5
Resident orca	4.92	0.015	0.05	8.67	0.00	-0.12	-0.2	0.2	54.4
Sleeper shark	4.88	0.110	0.07	3.65	0.00	-0.07	-14.2	6.5	265.3
Halibut	4.52	0.677	0.32	1.73	0.81	-0.02	-2.2	1.1	7.4
Pinnipeds	4.45	0.072	0.06	25.55	0.99	-0.96	-3.5	4.7	293.4
Porpoise	4.40	0.015	0.24	29.20	0.99	-4.26	0.5	4.3	1299.7
Lingcod	4.27	0.077	0.58	3.30	0.82	-0.07	-1.9	0.4	25.9
Adult arrowtooth	4.25	4.000	0.22	3.03	0.16	-0.14	-57.6	21.1	23.9
Adult salmon	4.18	3.410	1.31	13.00	0.94	0.02	22.6	5.9	7.8
Pacific cod	4.06	0.300	1.20	4.00	0.66	0.09	5.2	1.7	26.1
Sablefish	4.03	0.293	0.57	6.42	0.96	-0.05	0.7	1.8	27.9
Juv. arrowtooth	4.01	0.855	0.22	3.03	0.95	-0.63	-53.8	20.9	110.6
Spiny dogfish	3.96	0.110	0.09	4.77	0.83	-0.24	-3.3	0.9	38.2
Avian raptors	3.92	0.002	0.05	36.50	0.00	-108.59	-27.7	12.4	28064.8
Octopods	3.80	0.050	3.10	11.70	0.95	0.50	4.3	1.6	143.9
Seabirds	3.80	0.022	0.17	150.60	0.98	-5.15	-20.2	4.2	869.7
Deep demersal fishes	3.77	0.960	0.93	3.21	0.99	-0.17	-5.0	7.0	32.8
Adult Pollock (1+)	3.76	7.480	0.71	2.56	0.97	0.00	-12.6	9.0	5.4
Rockfish	3.74	1.016	0.17	3.44	0.99	-0.01	-0.2	1.1	4.9
Baleen Whales	3.65	0.149	0.05	10.90	0.54	-0.01	-0.4	2.2	66.3
Juvenile salmon (0-1)	3.51	0.072	3.91	62.80	0.99	0.59	18.7	5.8	367.1
Nearshore demersals	3.35	4.200	1.00	4.24	0.82	0.01	19.5	10.1	10.9
Squid	3.26	3.000	3.00	15.00	0.94	-0.03	-6.1	5.8	8.8
Eulachon	3.25	1.000	2.00	18.00	0.90	0.05	10.9	3.1	14.1
Sea otter	3.23	0.045	0.13	117.00	0.01	-1.65	-3.0	8.1	812.1
Deep epibenthos	3.16	30.000	3.00	10.00	0.96	-0.03	-42.7	29.4	4.4
Capelin	3.11	0.367	3.50	18.00	0.92	-0.02	1.5	0.8	10.3
Adult herring	3.10	2.810	1.54	18.00	0.98	-0.08	10.3	13.4	21.7
Juvenile pollock (0)	3.07	0.110	2.34	16.18	0.97	-0.52	-12.8	9.3	385.0
Invert-eating birds	3.07	0.005	0.20	450.50	0.00	-3.08	0.2	0.8	689.2
Sandlance	3.06	0.595	2.00	18.00	0.95	-0.01	1.0	0.8	6.2
Shallow lg epibenthos	3.06	3.100	2.10	10.00	0.79	-0.06	-20.6	8.4	12.3
Juvenile herring	3.03	13.406	0.73	18.00	0.97	-0.02	9.7	13.4	4.5
Jellies	2.96	6.390	5.00	29.41	0.01	-0.03	-16.4	5.9	4.2
Deep sm infauna	2.25	49.400	3.00	23.00	0.92	-0.01	-53.3	15.2	1.4
Near omnivorous zoops	2.25	0.108	7.90	26.33	0.99	0.00	0.1	0.1	3.4
Omnivorous zooplank	2.25	24.635	11.06	22.13	1.00	0.00	31.1	11.6	2.1
Shallow sm infauna	2.18	51.500	3.80	23.00	0.94	-0.03	-77.5	35.9	3.2
Meiofauna	2.11	4.475	4.50	22.50	0.95	0.00	0.0	0.6	0.6
Deep lg infauna	2.10	28.350	0.60	23.00	0.93	0.00	4.6	3.7	0.6
Shallow sm epibenthos	2.05	26.100	2.30	10.00	0.98	0.01	24.9	11.0	1.9
Shallow lg infauna	2.00	12.500	0.60	23.00	0.53	-0.01	1.4	3.7	1.4
Near herbiv zooplank	2.00	0.136	27.00	90.00	0.98	-0.03	-0.2	0.2	6.0
Herbivorous zooplank	2.00	30.000	24.00	50.00	0.98	-0.05	-133.7	40.0	6.0
Near phytoplankton	1.00	5.327	190.00	-	0.95	0.05	15.2	6.7	5.7
Offshore phytoplankton	1.00	10.672	190.00	-	0.95	-0.14	83.0	82.2	34.9
Macrophytes	1.00	125.250	4.00	-	0.13	0.00	13.2	6.5	0.2
Nekton falls	1.00	2.000	-	-	0.77	-	-	-	-
Inshore detritus	1.00	19.520	-	-	0.54	-	-	-	-
Offshore detritus	1.00	114.480	-	-	0.59	-	-	-	-

Notes: Values in bold have been calculated with the *Ecopath* software; other values in the first four columns are empirically based inputs, or values that were adjusted from empirically based estimates during balancing. P/B and Q/B are the ratios of production and consumption to biomass, respectively; ecotrophic efficiency (EE) is the proportion of production not consumed or exported.

a. CI (*community importance* (i.e., Mills et al. 1993, Power et al. 1996)) is here the sum of the opposite (sign) of the real value of the predicted change of all affected living groups (at the end of a 30-year dynamic simulation in which group i was completely removed by year 10) divided by the percent of the overall biomass of living groups represented by species i before it was removed;

b. CLS (*community longevity support*) is the sum of the opposite (sign) of the real value of the predicted change of each affected group multiplied by its longevity (i.e., the inverse of the P/B);

c. ISI (*interaction strength index* or *trophic interaction strength*) is the sum of the absolute values of the predicted change of all affected groups;

d. The *keystone index* is the ISI divided by the percent of the system's overall living biomass represented by group i before it was removed.

The *keystone index* is the ISI expressed in terms of the relative biomass of group i before it was removed (Equation 4-4) (see also Power et al. 1996 for definition of keystone species).

Equation 4-4. $$Keystoneness = \frac{ISI_i}{\%B_i^{start}}$$

Frequency histograms of the rankings of all living groups were produced to qualitatively evaluate the sensitivity and apparent usefulness of each index. Groups were also ranked according to the indices, and according to trophic level, and presented in tables and figures to provide a view of the roles of various functional groups in the PWS biological community.

RESULTS

The basic parameters of the refined and balanced *Ecopath* model of Prince William Sound are shown in Table 4-1 along with the results of the full series of removal simulations in the form of calculated rankings according to the four indices employed here. The functional groups in Table 4-1 are ranked by trophic level calculated as the biomass proportion weighted average of the trophic levels of diet items plus one. Table 4-2 shows the summarized community characteristics of Prince William Sound, Alaska, according to the present iteration of the model. Table 4-3 is a quantitative characterization of the flows of biomass from primary producer and detritus sources to consumption, detritus, and respiration at each trophic level in the PWS food web. Throughput is also displayed at each trophic level.

Table 4-2. Basic flows and indices describing the 1994-1996 Prince William Sound, Alaska Ecopath model

Flows	$(t{\cdot}km^{-2}{\cdot}year^{-1})$
Calculated total net primary production	3,541
Net system production	1,022
Sum of all production	5,158
Sum of all consumption	6,705
Sum of all exports	1,087
Sum of all respiratory flows	2,519
Sum of all flows into detritus	3,749
Total system throughput	14,059
Total catches	8.68

Biomass	$(tonnes{\cdot}km^{-2})$
Total living biomass	453

Indices	
Total primary production/total biomass	$7.81\ year^{-1}$
Total biomass/total throughput	$0.03\ year^{-1}$
Total primary production/total respiration	1.4057
Proportion of flows originating from detritus	0.44
Connectance index	0.16
Mean trophic level of the catch	3.81
System omnivory index	0.21 TL units

Note: Flows and biomasses are expressed in wet weight

Table 4-3. Flows from primary production and detritus through the Prince William Sound, Alaska model

TL	From primary production				From detritus				
	Consumed	To detritus	Respiration	Throughput	Consumed	Export	To detritus	Respiration	Throughput
VI	1	2	2	5	1	0	1	1	3
V	5	8	14	28	3	0	4	5	12
IV	24	54	107	186	12	0	18	20	50
III	147	381	539	1068	48	0	89	89	227
II	1060	1213	683	2955.	226	0	885	1058	2169
I	2955	585	0	3541	2169	1083	0	0	3760
Sum	4192	2244	1346	7784	2459	1084	998	1173	6221

Notes: Flows are expressed in $(tonnes \cdot km^{-2} \cdot year^{-1})$. Some flows reach trophic level VI because some organisms within some functional groups are supported by energy that has traversed six links from primary producers. Export from primary production is not shown, as it was negligible (3).

The frequency distribution of *community importance* indicated that 46 of the 48 living functional groups in the PWS model had almost no effect on the system when they were removed entirely, while transient orcas and avian raptors had strong effects (they scored far from zero) (Figure 4-2a). In contrast, the frequency distribution of *community longevity support* included at least six modes of 'influence' (Figure 4-2b). The six secondary modes for *community longevity support* seen on this figure include at least ten strongly negatively affecting species and at least two strongly positively affecting species for this index (Figure 4-3).
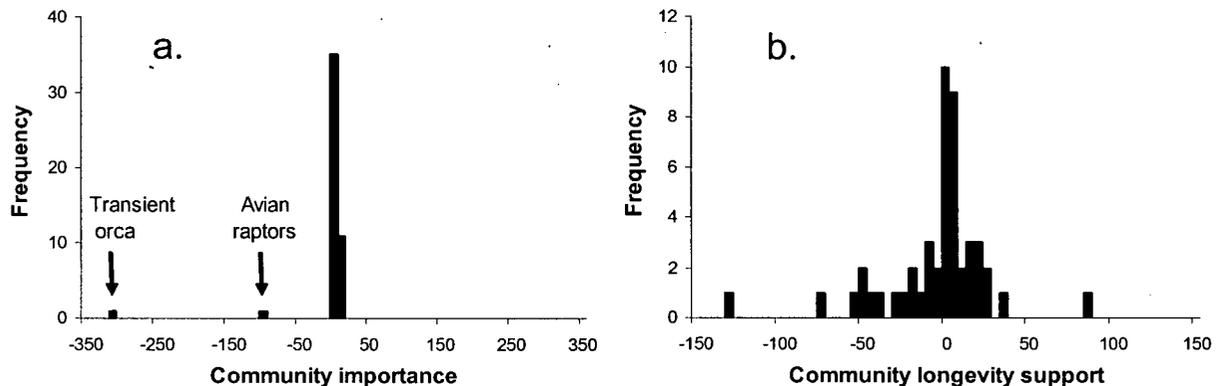
Figure 4-2. Frequencies of the *community importance* and *community longevity support* scores for all functional groups in the Prince William Sound model. *Community importance* is the sum of the opposite (sign) of the real value of the predicted change of all affected living groups (at the end of a 30-year dynamic simulation in which group i was completely removed by year 10) divided by the percent of the overall biomass of living groups represented by species i before it was removed (see Power et al. 1996). The two modes to the left of the central mode are transient orca and avian raptors. *Community longevity support* is the sum of the opposite (sign) of the real value of the predicted change of each affected group multiplied by its longevity (i.e., the inverse of the P/B).

By way of comparison to Figure 4-3, commercial fisheries had a very strong negative effect on community longevity (-301), while subsistence fisheries produced only a small effect (-15) and recreational fisheries had virtually no net effect (-1). This index of the effects of fisheries on the whole system also corresponded with a *pinniped support index* (PSI) applied to the three fisheries categories, PSI is the estimated relative support provided to pinniped biomass. Commercial fisheries produced a PSI
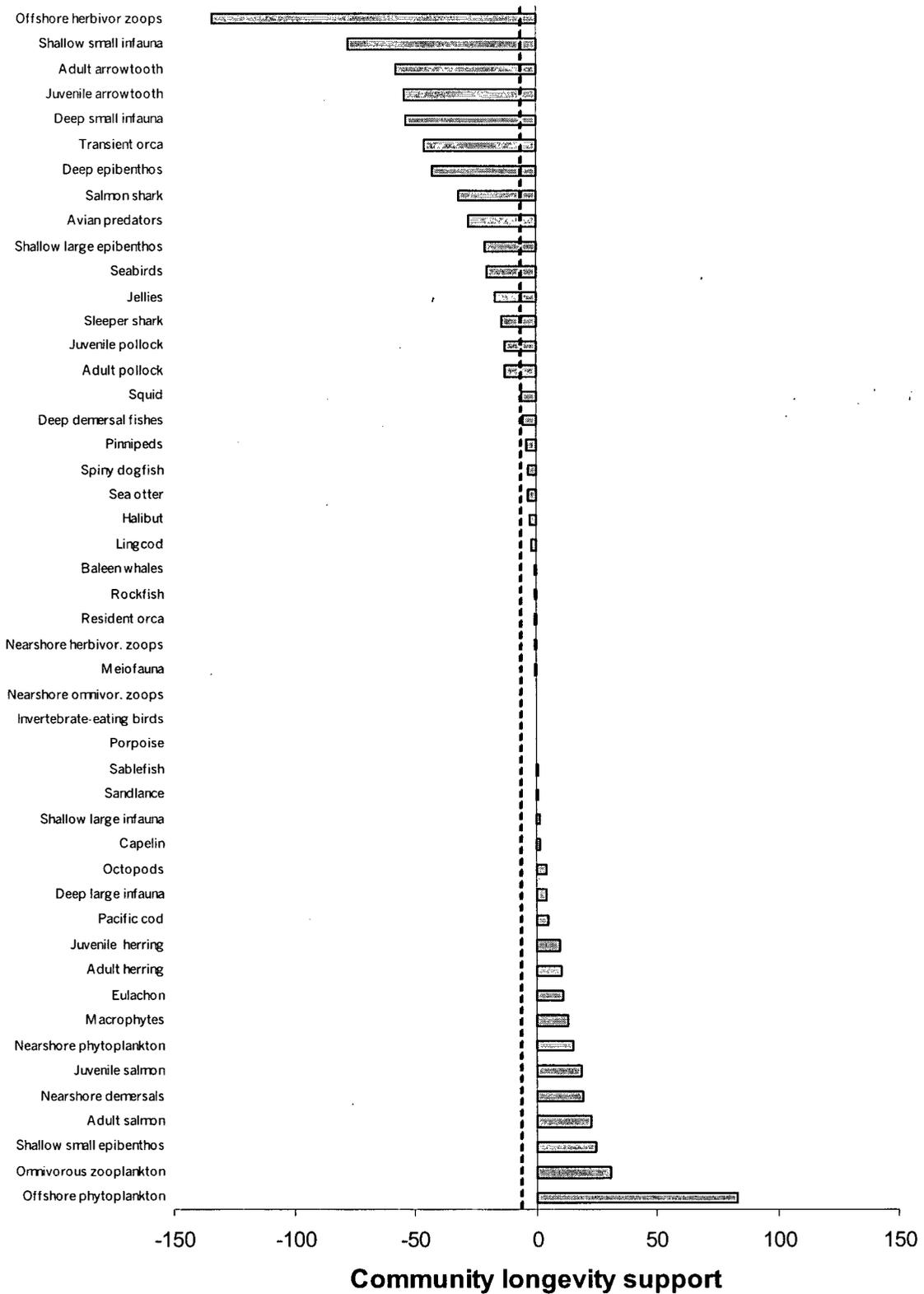
Figure 4-3. *Community longevity support* index rankings for all groups in the Prince William Sound model. The dashed line is the mean of the functional group values, and is negative (-7.7) as expected in predator prey-relationships (also shown by Paine 1992 for per capita interaction strength).

of -143, followed by subsistence (-98), and recreational fisheries (1.0), indicating that elimination of commercial fishing in PWS would allow a 143% positive increase from the baseline rate of pinniped change over the 30 year simulation; eliminating subsistence fishing would allow a 98% positive increase from the baseline rate of change; and eliminating the recreational fishery would cause a 1% decrease from the baseline rate of change (negligible effect on present trends). The pinniped functional group in PWS is comprised of 90% harbor seals (*Phoca vitulina richardsi*) and 10% Steller sea lions (*Eumetopias jubatus*).

More insight into the *community longevity support* index is provided when these results are plotted against the percent of the system biomass represented by each manipulated group (Figure 4-4).
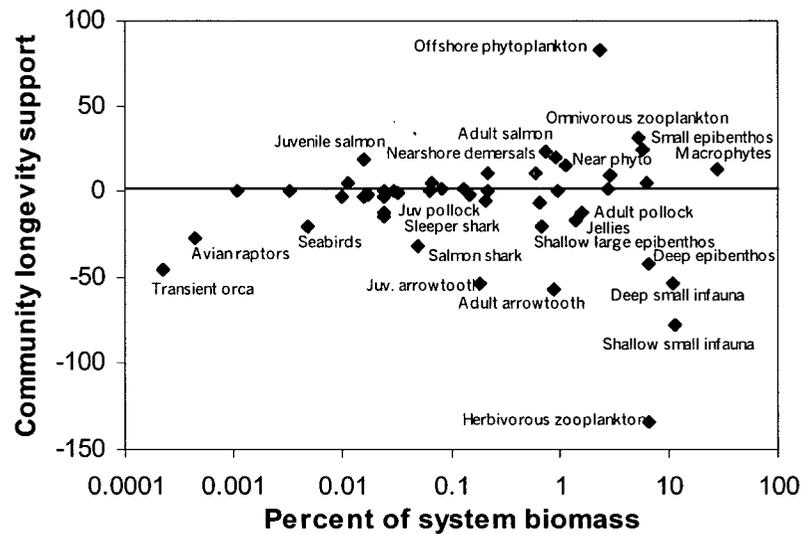
Figure 4-4. *Community longevity support* of a species (the sum of the longevity-weighted change in biomass of affected groups) versus the percent of the system's biomass it makes up before removal. Percent of system biomass was presented on a log scale. All functional groups with a change greater than 10 were labeled.

The *interaction strength index* and the *keystone index* appear at first glance to produce multiple modes, but these are displayed on log scales. Each of theses distributions thus indicates a small number of primary interactors and a larger group of secondary interactors (right side and middle of each abscissa in Figure 4-5). Still, these indices appear more sensitive to revealing the identity of potential secondary keystones than does *community importance* (Figure 4-2a). The top interactors and keystones that stand out on the right sides of Histograms 4-5a and 4-5b are listed from the tops of Graphs 4-6a and 4-6b, respectively.
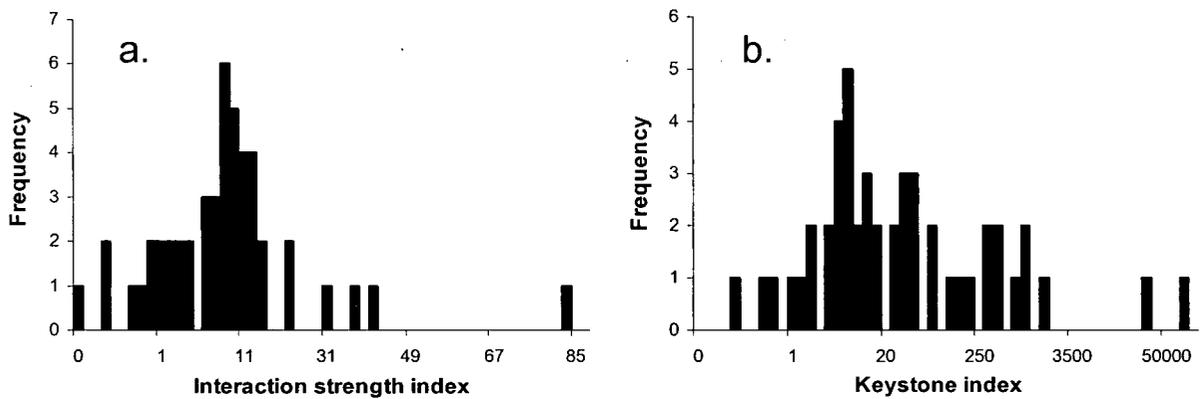
Figure 4-5. Frequencies of the *trophic interaction strength* index and *keystone index* scores for all functional groups in the Prince William Sound, Alaska model. Here *interaction strength index* is the sum of the absolute values of the predicted change of all affected groups. And *keystone index* is the ISI divided by the percent of the system's overall living biomass represented by group i before it was removed. Both of these indices are displayed on a log scale with the maximum value displayed near the top end of each scale.

Figure 4-6 shows all functional groups in the model ranked in order of trophic interaction strength (plotted on a normal scale) and keystoneness (displayed on a log scale). The term *keystoneness* was used by Hurlbert (1997). The contrast between these indices is clearly shown here in how the system's functional groups are ranked differently. This figure also shows the emergence of transient killer whales and avian raptors as the clear primary keystones in this iteration of the PWS model. Plotting the keystone index against the percent of the system biomass represented by each group (both on log scales) provides the most satisfactory view of keystones in the PWS system (Figure 4-7). Here, a secondary group of keystones (labeled groups above the diagonal) is apparent in addition to the two primary keystones.

DISCUSSION

This report presents the first example of a distribution of *community importance* values generated by a whole system trophic model, which are matched by the educated prediction of leading thinkers on the subject (Dayton 1984, Power et al. 1996), but the distributions generated using the three other indices employed here were perhaps even more interesting because of their apparently greater sensitivity to the removal experiments in terms of revealing additional species or groups with strong interaction effects on the system—a secondary cluster of strong interactors.

If the present analysis of the Prince William Sound biological community is reasonably correct, then the results represent an example that supports the suggestion of Power et al. (1996) that the distribution of *community importance* values for species or functional groups within communities should be commonly distributed such that fluctuations of the great majority of groups has almost no community-wide effects while a small number of groups (species) has very large effects (compare Figure 4-2a in the present contribution with Figure 1b in Power et al. (1996)) (see also Dayton 1984). The whole-food-web

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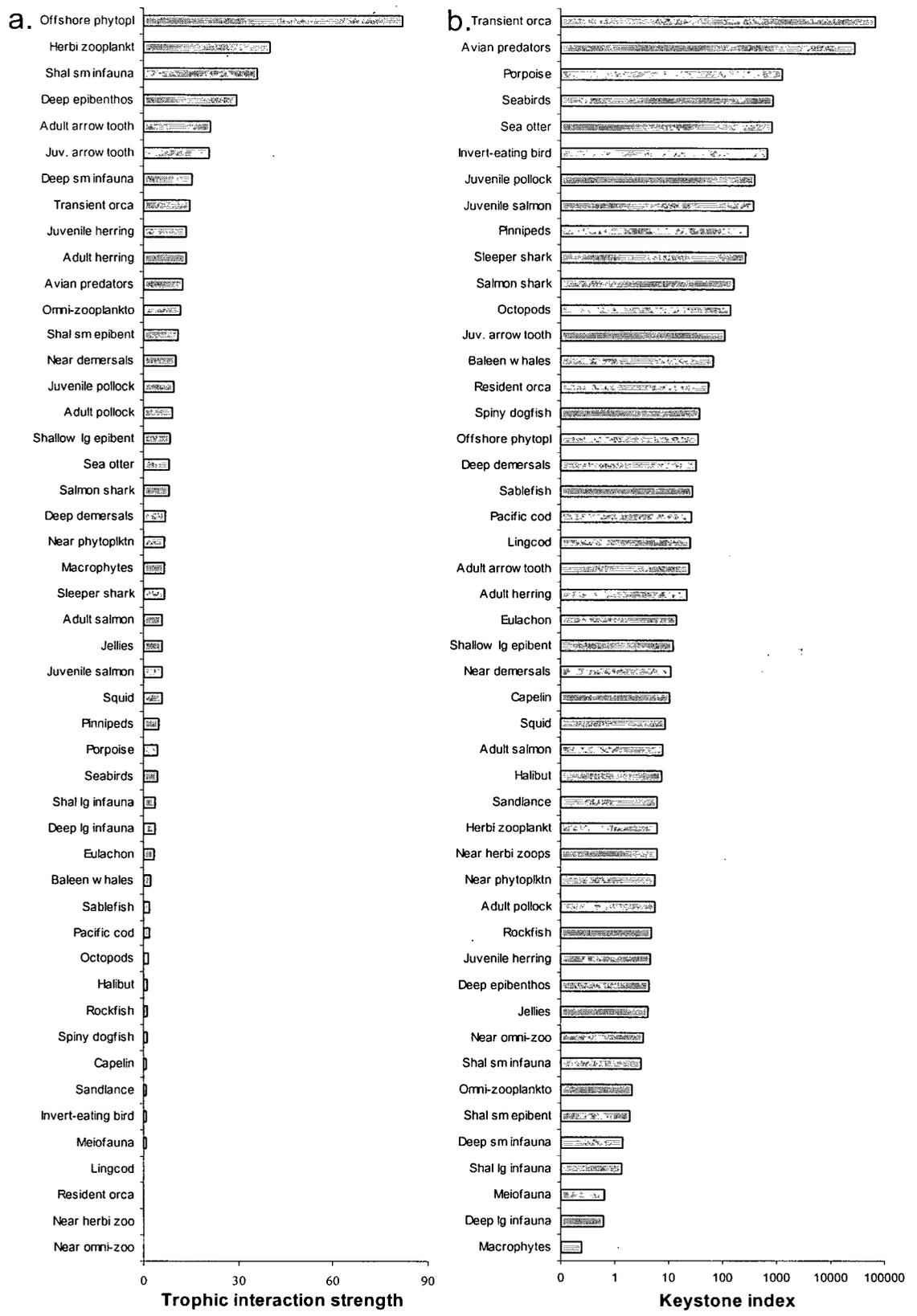
Figure 4-6. *Interaction strength index* and keystoneness of all living groups in the 1994-1996 Prince William Sound, Alaska Ecopath model. See Methods and Table 4-1 for explanation of indices.

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trophic modeling approach employed here enabled the estimation of such whole-system distributions and rankings because it allowed for sequential simulated removals of all functional groups in the system for a sufficiently long time period for all (direct and indirect) trophic effects to become evident. It also allowed for analyses of collective functional group responses. Many of the functional groups, especially at high and middle trophic levels, are individual species, but those at lower trophic levels are aggregated groupings of ecologically similar species. At the broad scale that this model is designed to examine, such aggregation does not detract from the information content of the simulation outputs. The notion of *keystone guilds*, for example, can be as useful as the notion of guilds for understanding ecosystems and for management purposes (Power et al. 1996). Still, this model can be re-structured in terms of disaggregating particular sub-webs (sensu Paine 1963) and aggregating other sub-webs, depending on the question at hand or the proclivities of particular researchers.
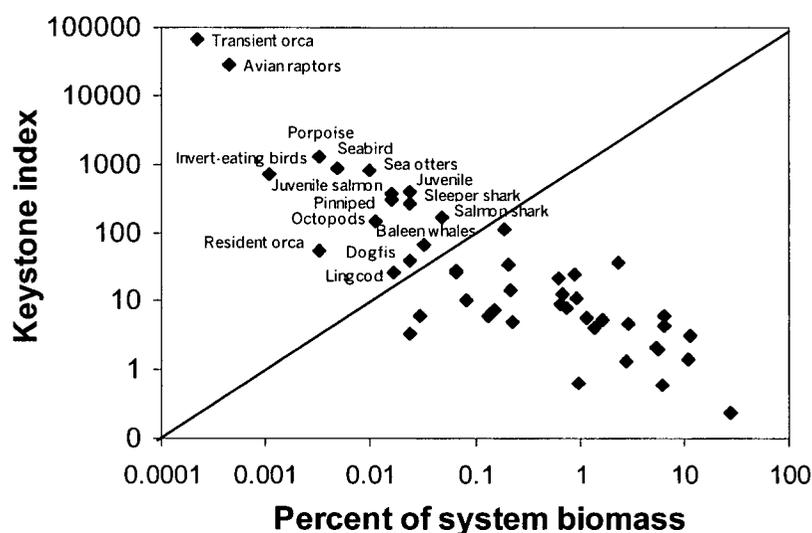
Figure 4-7. *Keystone index* ranking of a functional group (sum of the absolute change in biomasses of affected groups divided by the percent biomass of the affecting group before removal) versus the percent of the system's biomass it makes up before removal. Here, both axes are presented on log scales. The diagonal line is not x = y, but it roughly bisects the full range of system spread in this view of the system components. Groups in the upper left hand corner display the most keystoneness.

Transient killer whales (*Orcinus orca*) emerge from the removal simulations as super-predators. Some lines of evidence suggests that these transient orcas are dietary specialists on marine mammals (Bigg 1987, Matkin and Hobbes 1999, Saulitis et al. 2000), whereas resident orcas (also *Orcinus orca*) consume mostly fish (see also Pauly et al. 1998b on trophic levels of marine mammals). The estimated trophic level of transient orcas in the PWS model is 5.41, and the *keystone index* ranked them highest by far (Table 4-1, Figure 4-7). In addition, they were ranked eighth overall by the *interaction strength index* (Figure 4-6); they had the most negative *community importance* value (Table 4-1, Figure 4-2a); and the sixth most negative *community longevity support* value (Figures 4-3 and 4-4).

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If, in the past, transient orcas fed much more on baleen whales, as suggested by Estes et al. (1998) and Springer et al. (2003), then their trophic position might be almost one full level lower than currently estimated. This lower trophic level would, perhaps, make more sense in the context of the dynamic constraints (sensu Pimm 1984) and energetic constraints (Connell and Orias 1964, Paine 1966) of food webs. The intelligence and adaptiveness of orcas might prevent dynamic instability even at this high trophic level, but if orcas are the main cause of the observed pinniped (and other) declines in the North Pacific in recent decades, as postulated by Springer et al. (2003), then the current trophic position of transient orcas might well be energetically unstable. That is to say, large biomasses of baleen whales with a trophic level of approximately 3.5 could support transient orcas in an energetically stable manner, but smaller populations of pinnipeds with trophic levels of approximately 4.5 might not be able to. Considered in the simplest of trophic terms, trophic level 3.5 should support ten times more killer whales than trophic level 4.5, assuming the transfer of energy from one level to the next is 10% efficient (Lindeman 1942, Pauly and Christensen 1995). Thus, the removal of baleen whales might, in theory, leave behind almost 10 times too many orcas for pinnipeds to support (depending on aspects of diet, prey switching, and other aspects of whole food web energy allocation). If these predators are forced in this way to shift to previously untargeted prey, it is plausible that they mediate considerable ecological change (Mangel and Clark 1988, Springer et al. 2003, present contribution).

Avian raptors emerge from the removal simulations as super-predators in Prince William Sound as well. This group includes Bald Eagles (*Haliaeetus leucocephalus*) and Peregrine Falcons (*Falco peregrinus*). The emergence of avian raptors group as one of the two stand-out keystones in this iteration of the PWS model is surprising from a several standpoints. First, birds are simply not widely thought of as a group that strongly structures marine ecosystems. Although they stand out in their second position on the keystone index scale, they are ranked eleventh on the *trophic interaction strength* scale (Figure 4-6), and ninth, behind salmon sharks, in terms of negative *community longevity support*. Thus, avian raptors are indicated to have moderately large influences on the system. Their high keystone index ranking indicates their potentially strong influence at higher trophic levels if their populations were higher than in the present post oil spill model. However, the role of any given species is context dependent in terms of time, space, and community structure (Power et al. 1996) and so linear extrapolations of effects should not necessarily be expected (Piraino et al. 2002). Secondly, although the strongest indicated keystone group—transient orcas—also has the highest trophic level in the system, the avian raptor group ranks fifteenth in terms of trophic level (TL $=$ 3.92) while it is indicated to be the second strongest keystone in the system (Figures 4-5b and 4-6). This is consistent with the observations by Power et al. (1996) that keystones need not be the highest trophic level species in a system and by Piriano et al. (2002) that the identification of keystone species is not always predictable a priori. Still, avian raptors are the apex predators of their own sub-web, and the lower trophic level ranking is partially due to the omnivory and scavenging habits of Bald Eagles. The invertebrate-eating bird and seabird groups scored relatively low in

terms of trophic interaction strength, but they were both positioned towards the top of the secondary keystone cluster (Figures 4-6 and 4-7). Furthermore, the negative effects of seabirds on *community longevity* are comparable to those of Avian raptors. Invertebrate-eating birds are estimated to have no effect on *community longevity*.

The three shark groups, Pacific sleeper sharks (*Somniosus pacificus*), Salmon sharks (*Lamna ditropis*), and Spiny dogfish (*Squalus acanthias*) were ranked relatively high in terms of keystoneness (10th, 11th, and 16th, respectively) and a little lower in terms of trophic interaction strength (23rd, 19th, and 40th). They were respectively ranked 13th, 8th, and 19th in terms of *community longevity support*. The moderate rankings for sharks in these simulations were surprising because a series of removal simulations using the previous iteration of the PWS model indicated that the aggregated PWS shark group was a very strong interactor, ranking second to Transient orcas in terms of keystoneness. Those previous high rankings for the shark group were because the shark group accounted for a very large proportion of the mortality of Arrowtooth flounder—a dominant fish group in the model, a very strong interactor, and a moderate keystone itself. Furthermore, shark diets and consumption rates were updated with new site-specific information (e.g., Hulbert and Rice 2002), and the decision was made to use conservative values for consumption rates. For example, a daily ration of 2% for salmon sharks was taken from Nagasawa (1998), but since salmon sharks have high metabolic rates (like some pelagic sharks), their real daily rations might be closer to 5%, which would increase the estimated impact rankings for salmon sharks in the PWS model. Similarly, predation of pinnipeds by sharks is not included in the present iteration of the model, as the distribution and extent of this predation is currently highly uncertain, and such information has not been provided for any iteration of the PWS model. Some anecdotal information indicates that sleeper sharks might feed on pinnipeds in Alaska, and this would increase the scores of sleeper sharks in terms of keystoneness and interaction strength, in addition to changing the results of pinniped simulations, etc. The power of the present analytical approach is that re-assessments can be made with relative ease as such new information becomes available.

Simulations by Kitchell et al. (2002) indicated that neither reducing nor increasing shark biomasses through simulated fishery policies would have much effect on the pelagic fish community of the Central North Pacific, i.e., those sharks are not a keystone group in that setting. Pelagic systems are, however, fundamentally different from nearshore and coastal systems, and from any other kind of ecosystem (Dayton 1984). The central north Pacific (from the equator to 40° N latitude) is a pelagic system characterized mainly by a suite of fast fish predators, their fish prey, and the plankton communities supporting them, whereas PWS is a sub-polar coastal system with many benthic and demersal components and is characterized by a diverse spectrum of taxonomies and life histories. The negligible effect of removing the sharks group from the Central North Pacific model was due to the slow metabolism (and low consumption rates) of sharks relative to tunas and billfishes as well as emergent

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compensatory responses within the overall apex predator guild related to the considerable overlap of diets between sharks and the other fish predators.

Sea otters were ranked 5th overall in terms of keystoneness, towards the top of the secondary cluster (Figures 4-6 and 4-7). They were ranked 18th in terms of trophic interaction strength (Figure 4-6) and they had a very small overall negative effect on *community longevity support* (Figure 4-3). There are two reasons that sea otters ranked as only 'moderate keystones' (in secondary keystone cluster) in the PWS model rather than as strong keystone species. First, much of the substratum of Prince William Sound as a whole is comprised of soft bottoms, and infaunal bivalves are thus the main prey of sea otters there. The well known keystone role of sea otters in hard-bottom habitats (Estes and Palmisano 1974, Estes and Duggins 1995) hence does not manifest in simulations using the largely soft bottom PWS model; i.e., any strong keystone effect over hard bottoms is diluted by the scale and average 'habitat' of the model when run in Ecosm. An *Ecopath* model of a kelp forest would undoubtedly reveal the strong sea otter mediated cascade in kelp forests, and their strong keystone role there. Secondly, the sea otter population in the whole of Prince William Sound was reduced by acute mortality of the *Exxon* Valdez oil spill probably by somewhere between 19 and 38% (Garrott et al. 1993, Degange et al. 1994) though some estimates suggest overall PWS mortality as low as 6% (Garshelis 1997). This reduction might partially explain the moderate trophic interaction strength rankings. Nevertheless, the removal of sea otters from the Prince William Sound model does reveal a sea otter mediated trophic cascade over soft bottoms wherein the biomass of their bivalve prey increases leading to a bottom-up cascade where decreases in available phytoplankton and detritus (the bivalve's prey) leads to decreases in available zooplankton and small epifauna, and in turn decreases the biomasses of nearshore demersal fishes and their predators— lingcod. This is a strictly trophic cascade that could occur only in areas of the Sound that are not exposed to rapid onshore advection of phytoplankton and zooplankton. But the effects of sea otters transcend direct trophic effects in soft bottom habitat with at least two forms of non-trophic mediation: (1) discarded bivalve shells serve as hard substrate for the settlement of habitat-forming macroalgae, anemones, and other sessile organisms (Kvitek et al. 1992), and (2) their excavations for clams help other predators such as the asteroid *Pycnopodia helianthoides* capture smaller clams, as well as changing the conditions and opportunities for many other benthic organisms (Kvitek and Oliver 1986). These and other non-trophic effects are not captured in the simulations presented here, but the *Ecosim* does allow for specification of such non-trophic facilitation (e.g., Okey et al. 2004c) or interference. Such relationships can be specified in future attempts to identify and rank keystone species.

The large effects of commercial and subsistence fisheries on community longevity (and pinnipeds, for example) seems surprising at first considering that the fisheries catch makes up small proportions of net system production and system biomass (Table 4-2). Such a comparison is, however, misleading because the amount of primary production required to produce the annual 1994-1996 PWS catch of 8.68 tonnes of biomass (at an average trophic level of 3.81) was approximately 33 times that

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amount (283 tonnes), which is about 8% of the calculated total annual net primary production and 28% of the calculated annual net system production (after Pauly and Christensen 1995). The roles or impacts of fisheries in PWS in general are underestimated by the 1994-1996 *Ecopath* model since effort and catches were considerably lower than normal at this time due to the effects of the *Exxon Valdez* oil spill and due to the failure of the Sound's Pacific herring (species) population and fishery. Fisheries (and pinnipeds for that matter) have a larger trophic impact than a simple analysis of absolute flow of biomass to them would suggest because the organisms they consume integrate much larger percentages of the systems overall biomass and production than suggested by the summary statistics.

The comparison of fishery *community longevity support* (CLS) values to functional group CLS values calls for clarification of this particular index. It would be a mistake to confuse CLS with ecosystem, or community, integrity. It is natural for some predators to have an overall negative effect on *community longevity support* as formulated here, or similar impact indices (Paine 1992). Negative CLS values simply mean that these predators cause a net decrease the standing biomass of the relatively slower-growing and longer-lived organisms in the system. Such predation is akin to a natural disturbance that one could argue increases diversity and stability (sensu Levin and Paine 1974), and thus integrity. If a fishery has a strongly negative CLS value, this is likely to be an exotic disturbance (i.e., that the organisms in question did not co-evolve with) (*sensu* Sousa 1984), with the exception of (strictly) traditionally prosecuted subsistence fisheries that one could perhaps make a co-evolution argument for. This strongly negative fisheries CLS value represents use of slow-growing biomass in the system that could otherwise be used by, or become, higher trophic level organisms.

Aside from model structure (i.e., aggregation issues) errors in estimating basic parameters can influence a model's overall behavior in important ways. For example, J. Kitchell (pers. comm.) points out that overestimation of production/biomass (P/B) and consumption/biomass (Q/B) values are common in *Ecopath* models, and this can cause exaggerations in the responses of components in a system to perturbations. The PWS model is the result of a collaboration of over 30 individuals representing broad teams of scientists with expertise in the biota of the region (Okey and Pauly 1999a, b). The model underwent at least two official reviews in the context of the *Exxon Valdez* Oil Spill Restoration Project, as well as several unofficial reviews. C. Walters checked the model's parameters for inflated estimates of P/B, and the values for three of the 48 groups were subsequently re-visited and adjusted. Nevertheless, models are never completely accurate by definition and parameters will continue to be refined to be more accurate.

Ecosystems are complex and at the edge of our abilities to fully comprehend them. Human induced impacts to an ecosystem may well result in predictable outcomes, or they may result in unpredictable and possibly detrimental consequences. Computer modeling tools like *Ecopath with Ecosim* help us reveal possibilities of direct and indirect mechanisms that are initially elusive. Even the most complex ecosystem models, however, are simple and limited compared with real world dynamics. The

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best models can indicate only the possibility of real dynamics, which can then be tested and further evaluated. In light of the present approach, its inherent uncertainties, and the possibilities for big surprises in natural systems, marine resource managers might wish to consider the relative interaction strengths of species or functional groups or their relative keystoneness when developing policies that manage human activities.

Finally, one major caveat is called for, following a key point made by Piraino (2002). Ranking species as ecologically special automatically implies that other species are not important. This might be profoundly erroneous and might lead to unwise strategies for management and conservation. Clearly, strong keystone species are special. What happens to them and their populations, and what they are adapted to do, has important implications for the system. But those species that did not rank highly by any index we devise with our limited analytical approaches represents unknown potential and the very substance of biodiversity. Managers and policymakers are well advised to use caution when adjusting their strategies based on these types of analyses. If history and jellyfish are any guides, today's "unimportant" species will be tomorrow's important species.

CONCLUSIONS

The approach and results presented here are an example of how whole food web modeling approaches such as *Ecopath with Ecosim* can be used to identify and rank the species or functional groups in an ecosystem in terms of their *community importance*, overall trophic interaction strengths, keystoneness, and *community longevity support*—three indices adapted from previous work and one novel index for examining roles. Transient orcas and Avian raptors both stood out as keystone predators in the present iteration of the *Ecopath* model of Prince William Sound. The keystone and the *community longevity support* indices provided more sensitivity than the *community importance* to examine a secondary cluster of strong interactors.

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CHAPTER 5. Can oil spills shift marine ecosystems to alternate stable states?: Preliminary simulations with an *Ecopath* model of Prince William Sound, Alaska

ABSTRACT

Some of the adverse effects of the *Exxon Valdez* oil spill have persisted for 15 years in Prince William Sound (PWS), Alaska. The main challenge in detecting these effects is distinguishing lasting population impacts from background environmental fluctuations and ecological transients. Nevertheless, the consistent assumption is that the overall biological community is recovering, and that sooner or later it will be recovered. An alternate possibility is that this very large scale and severe spill shifted PWS's biological community to an alternative stable state from which it will not recover. I conducted a series of dynamic simulations that use a whole-food web mass-continuity model of PWS to approach this question. I simultaneously imposed different mortality trajectories on the various biotic components of the PWS ecosystem according to the character in which each of 48 living functional groups was affected by three different whole-system disturbances: the 1964 Great Alaska Earthquake (GAE), the *Exxon Valdez* oil spill (EVOS) using known effects information, and the EVOS including assumed, but unverified, effects. Overall system response patterns of the three scenarios differed characteristically. The GAE impacted mostly rapid-turnover species, and the corresponding simulation indicated rapid recovery. The impacts of EVOS on slow-turnover (charismatic) species are well documented, and this second simulation indicated much longer lasting impacts and a persistent shift of some functional groups to lower biomasses. Some suspected EVOS impacts went unverified due to inherent biases of a limited, albeit broad, science program. Enhancing the 'known' EVOS scenario with such 'assumed' effects led to a third scenario that more fully targeted both slow- and fast-turnover groups. This final scenario also indicated a persistent shift in the biological community to an alternate stable state from which the system did not recover during the 50-year simulation. If this community shift is not an analytical artifact, it indicates that the character of severe disturbances, in terms of the mix of direct impacts on slow versus fast organisms, has a strong bearing on the ecological destiny of Prince William Sound, Alaska.

INTRODUCTION

The notion that natural systems can persist in alternate stable states (Lewontin 1969, Sutherland 1974, May 1977) has fundamentally challenged classical ideas about ecosystem responses to anthropogenic and natural disturbances, and about nature in general. It implies that some systems, in some cases, will not recover from some perturbations. More specifically, it implies hysteresis, wherein a system is resilient to exogenous stressors up to a threshold level where a catastrophic shift (usually considered degradation) occurs, but shifting the system back to the previous state would require the exogenous

stressors to be decreased to levels much lower than those that triggered the forward shift. Hysteresis thus implies a lag between forward and backward catastrophic shifts in a system (Chapter 1).

Such theoretical discussions of alternate stable states have captured the imaginations of many ecologists and triggered a flurry of claims of alternate stable states in different ecosystems. The discussion was focused by Connell and Sousa's (1983) critical review of these examples through the application of rigorous criteria for judging ecological stability. The ensuing debate further refined the search for examples of alternate stable states in ecosystems (e.g., Peterson 1984, Sousa and Connell 1985) with some maintaining that modern ecological literature (and nature) is replete with examples of alternate stable states, even though they are not always fully demonstrated using the strictest criteria (Sutherland 1990). Renewed interest has produced a new population of candidate examples (see Chapter 1), and the evidence for some of these claims is reasonably convincing (Knowlton 1992, Petraitis and Dudgeon 1999, Carpenter 2000, Jackson et al. 2001, Scheffer et al. 2001). Putative examples of alternate stable states in marine ecosystems are growing as well (see Chapter 1), and the anemone barrens described in Chapters 2 and 3 is yet another example. Although not every one of this new collection of examples will stand up to rigorous tests for alternate stable states, they all represent shifts in marine ecosystems that appear to be persistent. Most authors on the subject agree that multiple lines of evidence should be examined, if possible, when judging the existence of alternate stable states.

The present chapter is a preliminary exploration of the effects of a large-scale and severe disturbance—the 1989 *Exxon Valdez* oil spill (EVOS)—on the whole marine community of Prince William Sound (PWS) Alaska. Two scenarios of the effects of the EVOS and one of the Great Alaska Earthquake (GAE) were simulated to compare their predicted marine community effects.

The 1989 *Exxon Valdez* oil spill bespoiled much of the intertidal zone of western Prince William Sound in addition to areas along the Alaskan Peninsula and parts of Kodiak Island with 40 million liters of North Slope crude oil. Numerous publications and several compendiums and overviews on the biological and ecological impacts of the EVOS have arisen from the scientific programs surrounding the natural resource damage assessment and the protracted legal controversies (e.g., Tables 5-1 and 5-2). This body of science was largely funded by the *Exxon Valdez* Oil Spill Trustee Council, but also by other science programs and interests.

Recent broad summaries of EVOS effects on Prince William Sound and adjacent marine ecosystems distinguished three major types of ecological effects: acute, chronic, and indirect (Peterson 2001) and concluded that both exposure to residual oil and adverse effects have persisted much longer than expected, that many effects are mediated indirectly through trophic cascades, and that modern toxicology and risk-assessment should be fundamentally changed to incorporate ecosystem-based considerations (Peterson et al. 2003). In addition to these syntheses, there are several volumes of collected work on the ecological impacts of the spill (Loughlin 1994, Wells et al. 1995, Rice et al. 1996, Warheit et al. 1997) as well as other notable reviews (e.g., Paine et al. 1996, Spies et al. 1996, Rice et al. 2001) and

more up-to-date summaries of the status of particular species or habitats (cited in Discussion). The ecological effects of the EVOS were both broad and severe, but they varied considerably depending on the habitat, physiology, diet, and life history of each species. Accordingly, the magnitude and persistence of exposure and effects varied, as did the recorded trajectories of population change after the EVOS.

Another large scale and severe disturbance was the massive (magnitude 9.2) Great Alaska Earthquake (GAE), which occurred in the spring of 1964, 25 years before the EVOS. It resulted in a number of acute ecological effects throughout the coastal zone of South Central Alaska, some of which are still conspicuous. Fortunately, some of the biological impacts of the GAE in Prince William Sound were documented (NRC 1971, Wheelwright 1994). This earthquake tilted Prince William Sound such that some intertidal communities were lowered 2 meters and others were stranded above the tides by as much as nine meters. Most areas experienced intermediate changes in topographic/bathymetric heights, but much of PWS also moved many meters horizontally. A major tsunami and many local ones swept through the Sound and adjacent regions, and submarine slides, flows, and slumps likely occurred in many soft sediment areas (NRC 1971, Okey 1997). In general, the biological impacts of the earthquake were focused on relatively fast turnover (low trophic level) organisms inhabiting both rocky and soft bottom intertidal and subtidal habitats. In addition to benthic plants and invertebrates, small fishes and salmonids that depend on intertidal spawning habitats, or low-lying stream gravels, were affected. Some adult teleost fish mortality was also observed to occur through sudden depth displacements, though the extent of impacts on fishes is uncertain (NRC 1971). The earthquake disturbance simulation was based on documented information on impacts to specific groups of organisms as well as some assumptions about additional impacts that may not have been documented. The GAE was a natural experiment of a catastrophic disturbance and it became, "the best documented and most thoroughly studied earthquake in history" (NRC 1971).

Classical equilibrium theory has detrimental effects on ecosystems because the presumption of inevitable recovery gives humans justified free-reign in their interactions with nature. The central point of Holling's (1973) resilience viewpoint is an applied one, in which disturbances, or extraction of biological resources, can erode a system's resilience leading to loss of structural integrity. A system can thus settle at an alternate domain of attraction, rather than recovering to a pre-disturbance state. The default expectation of ecological recovery after catastrophic disturbances like the *Exxon Valdez* oil spill might have assuaged ecologists into pursuing questions of when system recovery will take place, rather than more important questions of whether recovery will take place.

In reality, biological communities are shaped by the interaction of deterministic forces with random events (i.e., stochasticity) (Holling 1973). Despite the apparent erroneousness and detrimental implications of a strict equilibrium viewpoint, it is still a useful convenience for ecologists because it can be employed to distinguish between deterministic biological forces and externally-imposed physical or

chemical forces, which could take on the stochastic character of 'historical accidents.' Deterministic analytical tools can also be used to explore the nature of ecosystem structure and function.

My initial question was, 'Is it plausible that a large oil spill, such as the EVOS, could shift the PWS biological community to an alternate stable state?' This chapter, in addition to addressing this question, is an exploration of the specific characteristics of a disturbance that might be required for such a shift to occur. I note that Carpenter's (2000) discussion of how alternating regimes can be created through feedbacks between slow and fast variables in a system is particularly germane to the present exercise because, as we shall see, the scenario that strongly impacts both of these types of components in the PWS model is the only one that leads to an apparent alternate stable state.

METHODS

Study location

The location of Prince William Sound, Alaska is shown in Figure 5-1 and its physical and ecological setting is described in Chapter 4 as well as by Okey and Pauly (1999b).

The modeling approach

I used the dynamic simulation modeling approach *Ecosim* (Walters et al. 1997) to simulate and compare the broad ecological impact of three scenarios of severe perturbations to the Prince William Sound, Alaska biological community. These included the 1964 Great Alaska Earthquake (GAE), an *Exxon Valdez* oil spill (EVOS) scenario using known effects information, and an EVOS scenario that included assumed (but unverified) ecological effects information in addition to known effects information.

Ecosim is a bundle of dynamic simulation routines in the ecological modeling suite *Ecopath with Ecosim* (Polovina 1984, Christensen and Pauly 1992, Christensen et al. 2000, Pauly et al. 2000, Christensen and Walters 2004) in which a whole-system food web model is constructed to describe a snapshot of biomass flows in an ecosystem. This empirically-based *Ecopath* model is then a starting baseline for temporal and spatial dynamic *Ecosim* simulations that are conducted to explore ecological questions or policy alternatives. The basic *Ecosim* utility allows the exploration of the potential temporal responses of the various biotic components in the model to simulated changes in other components uses by manipulating the matrix of simultaneous differential equations taken from a given *Ecopath* model. Functional groups respond to such manipulations because of the thermodynamic limitations expressed by each functional group and the whole system. An investigator can thus use *Ecosim* to specify changes in the mortality rates imposed on selected groups, either individually or simultaneously, to examine the simulated response of those groups, other groups, or the whole food web based on the direct and indirect trophic effects of the specified manipulation. We can thus estimate indirect effects given information on direct effects. Details of the *Ecopath with Ecosim* modeling approach are provided in Chapter 1.

The Prince William Sound model

The Prince William Sound *Ecopath* model characterizes the average annual flows of biomass throughout the food web, based on the best available information from the time period 1994 to 1996, five to seven years after the EVOS. It was constructed through a collaborative process described in Okey and Pauly (1999a), wherein over thirty-five experts on the various components of the Prince William Sound ecosystem were assembled from numerous agencies and institutions for collaboration at workshops, through e-mail and telephone communications, and by contributing to an edited volume that describes the model and documents its construction and refinement through an iterative and interactive thermodynamic balancing process and continuous review (Okey and Pauly 1999b). The model is mass-balanced, in that some of the given parameters are adjusted such that the static *Ecopath* model is a thermodynamically likely scenario of trophic structure and flows. Its trophic level estimates (an output) were verified using a nitrogen stable isotope method described by Kline and Pauly (1998). Recent additional changes to the PWS model are described in Chapter 4.
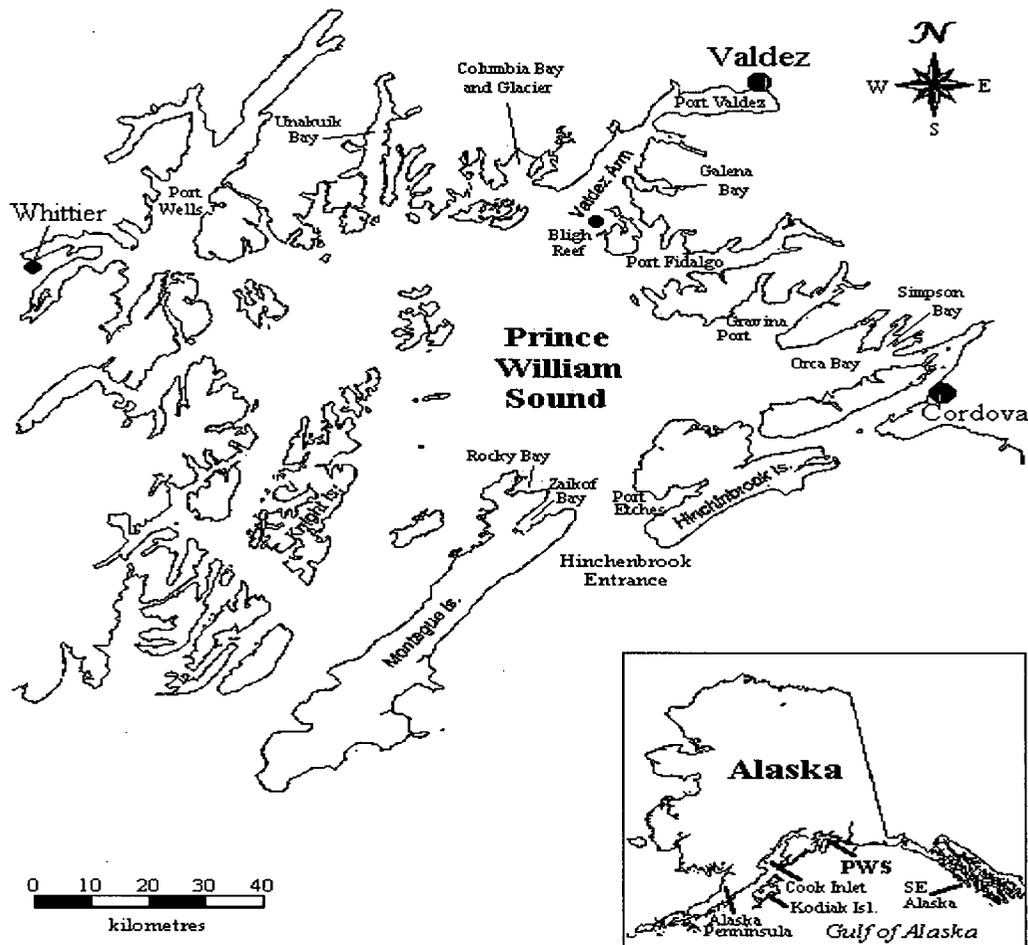
Figure 5-1. Map of Prince William Sound (PWS), Alaska (modified from Braddock et al. 1996).

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The three scenarios explored in this chapter were constructed to compare the ecological effects of the

1989 *Exxon Valdez* Oil Spill (EVOS) with those of another severe disturbance that affected Prince

William Sound—the 1964 Great Alaska Earthquake (magnitude 9.2). This earthquake caused catastrophic

alterations to Prince William Sound exactly 25 years before the catastrophic EVOS (NRC 1971,

Wheelwright 1994). Thus, the first two simulations were constructed based generally on documented

impacts of the GAE and the EVOS; the third simulation was based on assumptions of likely, but

unverified, ecological impacts of EVOS, in addition to the documented impacts. Table 5-1 lists the main

sources of the effects information used for these simulations.

Table 5-1. General sources of mortality estimates and the general segment of the food web affected by the three catastrophic disturbance scenarios compared.

Scenario	Impacted organism turnover rates	Sources of specified mortality trajectories
GAE	Mostly fast	(NRC 1971, Wheelwright 1994)
EVOS known	Mostly slow	(Loughlin 1994, Wells et al. 1995, Paine et al. 1996, Rice et al. 1996, Spies et al. 1996, EVOSTC 1997, Lord 1997, EVOSTC 1999, NOAA 1999, Okey and Pauly 1999b)
EVOS enhanced	Fast and slow	'EVOS known effects' specifications plus additional assumed impacts

Mortalities of PWS marine organisms associated with the GAE were focused mainly on lower

trophic level organisms that generally have a fast turnover. This scenario was specified accordingly by

sketching sudden (brief) pulses of increased mortality rates into the mortality input interface for only the

particular groups that were directly affected and in the ways they were affected, based on the

documentation of direct effects (NRC 1971). The 'EVOS known effects' scenario focused more on

impacts to mid and upper trophic level organisms that generally have a slower turnover, since much of the

interest and early research was focused on those segments of the ecosystem (though impacts to low and

relatively low trophic level species such as intertidal organisms were also included when they were

documented). The 'EVOS enhanced' scenario included all the mortality profiles from the 'EVOS known

effects' scenario, as well as mortality profiles on additional biotic components that could be reasonably

assumed to have been affected by such a spill without being detected. This enhanced scenario thus

included impacts on both low trophic level groups (fast turnover) and middle and high trophic level

groups (slower turnover). Mortalities specified for each group are shown in Table 5-2.

Although mortality trajectories associated with the GAE were specified as 'pulse' effects, some

of those for the EVOS were specified to have an initial pulse followed by a tapering effect representing

persistent, but declining, effects. These mortality trajectories (pulses and tapers) were specified

individually for each affected functional group, according to the different character of effects experienced

by each group. These tapering effects were rarely specified to last longer than 15 years. Simulations were

run for 50 years, and universal prey vulnerabilities (for all trophic interactions) were wet at 0.4, which

represents an overall mixture of 'top down' and 'bottom up' forces in the system, and this level is known to be reliable based on sensitivity tests that evaluated model behavior (Okey and Wright in press). The 50-yer time frame was considered to be beyond the normal time horizon of interest, but it was used here in the interest of exploring the persistence of the community shifts indicated by the EVOS scenarios. Exploratory 100-year simulations also yielded essentially the same results.

Table 5-2. Specified direct mortalities imposed on each functional group presented with the basic input parameters for each group of the 51 compartment Ecopath model of the 1994-1996 Prince William Sound food web.

Group name	Trophic level	Biomass (t·km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	Specified percent direct mortality		
					GAE	EVOS #1	EVOS #2
Transient orca	5.41	0.001	0.05	6.04			10
Salmon shark	5.10	0.221	0.10	7.30			10
Resident orca	4.92	0.015	0.05	8.67		20	20
Sleeper shark	4.88	0.110	0.07	3.65			10
Halibut	4.52	0.677	0.32	1.73			10
Pinnipeds	4.45	0.072	0.06	25.55		20	20
Porpoise	4.40	0.015	0.24	29.20			20
Lingcod	4.27	0.077	0.58	3.30			20
Adult arrowtooth	4.25	4.000	0.22	3.03			10
Adult salmon	4.18	3.410	1.31	13.00			
Pacific cod	4.06	0.300	1.20	4.00			10
Sablefish	4.03	0.293	0.57	6.42			10
Juv. arrowtooth	4.01	0.855	0.22	3.03			20
Spiny dogfish	3.96	0.110	0.09	4.77			10
Avian raptors	3.92	0.002	0.05	36.50		10	10
Octopods	3.80	**0.050**	3.10	11.70			10
Seabirds	3.80	0.022	0.17	150.60		20	20
Deep demersal fishes	3.77	0.960	0.93	3.21			10
Adult Pollock (1+)	3.76	7.480	0.71	2.56			10
Rockfish	3.74	1.016	0.17	3.44	20	20	20
Baleen Whales	3.65	0.149	0.05	10.90			10
Juvenile salmon (0-1)	3.51	0.072	3.91	62.80	20	20	20
Nearshore demersals	3.35	4.200	1.00	4.24	20	20	20
Squid	3.26	3.000	3.00	15.00			10
Eulachon	3.25	1.000	2.00	18.00			10
Sea otter	3.23	0.045	0.13	117.00		20	20
Deep epibenthos	3.16	30.000	3.00	10.00			10
Capelin	3.11	0.367	3.50	18.00			10
Adult herring	3.10	2.810	1.54	18.00			10
Juvenile pollock (0)	3.07	0.110	2.34	16.18			10
Invert-eating birds	3.07	0.005	0.20	450.50		20	20
Sandlance	3.06	0.595	2.00	18.00			10
Shallow lg epibenthos	3.06	3.100	2.10	10.00	50	50	50
Juvenile herring	3.03	13.406	0.73	18.00	50	50	50
Jellies	2.96	6.390	5.00	29.41			10
Deep sm infauna	2.25	49.400	3.00	23.00			10
Near omnivorous zoops	2.25	0.108	7.90	26.33	50		50
Omnivorous zooplank	2.25	24.635	11.06	22.13			10
Shallow sm infauna	2.18	51.500	3.80	23.00	50	50	50
Meiofauna	2.11	**4.475**	4.50	22.50	20		20
Deep lg infauna	2.10	28.350	0.60	23.00			10
Shallow sm epibenthos	2.05	26.100	2.30	10.00	50	50	50
Shallow lg infauna	2.00	12.500	0.60	23.00	20	20	20
Near herbiv zooplank	2.00	0.136	27.00	90.00	50		50
Herbivorous zooplank	2.00	30.000	24.00	50.00	20		20
Near phytoplankton	1.00	**5.327**	190.00	-	50		50
Offshore phytoplankton	1.00	**10.672**	190.00	-			10
Macrophytes	1.00	125.250	4.00	-	30	30	30
Nekton falls	1.00	2.000	-	-			10
Inshore detritus	1.00	19.520	-	-			
Offshore detritus	1.00	114.480	-	-			

Notes: Values in bold have been calculated with the *Ecopath* software; other values in the first four columns are empirically based inputs, or values that were adjusted from empirically based estimates during balancing. P/B and Q/B are the ratios of production and consumption to biomass, respectively. Many of the oil spill mortalities 'shapes' represented effects that taper off over time.

Each of the three disturbance scenarios specified for this exercise have a signature of initial impacts that is unique trophically, and in terms of life history strategies: the GAE affected mostly fast-turnover groups, EVOS 'known effects' scenario affected a mix of slow and fast turnover groups, but it was biased towards slow-turnover groups, and EVOS 'enriched effects' scenario affected both slow and fast turnover species. The GAE scenario resulted in relatively swift recovery while the EVOS scenarios resulted in a persistent shift, at least for some groups, to lower abundance levels.

RESULTS

The first simulation described here suggests that the biological community of Prince William Sound, Alaska, as a whole, can recover quickly from the known effects of a large earthquake such as the 1964 Great Alaska Earthquake (GAE). Even though this earthquake triggered devastating tsunamis and changed elevations; the simulation indicated a quick rebound of the marine biota because damage was generally limited to components with fast turnover rates. In contrast, the simulation of the *Exxon Valdez* oil spill (EVOS) based on documented information on the direct biotic impacts of the spill suggested much slower recovery trajectories than indicated for the GAE, probably because documented EVOS impacts were focused mostly on higher trophic level organisms with slower natural turnover rates. The existence of tapering effects in the EVOS simulations did not account for the characteristic differences as indicated by the long time scale of the simulation relative to the short time scale of the tapering. The simulation of an EVOS scenario in which the direct impacts of the oil spill were enhanced beyond documented impacts resulted in even more severe effects. Both of the EVOS scenarios suggested that such an oil spill might shift the overall PWS biotic community to an 'alternate stable state' from which the system does not recover. The results of these scenarios are summarized below.

The Great Alaska Earthquake scenario—The biomass of many biotic components in the PWS model were responsive to the simulated 1964 earthquake, but projected recovery of these components to a pre-earthquake state was relatively rapid (Figure 5-2a). Several groups declined immediately, including intertidal and subtidal benthic groups, some small pelagic fishes, and salmon. Other groups, such as some plankton groups and squid, were predicted to undergo synchronal increases due to declines of competitors or predators. Many components were rapidly recovering as quickly as three years after the earthquake, and in some cases more quickly. Most components had recovered to near their pre-earthquake condition 10 years after the quake, and the model system had returned to the pre-earthquake state by 30 years. These patterns are generally consistent with the patterns of recovery from the GAE found in the real PWS (NRC 1971).

EVOS 'known effects' scenario—The biomass of many PWS ecosystem components responded strongly to the EVOS 'known effects' scenario (Figure 5-2b). High and relatively high trophic level organisms, as

well as some intertidal and shallow subtidal benthic organisms, declined as a direct result of the oil spill, while some plankton groups and squid were predicted to increase concurrently with decreases in the directly affected organisms, as in the GAE scenario. The character of this EVOS simulation departs from the GAE simulation after approximately year 10 when the biomass of several less impacted competitors (e.g., Pacific cod, sablefish, lingcod, clams) of the impacted charismatic species became elevated for approximately 20 years. A conspicuous feature of this simulation is the persistent downward shift of a number of groups that do not appear recover to their previous levels. These groups include resident killer whale (*Orcinus orca*), porpoise (Dall's porpoise, *Phocoenoides dalli,* and harbor porpoise, *Phocoena phocoena)*, pinnipeds (mostly harbor seal, *Phoca vitulina richardsi*), avian raptors (Bald Eagles, *Haliaeetus leucocephalus,* and Peregrine Falcons, *Falco peregrinus*), invertebrate-eating birds (e.g., sea ducks), shallow large infauna (clams), Pacific halibut (*Hippoglossus stenolepis*). The recovery trajectories of other functional groups appear to track actual recoveries of organisms documented since the EVOS, even though these simulations were conducted on a post-spill (1994-1996) model rather than a pre-spill model.

EVOS 'enhanced effects' scenario —The biomasses of a number of functional groups in the system fluctuated more strongly to the EVOS 'enhanced effects' scenario than to the 'known effects' scenario. Like the EVOS 'known effects' scenario, several groups stabilized at levels lower than their initially-specified baselines for the duration of the 50-year simulation (Figure 5-2c). These include lingcod (*Ophiodon elongatus*) and Pacific cod (*Gadus macrocephalus*) in addition to the groups listed previously. Almost all groups declined initially due to specified impacts across all trophic levels. Many of the fast turnover groups rebounded to levels far above their initial state within two years of the disturbance. The stabilization of many groups at shifted levels occurred by 15 years after the simulated spill. By the end of the 50 year simulation, these shifted groups were not tending toward recovery from their shifted states.

DISCUSSION

The question of whether oil spills can shift marine ecosystems to alternate stable states is a different question than whether the *Exxon Valdez* oil spill shifted the Prince William Sound ecosystem to an alternate stable state. The simulations presented here illustrate the possibility that alternate stable states can be produced when a disturbance severely impacts both slow and fast turnover species (sensu MacArthur and Wilson 1967, Pianka 1970, 1972), or at least enough of the total number of biotic components in a system. This scenario was part of a preliminary attempt to simulate the effects of the EVOS on the PWS biological community using an empirically-based model (presently the only existing whole-PWS trophic model) and informed estimations of EVOS effects trajectories on the Sound's biological components. Although they ought to be explored further by updating specified mortality trajectories with the latest effects information, these simulations are currently the best existing estimates

of whole PWS ecological impacts of the EVOS because they are the *only* existing estimates of whole PWS ecological impacts of the EVOS. In this sense, the simulations presented here support the hypothesis that alternate states can exist in the real PWS, and they provide some insights into the character of disturbance mechanisms that might cause such shifts.
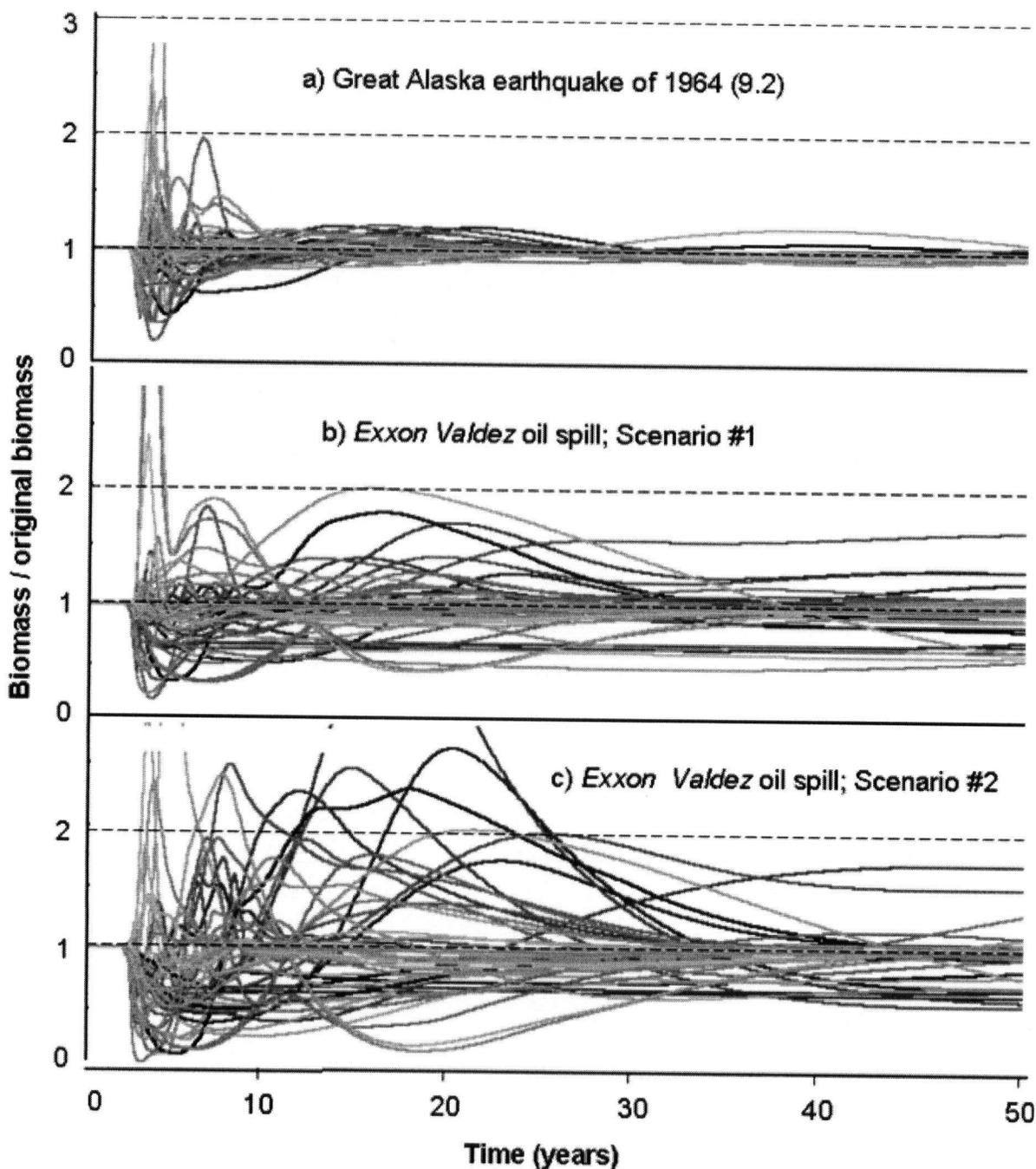
Figure 5-2. Simulations of three catastrophic disturbances in Prince William Sound, Alaska: (a) the Great Alaska Earthquake of 1964 (magnitude 9.2), which shook and tilted Prince William Sound causing tsunamis, and which mostly impacted fast turnover organisms; (b) An *Exxon Valdez* oil spill scenario based on documented impacts of the spill, which focused on impacts to slow turnover organisms (and some fast turnover organisms for which information was available); and (c) An *Exxon Valdez* oil spill scenario that was enriched with assumed impacts of the spill that went unverified, in addition to documented impacts of the spill. Both slow and fast turnover organisms were impacted in the EVOS scenarios.

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The question, 'Did the EVOS actually shift the system to an alternate stable state from which some components will not recover' cannot be answered with the results of these preliminary simulations. To approach this, it will be necessary to not only refine the simulations with the latest effects information (Table 5-3), but to compare the resulting trajectories of each simulation to independently-estimated trend information to validate the various answers that the simulations are providing. Such a comparison of the simulation outputs with empirical data on the recovery of organisms in PWS ecosystem can inform us about whether the system actually has shifted to a new stable state, and more generally the mechanisms and indirect effects involved in the shifting or temporary effects experienced by the system. Still, some of the trajectories appeared to track known trajectories from the GAE and the EVOS, providing a preliminary indication of the reliability of the model and dynamic approach.

The trajectories of the biotic components depicted in Figure 5-2 represent the response of the model components to simulations of qualitatively different catastrophic disturbances. Based on available information, and assumptions of unavailable information about the two disturbances, the suite of effects-mortality trajectories were applied to different ranges of trophic levels (and life history strategies): the GAE of 1964 mostly impacted lower trophic levels; documentation of *Exxon Valdez* oil spill impacts focused on higher trophic levels; and an enriched scenario of the *Exxon Valdez* oil spill (including possible unverified impacts) included impacts on both fast and slow biotic components. The main purpose of this exercise is to test the effects of these three characteristically distinct catastrophes on the general response of this representation of the PWS food web. Figure 5-2, therefore, should first be viewed in terms of the general patterns and differences among the three scenarios. These scenarios resulted in an ascending gradient of impacts to the initial (post spill) model system, ranging from rapid recovery from the GAE (and associated tsunamis) to a pattern representing an 'alternate stable state' resulting from the EVOS scenarios.

Results from numerous studies presented at the 10th annual conference of the EVOS science program in March of 1999 (EVOSTC 1999) indicated that only two of numerous species of concern had recovered at that time—Bald Eagles and river otters (*Lutra canadensis*)—and that system-level impacts of EVOS were persisting after 10 years. More recently compiled information (e.g., Peterson 2001, Peterson et al. 2003) confirms that some EVOS exposure and effects have lasted much longer than previously suspected. Such results match either of the two oil spill scenarios presented here. The inputs and results of the two oil spill scenarios should be considered, at the present juncture, to have equal validity since it is not reasonable to assume that all EVOS impacts were documented. It is notable that even the scenario based only on early documented impacts—a conservative scenario—indicates that overall system recovery from the EVOS will take longer than 50 years. It is also worth noting that

assumed impacts of the spill in the enriched simulations were conservative (Table 5-2), and that specifying scenarios that are more severe might be useful for further exploring system behavior.

One reason for caution when interpreting the results of the simulations is the 'bounded' nature of the output. For example, the flat lines observed in the two EVOS scenarios should not imply that the proper interpretation from this simulation is that these populations (groups) would be stable in time. The mortality trajectories imposed on each scenario represent the results of changes in only the imposed forces of interest, and the resulting trajectories are the result of these imposed forces combined with the trophic forces that are based on initial biomasses and specified flow rates among groups. Other physical forces in the system, such as seasonal fluctuations and oceanographic regime shifts and cycles, are not included in these preliminary simulations, though this can now be done explicitly, and multi-year trends can be accounted for in the master equation by setting a bioaccumulation factor. By experimenting with the various combinations of the various types of forces that exist in the system, future simulations will go much further in explaining observed changes and informing us about the best policy and management strategies for achieving particular goals.

The stabilized shift in these two scenarios do indicate that specified trophic forces combined with specified mortality trajectories are adequate to produce an outcome that appears as an alternate stable state in the trophic model (not including exogenous oceanographic forces) given the specified time frame. Inclusion of all forces in the ecosystem into the model would either dampen or exaggerate this putative alternate state. True alternate stable state dynamics could emerge in these simulations if the juvenile stages of previously dominant groups exhibit 'cultivation-depensation effects' (Walters et al. 2000) at the hands of their predators or competitors after the 'dominant' predator was pushed to very low biomasses by the disturbance. That is to say, a prey species whose population was previously controlled by predators could switch roles and control the predators (which then become the prey) either by consuming young life stages of the now depleted predator, or simply by virtue of abundance (e.g., Barkai and McQuaid 1988). Such effects would imply a truly hysteretic dynamic. An alternate explanation to such a 'reinforced stable state' explanation, however, is that disturbances that are as severe and broad as large oil spills can cause a *considerable* lag in the return of functional groups to levels associated with the previous global equilibrium state.

The indicated slow recovery rates after the oil spill scenarios relative to the more rapid recovery trajectories following the earthquake scenario indicates that high trophic level organisms are important for maintaining the structure of this community. This is likely due to the strong interaction effects of apex predators (Chapter 4). Stated another way, it is because the slow-turnover components of a community can control the dynamics of the faster components (Carpenter 2000, Carpenter and Turner 2000). The results of these simulations also indicate that the relatively low resiliency of high trophic level organisms to oil spills and their prominent role in maintaining community structure makes the broader system vulnerable when these key components are severely impacted. Ecosystem integrity is thus more eroded

when high trophic levels are impacted than when low trophic levels are impacted. However, the greatest erosion of ecosystem integrity appears to come about through forces that cause broad impacts across multiple trophic levels (Figure 5-2c).

The ultimate application of this type of approach in ecology and management relates to the extent to which the model of PWS actually represents the real PWS ecosystem, and the extent to which dynamic modeling (e.g., *Ecosim*) can represent real ecological processes. These questions, the answers to them, as well as the confusion surrounding them, are at the core of discomfort that ecologists might have in employing modeling approaches to real systems. The key to optimizing the usefulness of such approaches lies in the interpretation of the simulations and the model itself. Although the PWS model is one of the most explicit and refined *Ecopath* models constructed to date, it is an inherently simplified representation of the food web and its biomass flows. The important question is whether the modeling approach can capture the character, or the core, of these processes at the scale of interest (the whole system) thereby revealing the potential operation of mechanisms, if not the details of the magnitude of those processes. In addition, some of the functional groups in the model represent an aggregation of species, and the character of that aggregation influences both the description of the system and the behavior of the model in simulations. Aggregation, therefore, must make ecological sense, and tailoring a model's aggregation to the system and questions of interest is crucial.

Table 5-3. Peer-reviewed *Exxon Valdez* oil spill biological effects and population trajectory information.

Species or functional group	Source
Harbor seals	Frost et al. (1999); Hoover-Miller et al. (2001)
Marine birds	Irons et al. (2000); Lance et al. (2001); Wiens et al. (2001)
Pigeon Guillemots	Golet et al. (2002)
Common Murres	Piatt and Anderson (1996)
Nearshore demersal fishes	Jewett et al. (2002)
Pink salmon	Murphy et al. (2000); Heintz et al. (2000)
Black Oystercatchers	Murphy and Mabee (2000)
Harlequin Duck	Lanctot et al. (1999); Esler et al. (2002)
Sea ducks	Trust et al. (2000)
Developing fish	Short et al. (2003)
Sea otters	Garrott et al. (1993); Degange et al. (1994); Eberhardt and Garrott (1997); Garshelis (1997); Monson et al. (2000); Bodkin et al. (2002); Dean et al. (2002)
Pacific herring	Pearson et al. (1999); Carls et al. (2002)
Shallow subtidal communities	Dean and Jewett (2001)
Deep benthos	Feder and Blanchard (1998)
Soft-bottom benthos	Jewett et al. (1999)
Protothaca staminea	Fukuyama et al. (2000)
Urchins and kelp	Dean et al. (2000)
Intertidal community	Driskell et al. (1996); Houghton et al. (1996); Lees et al. (1996); Driskell et al. (2001); Skalski et al. (2001)
Mussel beds	Carls et al. (2001)
Eelgrass	Dean et al. (1998)
Fucus gardineri	Stekoll and Deysher (2000); Driskell et al. (2001)
General reviews & syntheses	Steiner et al. (1990); Paine et al. (1996); Spies et al. (1996); EVOSTC (1997); Lord (1997); Peterson et al. (2003)
Compendia	Loughlin (1994); Wells et al. (1995); Rice et al. (1996); Okey and Pauly (1999b); Peterson (2001)

The primary contribution that this modeling approach makes to our understanding of natural systems, and the effects of human activities, is that it provides a view of the potential effects of the trophic forces in a system relative to other forces (e.g., oceanographic) that can also be incorporated into the modeling approach. Researchers can thus begin understanding the overall effects of a given set of human actions by better understanding both the direct and indirect effects of those actions and other phenomena. The spectra of indirect effects that manifest in a given community, under different conditions, are the key to understanding how communities function within the purview of human stewardship and recklessness because these indirect effects are the key mediators of most of the biological changes that humans are concerned with. As suggested by Yodzis (2001), these indirect effects cannot be revealed adequately without such whole-system modeling approaches. The usefulness of such models, again, hinges on the availability of empirical information that will improve their performance.

This debate between single possible stable states vs. alternate stable states and the corollary debate of strict determinism vs. the existence of indeterminism in nature is of central importance to ecosystem-based management and conservation because of the philosophical implications of these alternative views. The existence of a single stable state, or "global attractor", implies that the states of ecosystems are fundamentally pre-determined, and their fate cannot, ultimately, be changed. From this it would follow that ecosystems cannot be degraded, or if they are, they will always return to the pre-determined state. This single-stable-state would affirm transcendental fatalism and inevitability, or a strict determinism whether externally-imposed or not. In contrast, a multiplicity of stable states implies that ecosystems can be changed or degraded to states from which they might not return, and that humans have real choices among actions that will influence the destiny of ecosystems. The latter view affirms existential liberty and responsibility in nature. The adherence of society to one view over another undoubtedly influences ecosystems because fundamental philosophical frameworks, as in religions, influence human-ecosystem interactions (Nash 1968, Botkin 1990, Sullivan 1997), especially in systems that are highly exploited or exposed to a high risk of catastrophic disturbance.

Leading thinkers in modern ecology express similar views with Holling (1973) when suggesting that the solution to the question of strict determinism vs. stochasticity in the organization of natural communities can be found through examining the completeness of our knowledge of natural phenomena, and the scales at which they occur. Wilson (1998) argues that even if Laplace's mechanistic determinism is conceded, nature still might as well be influenced by stochastic events or historical accidents, simply because of the impossibility of understanding all causes and effects. Bodkin (1990) is stronger in his practical rejection of strict determinism, for the similar reason that individual organisms and assemblages (including scientists and camps) experience natural events on scales of time and space that are less than the whole. Stochasticity is therefore experienced by individual organisms and communities, effectively making the phenomenon real on scales that matter. Whether complex dynamics and stochasticity result

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entirely from deterministic chaos, or have help from irreducible indeterminacy, recognition of complex dynamics in ecological systems can lead to hypothesis development and prediction that are less biased by classical deterministic views (Pimm 1991), in addition to improved management strategies (Holling 1973, Done and Reichelt 1998).

It is possible that the news media, policy professionals, resource agency representatives, the general public, and scientists have all been asking the wrong, albeit hopeful, questions: "Has the ecosystem recovered yet?" or 'When will the ecosystem recover?" These questions assume a single possible stable state, and inevitable recovery to that state. This sentiment is a static, or "equilibrium", view of nature, which is deeply imbedded in western religion and science. Perhaps a more interesting and realistic question is "Will the system recover to a pre-oil spill state," or "Has the system been pushed to an alternate state from which it will not recover?"

Two interesting details of the present approach must be highlighted. First, a shifted, or alternate, state emerged during this exercise using a linear model that is based on a global equilibrium point. This is surprising and it implies that the emergent dynamics resulting from this imposed broad and severe disturbance strongly resist the natural tendency of such a model to eventually recover to its base equilibrium point, at least on the time scale examined here. This alternate state might even reflect aspects of stability due the endogenous reinforcement of the cultivation-depensation mechanism discussed previously. Second, these simulations were conducted using a post-spill model, rather than a pre-spill model, to explore the impacts of a large oil spill. Thus, the explorations of oil spill impacts described here more strictly address the effects of a *second* severe oil spill in PWS, which is a distinct possibility—even a likelihood.

There are two obvious next steps for refining the present exercise. First, these whole system simulations should be conducted using a variety of updated effects information that has recently become available (Table 5-3). Second, the predicted trajectories of particular species and functional groups should be compared to independently estimated time series of population changes, and this fitting to observed 'recovery' patterns should be repeated for each of the three scenarios. *Ecosim* includes a routine for fitting simulated trajectories against independently-estimated time series of biomass estimates to verify the model's dynamic behavior and to distinguish the relative importance of the various forces acting on the populations, in this case oil, fishing, and oceanographic changes. Although not all observed 'recovery' patterns will be strictly independent of sources of effects information, such time-series fitting would provide some degree of verification of the broad-system dynamic patterns discussed here. This would be an extremely worthwhile endeavor, especially since the PWS model is rigorously constructed and maintained. Such a synthesis would, however, require support and funding that is beyond the scope of this dissertation work.

CONCLUSIONS

A general conclusion from the preliminary simulations presented here is that the resilience of biological communities to disturbance might well depend on the character of the disturbance in terms of its breadth of impacts across trophic levels, or more precisely its breadth of impacts across life history strategies, in addition to the disturbance's physical characteristics of magnitude, frequency, and severity. These simulations represent evidence that very severe disturbances that simultaneously affect both fast and slow turnover components can shift systems to alternate stable states (sensu Carpenter 2000, Carpenter and Turner 2000). This is, however, just one type of evidence, and particular situations should be subjected to multiple lines of evidence to properly judge whether alternate stables states exist in that situation. In addition, the simulations presented in this chapter are too preliminary to adequately judge the plausibility that the *Exxon Valdez* oil spill shifted the Prince William Sound biotic community to an alternate stable state from which it will not recover. A more in-depth program based on a whole-system dynamic simulation approach, and including the latest effects and trends information listed herein, should be developed to address this broader question and to better understand the specific mechanisms that might help or hamper recovery of damaged biological resources.

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ABSTRACT

Phytoplankton blooms are increasingly conspicuous along the world's coastlines, and the toxic effects of these blooms have become a major concern. Nutrient enrichment often causes phytoplankton blooms, which decrease water transparency, but little is known about the effects of such light regime changes on whole communities of the continental shelf. A series of simulations designed to evaluate the potential effects of shading by phytoplankton blooms on community organization were conducted using a balanced trophic model of the West Florida Shelf ecosystem and the *Ecopath with Ecosim* modelling approach. Many functional groups in the system were predicted to decline as benthic primary production was inhibited through shading by phytoplankton, especially when associated biogenic habitat was lost. Groups that obtain most of their energy from planktonic pathways increased when shading impact and associated structural habitat degradation were complemented by enhanced phytoplankton production. Groups predicted to decline as the result of shading by plankton blooms include seabirds, manatees, and a variety of demersal and benthic fishes and invertebrates. Some counterintuitive predictions of declines (mackerel, seabirds, and surface pelagics) resulted because these groups are somewhat dependent on benthic primary production. The overall effect of the simulated bloom-associated shading of benthic primary producers resembled a trophic cascade where the number of full cycles of biomass gains and losses was about five, approximately equal to the number of trophic levels in the system.

INTRODUCTION

Benthic primary production can be a significant portion of the overall primary production in a system, but the community effects of sea floor shading by plankton blooms is underemphasized despite an early recognition of the key role of water clarity (Verwey 1931). Eutrophication and associated reductions of light penetration has long been known to decrease the maximum depth of macrophyte colonization in lakes (Maristo 1941, Spence 1982). Indeed, irradiance is the principal environmental characteristic determining depth distributions of marine and freshwater macrophytes (Sears and Cooper 1979, Chambers and Kalff 1985) as well as their seasonal and life history characteristics (e.g., Gomez 2001). Examples of light reduction impacts on marine macrophytes are becoming common (e.g., Dennison and Alberte 1985, Johansson and Snoeijs 2002, Nielsen et al. 2002, Hauxwell et al. 2003).

Irradiance is presumably as crucial for 'microphytobenthic' primary producers as it is for macrophytes (e.g., Blanchard and Montagna 1992, Daviescolley et al. 1992). Microphytobenthos consist of photosynthetic microorganisms on the sea floor and on lake and stream bottoms includeing cyanobacteria, benthic diatoms, euglenoid flagellates, and dinoflagellates (which include zooxanthellae—the photosynthetic endosymbionts of anthozoans). Enrichment of marine surface waters now appears to

be the main mechanism inhibiting benthic photosynthesizers in coastal systems (e.g., Tomasko and LaPointe 1994, Hall et al. 1999, Hillman et al. 1995, Meyercordt and Meyer-Reil 1999).

Organic enrichment has been recognized for some time as a major cause of faunal change in marine systems (Pearson and Rosenberg 1978), but it has been recognized for much longer that the penetration of light in water controls the depth of coral reefs (Verwey 1931). Still, whole marine ecosystems have been considered somewhat immune to enrichment by nutrients and organic material due to their large size and potential for dilution. This immunity view began to lose popular credence with cases such as Kaneohe Bay, Hawai'i, where organic pollution caused profound changes to coral and algal assemblages and the system as a whole (Banner 1974, Laws and Redalje 1979, Hunter and Evans, 1995). There are now many examples of adverse effects of eutrophication and shading on coral reef systems (e.g., Loya 1976, Rogers 1979, Walker and Ormond 1982, Tomascik and Sander 1985, 1987, van Woesik et al. 1999). Only recently, however, have sunlight and water transparency been labeled as cornerstones of coral research based on findings that Florida corals exist at depths near their respiration-production compensation point (Yentsch et al. 2002). This implies that small changes in water transparency might cause broad ecological changes on continental shelves.

Fundamental ecological changes triggered by enrichment-related phytoplankton blooms are now evident in large coastal systems (e.g., Johansson and Snoeijs 2002, Rabalais et al. 2002). 'Harmful algal blooms' (HABs) are common and increasing along much of the world's coastlines, and various toxicological, economic, and ecological effects are recognized. The growing concern is underscored by the recent development of broad-based scientific assessments and research programs (e.g., Boesch et al. 1997, CENR 2000, NRC 2000, Anderson et al. 2002, Conley et al. 2002). One notable program— ECOHAB—is a multidisciplinary research project designed to study the ecology and oceanography of HABs (Anderson 1995). One result of this research is the realization that aeolian subsidies of iron from Saharan dust can trigger red tide events on the West Florida Shelf by stimulating nitrogen fixation by cyanophytes (Lenes et al. 2001, Walsh and Steidinger 2001). Concerns surrounding nutrient enrichment and HABs have focused on human health (e.g., shellfish poisoning), economic impact of fisheries losses, and toxicological impact on marine life as the toxic effects propagate through the food web. One example, given by Landsberg and Steidinger (1998), is that a large bloom of the dinoflagellate *Karenia brevis* (formerly *Gymnodinium breve*) caused the deaths of large numbers (about 10%) of the remaining endangered Florida manatees (*Trichechus manatus latirostris*) in 1996.

Benthic primary production is underemphasized in marine ecosystems because phytoplankton is the main source of primary production in the world's oceans. In coastal settings however, macrophyte primary production has been recognized as an important component of overall primary production as well as serving as structural habitat (Mann 1972, Smith 1981, Duggins et al. 1989, Hacker and Steneck 1990, Duffy and Hay 1991, Vetter 1994, 1995, Okey 1997, Vetter and Dayton 1998, 1999, Okey 2003, Epifanio et al. 2003, Adams et al. 2004). A particularly underemphasized component of benthic primary

production is that accounted for by microphytobenthos. Recent work has demonstrated that this inconspicuous component can contribute a considerable portion of overall continental shelf primary production (Colijn and de Jonge 1984, Cahoon and Cooke 1992, MacIntyre and Cullen 1995, MacIntyre et al. 1996, Nelson et al. 1999). High rates of marine microphytobenthic primary production have been recognized for 30 years (e.g., Bunt et al. 1972, Sournia 1976, Hartwig 1978).

High production of microphytobenthos occurs on tropical and subtropical shelves where overlying water is relatively clear. The rate of primary production by microphytobenthos, as well as its biomass, is strongly limited by the light reaching the sediment (Hartwig 1978). This light limitation is expressed in nature as a declining gradient of microphytobenthos production with increasing depth off Madagascar, for example (Plante-Cuny 1973 in Colijn and de Jonge 1984), but also on the West Florida Shelf (Vargo, unpublished data) where these primary producers likely occur below the 200 m depth contour. Tropical and subtropical 'clear water' shelf systems might in fact be particularly susceptible to the impacts of pollution that causes increased shading because sea floor primary production in these shelf areas can comprise a considerable portion of overall primary production, and because declines in the water transparency of these naturally oligotrophic systems might fundamentally shift patterns of energy flow as light fades below the minimum necessary thresholds of acclimated benthic primary producers. Many corals and foraminiferans rely on symbiotic zooxanthellae to provide them with photosynthetic energy that is integral to the production and maintenance of tropical marine habitats and biodiversity. These organisms and habitats are degraded (or changed) by transparency declines related to nutrient enrichment (Hallock and Schlager 1986, Hallock 1987, 1988, Hallock et al. 1993, Hallock 2000).

Microphytobenthic production is known to decrease when the biomass of overshading plankton increases, even though microphytobenthos can persist at low light levels (Cahoon and Cooke 1992, Meyercordt and Meyer-Reil 1999). This spatial and temporal primary production compensation by microphytobenthos should distribute primary production evenly across horizontal space and time, or at least moderate its overall variability. Similar compensation patterns are now emerging in other systems (e.g., Blanchard and Montagna 1992, Clavier and Garrigue 1999). Both horizontal and vertical distributions of micro-photosynthesizers within sub-systems undoubtedly mediate the character of secondary and higher level production. As phytoplankton increases across a shelf, microphytobenthos tends to decrease.

Many organisms living over continental shelves utilize the primary production of microphytobenthos directly (Nelson et al. 1999) or indirectly. Shading by nutrient enrichment along coastal zones can, in theory then, shift communities from assemblages that rely on benthic primary production towards those that rely on planktonic primary production. This is consistent with simulations by Blanchard and Montagna (1995), which indicated that shading by phytoplankton blooms in Baffin Bay, Texas could profoundly decrease the production rate of microphytobenthos and the abundance of the benthic macrofauna supported by them. This shift along a benthos-based to plankton-based continuum

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could have far reaching implications for community organization and benthic-pelagic coupling since a whole suite of organisms rely directly or indirectly on microphytobenthos.

Continental shelves cover about 8% of the world's ocean area, but produce almost one quarter of the world's plankton (Pauly and Christensen 1995). Marine macrophytes on continental shelves add an additional 5% to the oceans' primary production, and make up fully two thirds of the oceans' plant biomass, despite inhabiting about one quarter of one percent of the total area inhabited by plankton (Smith 1981). Benthic microflora on continental shelves add even more to oceanic primary production. Shading related shifts in the assemblages of these continental shelf primary producers and dependent biological communities are especially important to humans because, for example, fisheries are concentrated near coasts. Of even greater concern than such pollution-induced shifts is the distinct possibility that such shifts might lead to degraded systems that are stable (i.e., do not recover). Not only could eutrophication and shading lead to large changes in flora and fauna, but certain changes in fauna (i.e., removal of filter feeders) could exacerbate cultural eutrophication in marine systems (Lenihan and Peterson 1998, Lenihan 1999, Jackson et al. 2001). Thus, positive feedbacks between nutrient enrichment and filter feeder degradation could potentially lead to 'alternate stability domains' in these marine systems (see Scheffer et al. 2001). In addition, Smith (1981) plausibly suggested that a good portion of the $9 \cdot 10^8$ tonnes of carbon captured annually by marine macrophytes could be entrained in marine carbon sinks because the fate of much of this material is unused detritus. Decreases in macrophyte production resulting from increases in shading by plankton could slow the flux to such a sink, thus slowing oceanic absorption of atmospheric carbon.

The West Florida Shelf

The West Florida continental shelf covers over 170 000 km^2 extending more than 200 km west from the intertidal zone to the 200 m isobath across a very gentle slope of ancient limestone platforms (slope <<1°). These platforms are overlain with a veneer of old carbonate sediment and more recent riverine sediment. To the north, the shelf extends to DeSoto Submarine Canyon near the Alabama-Florida border, and to the south the delineation is drawn at the transition to the Florida Keys.

The nutrient content and optical properties of West Florida Shelf waters are strongly influenced by input from the Mississippi, Mobile, Apalachicola, Suwannee, and Caloosahatchee rivers (Muller-Karger et al. 1991, Gilbes et al. 1996, Del Castillo et al. 2000). Most Gulf waters are naturally poor in nutrients except adjacent to rivers and estuaries or when river flow is high, and except for seasonal patterns of upwelling and impingement of deeper nutrient-rich water from beyond the shelf break related to Loop Current frontal eddy intrusion and other forces (Paluszkiewicz et al 1983, Weisberg et al. 1996, Weisberg et al. 2000, Meyers 2001). Enrichment by riverine, estuarine, and upwelled nutrients is episodically complemented by aeolian deposits of iron from Sahara dust.

Florida Bay lies at the inner edge of the southwest Florida shelf. Documented recent events in the Bay provide clues to the types of changes that might be occurring on the broader shelf. Since the middle to late 1980s, Florida Bay has undergone massive die-offs of several species of seagrasses. A reasonable explanation for this die-off is that increased nutrient inputs led to shading of these plants by macroalgal epiphytes (Fong and Harwell 1994, Lapointe et al. 1994) and blooms of phytoplankton (Tomasko and LaPointe 1994, Boyer et al. 1999, Fourqurean and Robblee 1999, Hall et al. 1999). Phytoplankton blooms can increase water-column temperatures by absorbing solar radiation (Tomasko and LaPointe 1994). Changes in salinity from freshwater diversion can influence the oxygen saturation in the water column (Gunderson 2001). Furthermore, the die-off of seagrasses can increase sediment re-suspension in settings like Florida Bay, thereby causing more shading and seagrass die-off (Hall et al. 1999). Such a positive feedback can help explain the apparent shifts in stability domains in Florida Bay, in addition to the explanations presented by Gunderson (2001). Still another explanation that might have worked in concert with such scenarios is that sea turtle depletion led to outbreaks of epiphytes and diseases that kill seagrasses because naturally high densities of sea turtles cropped seagrass blades that would otherwise become susceptible (Jackson et al. 2001).

Whatever the exact mechanisms, the ichthyofauna of Florida Bay appears to have undergone a shift from benthic species toward more planktonic-feeding species during the same period (Thayer et al. 1999), and sponges also died in parts of the area (Butler et al. 1995). Similar changes have been observed in seagrass areas of Western Australia for apparently similar reasons (Hillman et al. 1995). Livingston (2001) has described the mechanisms behind such processes in Gulf Coast estuaries.

The widespread loss of seagrasses related to shading and related factors is a very conspicuous ecological change in Florida Bay, but analogous though less conspicuous changes might have occurred in deeper zones of the West Florida Shelf. An analysis of imagery from Advanced Very High Resolution Radiometry showed that reflectance and light attenuation increased between 1985 and 1997 in an area of the shelf west of Florida Bay (Stumpf et al. 1999). The present paper combines a new exploration of trends in water transparency over the West Florida Shelf with some preliminary dynamic simulations of broader community effects of shading using an up-to-date trophic model of the West Florida Shelf (*Ecopath with Ecosim*). Browder (1993) called for refinement of information about the Gulf of Mexico continental shelf after presenting a pilot model of the shelf using the *Ecopath* approach. Her preliminary modelling exercise indicated the existence of more benthos and higher benthic production than previously thought. The present exercise can be seen as following up on this, presenting results of a more recent synthesis of West Florida Shelf ecosystem information. The general questions addressed in this study were: (1) Are there multiyear trends in water transparency over the West Florida Shelf? (2) What proportion of the overall primary production on the West Florida Shelf is made up by microphytobenthos? (3) What broad community effects might result from nutrient enrichment and phytoplankton blooms? The preliminary simulations described below indicated that broad community

effects should be expected from a mechanism that decreases benthic primary production, such as shading by phytoplankton blooms.

METHODS

This investigation consisted of two components: (1) exploration of trends in water transparency over the West Florida Shelf, and (2) simulations of community-wide effects of seafloor shading by phytoplankton blooms using a recently constructed balanced trophic model of the West Florida Shelf.

Trends in water transparency

Changes in water transparency were investigated with two approaches. The first was a review of phytoplankton production estimates from the vicinity of the West Florida Shelf. The second approach was to examine trends in water quality parameters in the Southeast Area Monitoring and Assessment Program (SEAMAP) data for a chosen portion of the West Florida Shelf. The examined area extends between 24° to 26° N and between 83° to 85° W, and is located just to the northwest of the Dry Tortugas. It was named the 'Hemingway Quadrant,' and was chosen because it encompassed an area of the seafloor covered by living coralline algal nodules (e.g., *Peyssonnelia rubra* and *P. simulans;* Phillips and Thompson 1990) that can be used in the future as a proxy to document changes in shelf photosynthetic communities. The water quality data within this area were extracted from SEAMAP ichthyoplankton survey data collected during cruises in the Gulf of Mexico by the Florida Fish and Wildlife Conservation Commission (data held by C. Meyer and B. Mahmoudi, Florida Marine Research Institute, St. Petersburg). Temporal trends of chlorophyll at three depths, turbidity at three depths, and Secchi depth at the surface were analyzed with simple linear regression.

The West Florida Shelf model

The *Ecopath* model of the West Florida Shelf was constructed at the Florida Marine Research Institute during 2000 as an initiative by the Florida Fish and Wildlife Conservation Commission to synthesize existing ecosystem information in a format that would allow simulations of ecosystem dynamics related to living resource management along the Gulf coast of Florida (Mahmoudi et al. 2002). This model was constructed by combining extensive literature reviews of local, regional, and global information with a coordinated collaboration of marine scientists with expertise in West Florida Shelf biota. The basic parameters for the 59 functional groups in the West Florida Shelf *Ecopath* model are shown in Table 6-1. Diet compositions and full documentation of sources for all parameter estimates are available from the Florida Marine Research Institute (Okey and Mahmoudi 2002). A slightly updated diet composition is presented here in Appendix E.

Benthic primary producers were estimated to make up 35% of the overall primary production and 91% of the primary producer biomass on the West Florida Shelf, with microphytobenthos making up 10%

and 11% of the respective totals (though the biomass and production of macroalgae might be underestimated in this analysis).

Simulations

Seven scenarios were developed to investigate community-wide effects of shading interference of benthic primary producers by phytoplankton blooms:

1. Shade microphytobenthos;
2. Shade macroalgae;
3. Shade seagrasses;
4. Shade all three benthic primary producer groups;
5. Shade all three and include prey protection effects of biogenic structure;
6. Shade all three and include enrichment of phytoplankton production;
7. Shade all three; include refuge effects; include phytoplankton enrichment.

Shading mortality was evenly increased from 0 to 50% of the production rate (P/B) for each of the three benthic producer groups between 2.5 and 10 years after the beginning of of 30-year simulations. Scenario 5 added refuge effects of biogenic structure to the simulated shading of all three benthic primary producers. Seagrasses, macroalgae, drifting macrophytes, and sessile epibenthic fauna benefit many prey organisms through refuge effects. Small demersal fishes, for example, are less vulnerable to predators when they associate with this biogenic habitat structure, which is why they are found in higher abundances in such refugia (Holmquist 1994, Levin and Hay 1996). *Ecosim* allows specification of such a protective 'mediation,' such that prey organisms become more vulnerable to predators when their protective biogenic habitat declines. This is achieved by modifying their relationships within *Ecosim* by choosing or sketching a 'shape' of the relationship in the mediation interface representing how specified trophic interactions are modified by changes in the biomass of a 'mediating' group. This protective effect was specified to be qualitatively equal for the four biogenic structures listed above, and the same mediating relationship (biogenic habitat protection) was applied to the prey vulnerabilities for a variety of demersal and structure-associated fishes and other organisms in the system. This relationship was specified with a negative sigmoid function that was automatically scaled relative to *Ecopath* baseline inputs (see Christensen et al. 2000). Scenario 6 combines simulated shading of the three benthic primary producers with concomitant increases in surface phytoplankton at the approximate rate indicated by revealed trends in SEAMAP data (discussed later). Scenario 7 resembles bloom related shading best in that it combines overall shading with both refuge effects (loss of refuge) and phytoplankton enhancement. The system-wide prey vulnerability was set at 0.4 for all scenarios representing a mixture of top-down and bottom-up forces shaping the community.

Table 6-1. Basic parameters of the Ecopath model of the West Florida continental shelf. OI is the omnivory index, which is the variance of prey trophic levels; P/B and Q/B are the ratios of production (P) and consumption (Q) to biomass; EE is the ecotrophic efficiency, or the proportion of production consumed by predators or exported. Values in bold have been calculated by the *Ecopath* algorithm; other values are empirically based inputs, or values that were adjusted from empirically based values during balancing. Documentation of the derivations of these estimates is available in Okey and Mahmoudi (2002).

Group name	Trophic level	OI	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE
Large oceanic piscivores	4.7	0.313	0.070	0.680	7.400	0.845
Pelagic oceanic piscivores	4.5	0.266	0.150	1.057	8.500	0.829
Dolphins	4.4	0.283	0.038	0.099	40.439	0.082
Coastal sharks	4.3	0.732	0.090	0.410	3.290	0.909
Large groupers	4.3	0.252	0.119	0.458	4.103	0.880
Pelagic coastal piscivores	4.3	0.240	0.230	0.640	10.230	0.972
Benthic oceanic piscivores	4.2	0.331	0.045	0.450	7.940	0.961
Mackerel (adult)	4.2	0.097	0.183	0.384	8.000	0.938
Mackerel (juvenile)	4.2	0.051	0.126	0.769	9.000	0.970
Nearshore associated piscivores	4.2	0.263	0.013	1.057	7.670	0.900
Seabirds	4.2	0.289	0.001	0.100	80.000	0.000
Pelagic oceanic jelly eaters	4.1	0.045	2.200	1.560	8.071	0.674
Structure associated coastal piscivores	4.1	0.271	0.220	0.630	5.400	0.736
Benthic coastal piscivores	4.0	0.304	0.245	0.550	8.386	0.938
Demersal coastal piscivores	4.0	0.903	0.120	0.642	6.334	0.977
Squid	3.8	0.184	1.100	3.000	35.000	0.987
Large oceanic planktivores	3.7	0.305	0.043	0.110	1.800	0.500
Rays and skates	3.7	0.340	0.238	0.380	7.720	0.651
Octopods	3.6	0.400	0.074	3.100	11.700	0.950
Benthic coastal invertebrate eaters	3.5	0.129	0.860	0.860	10.110	0.991
Benthic oceanic invertebrate eaters	3.5	0.203	0.190	1.200	15.780	0.988
Demersal coastal invertebrate eaters	3.5	0.223	1.400	0.654	7.920	0.999
Structure associated coastal invertebrate eaters	3.5	0.169	1.200	0.748	7.330	1.000
Structure associated coastal planktovores	3.5	0.081	0.050	2.000	10.000	0.851
Carnivorous jellyfish	3.4	0.091	0.265	40.000	80.000	0.928
Demersal oceanic invertebrate eaters	3.4	0.069	0.045	1.200	15.760	0.971
Lobsters	3.4	0.246	0.028	0.900	8.200	0.858
Other fishes	3.4	0.225	3.870	1.300	7.040	0.950
Pelagic oceanic planktivores	3.4	0.509	1.500	0.872	11.710	0.949
Stomatopods	3.3	0.469	0.994	1.335	7.432	0.414
Turtles	3.3	0.639	0.007	0.192	3.500	0.417
Nearshore planktivores	3.2	0.262	2.215	2.000	15.920	0.990
Large crabs	3.1	0.189	0.705	2.800	8.500	0.990
Sardine and herring	3.1	0.471	2.400	1.050	12.106	1.000
Carnivorous zooplankton	3.0	0.171	21.600	8.700	20.000	0.250
Adult shrimps	2.9	0.443	0.550	5.380	19.200	0.987
Demersal coastal omnivores	2.9	0.490	0.700	1.340	15.130	0.784
Ichthyoplankton	2.9	0.427	0.048	50.448	132.130	0.748
Surface pelagics	2.9	0.859	0.099	2.600	11.700	0.950
Other mesozooplankton	2.6	0.277	6.700	17.300	50.000	0.851
Structure assoc. coastal omnivores	2.5	0.466	0.312	1.329	24.370	0.980
Echinoderms	2.4	0.347	19.246	1.200	3.700	0.277
Meiofauna	2.4	0.236	13.000	12.500	25.000	0.822
Sessile epibenthos	2.4	0.273	219.000	0.800	9.000	0.236
Small mobile epifauna	2.4	0.284	12.614	7.010	27.140	0.950
Small infauna	2.3	0.273	19.032	4.600	15.900	0.401
Small copepods	2.2	0.133	8.300	17.300	50.000	0.939
Bivalves	2.1	0.106	48.596	1.209	23.000	0.168
Mullets	2.1	0.101	0.329	0.701	11.030	0.512
Manatees	2.0	0.000	0.001	0.100	36.500	0.000
Microbial heterotrophs	2.0	0.000	60.000	100.000	215.000	0.235
Dead carcasses	1.0	0.421	1.000	-	-	0.906
Drift macrophytes	1.0	0.000	2.659	-	-	0.324
Macroalgae	1.0	0.000	36.050	4.000	-	0.396
Microphytobenthos	1.0	0.000	29.778	23.725	-	0.623
Phytoplankton	1.0	0.000	25.000	182.130	-	0.304
Seagrasses	1.0	0.000	175.617	9.014	-	0.017
Sediment detritus	1.0	0.274	390.000	-	-	0.884
Watercolumn detritus	1.0	0.347	125.000	-	-	0.910

RESULTS

A general trend of increasing phytoplankton production from the early 1970s to the early 1990s in the vicinity of the West Florida Shelf emerged during a literature survey (Figure 6-1). This was consistent with the finding of significant increases in surface and middle-depth chlorophyll from the early 1980s to the late 1990s, significant increases in surface turbidity from 1993 to 1999, and the trend of declining surface clarity (Secchi depths) from 1983 to 1997 in SEAMAP data from the 'Hemingway Quadrant' (Table 6-2). Very small proportions of the total variations in these data are explained here, but sample sizes are high enough to reveal significant differences, or trends.

Table 6-2. Results of regressions of water column measurements against time in the Hemingway Quadrant of the West Florida Shelf. Chlorophyll data spanned from early 1980s to late 1990s; turbidity from 1993-1999; and clarity from 1983-1997.

Water column depths	Intercept a	Slope $b \pm s.e.$	n	R^2	p
Chlorophyll					
Surface	-66	0.03 ± 0.01	210	0.05	0.001
Middle	-517	0.26 ± 0.11	33	0.16	0.02
Maximum	-34	0.02 ± 0.04	34	0.01	0.65
Turbidity					
Surface	-4663	2.37 ± 1.16	93	0.04	0.04
Middle	2572	-1.25 ± 1.28	93	0.01	0.33
Maximum	2181	-1.06 ± 1.34	93	0.01	0.43
Clarity (Secchi depth)					
Surface	395	-0.19 ± 0.15	89	0.018	0.208

Benthic primary producers were estimated to comprise 35% of the overall primary production on the West Florida Shelf, with microphytobenthos accounting for 10%, macroalgae 2%, and seagrasses 23%, based on a literature review by Okey (2002). In contrast, benthic primary producers make up an estimated 91% of the shelf's overall primary producer biomass, with microphytobenthos accounting for 11%, macroalgae 14%, and seagrasses 66% (Table 6-3). The distribution of flows at each trophic level is shown in Table 6-4.

Table 6-3. Estimated production and biomass of the four primary producers in the West Florida Shelf ecosystem

Primary producer	Production $(t \cdot km^{-2} \cdot year^{-1})$	Biomass $(t \cdot km^{-2})$
Phytoplankton	4553 [a]	25.0 [b]
Microphytobenthos	706	29.8
Macroalgae	144 [c]	36.1 [c]
Seagrasses	1583	175.6

Notes: Estimates were chosen or derived based on a literature review by Okey (2000). Sources are indicated when chosen from a range of estimates, rather than derived;
a. Steidinger (1973) and Tomas (1995);
b. Steidinger (1973);
c. Likely an underestimate for WFS.

Table 6-4. Flows from primary production and detritus ($t \cdot km^{-2} \cdot year^{-1}$). System imports and exports are not shown. Some flows reach trophic level six because some organisms within some functional groups are supported by energy that has traversed five links from primary producers.

Trophic level	From primary production				From detritus			
	Consumed	To detritus	Respiration	Throughput	Consumed	To detritus	Respiration	Throughput
VI	0	0	0	0	0	1	1	2
V	0	1	3	5	2	8	12	22
IV	5	15	18	38	22	91	71	184
III	38	138	83	259	184	952	393	1529
II	259	1109	540	1909	1529	8169	4854	14552
I	1907	5080	0	6987	14551	0	0	17164
Sum	2209	6344	645	9198	16289	9220	5332	33454

The biomass values of almost all functional groups in the system were predicted to decline when shading mortality on benthic primary producers was simulated without including concomitant refuge effects of biogenic structure or enhancement of phytoplankton (Figure 6-2) (the specified shading mortality of half the P/B values resulted in an approximate 50% reduction in the biomass of each or all of the benthic primary producers). Of the 55 living groups in the model, only phytoplankton, small copepods, ichthyoplankton, and carnivorous jellyfish never declined as the result of the specified simple seafloor shading mortalities. These were the only groups in the model whose food sources originated entirely with phytoplankton (and detritus).
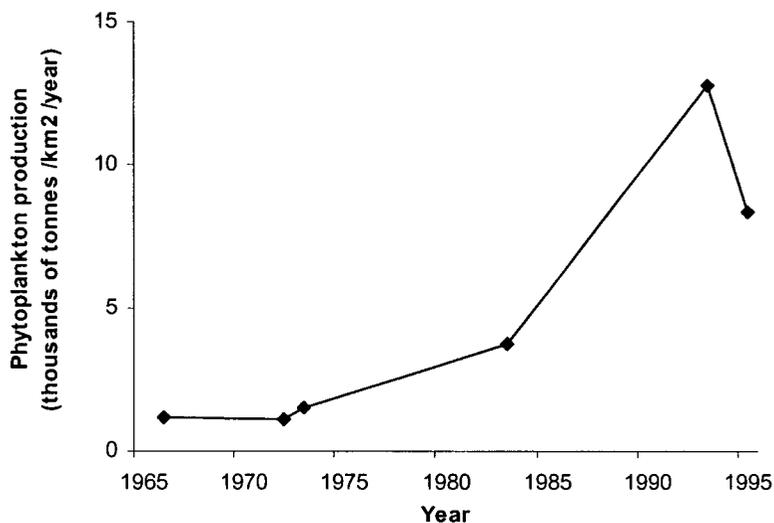
Figure 6-1. Changes in estimates of phytoplankton production from 1966 until 1995 (from Kondratyeva & Sosa 1966 in Vargo and Hopkins 1990, El-Sayed 1972, Steidinger 1973 in Vargo and Hopkins 1990, Yoder & Mahood 1983, Vargo, unpublished data from 1993, Brian Bendis, Florida Fish and Wildlife Conservation Commission, unpublished data from 1994-1996).

Declines were generally more severe when refuge effects of benthic groups (biogenic habitat structure) were specified using the 'mediation' function in *Ecosim*. Most groups declined more as the now 'habitat-providing' benthic primary producers declined. This occurred whether or not a species directly benefited from these habitat structures. Five groups, however, increased as the habitat-providing benthic

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primary producers declined. These were lobsters, large crabs, stomatopods, nearshore planktivores, and turtles, all clustered between trophic levels 3.1 and 3.4. The addition of simulated phytoplankton enrichment to the shading and habitat scenarios led to predicted increases in groups that obtain most of their energy from phytoplankton pathways and decreases in groups that obtain most of their energy from benthic primary production. The direction of effects alternated regularly as they propagated to higher trophic levels. The number of full cycles of alternating effects appears to match the number of trophic levels in the system (4.7 trophic levels) (Figure 6-2).

DISCUSSION

The mechanism of community change via shading

The separate articulation of four primary producer groups in the West Florida Shelf *Ecopath* model (out of 59 functional groups) enabled exploration of the potential community effects of long-term declines of water-column transparency in this historically clear-water system. Three of these primary producers are benthic and one is pelagic (i.e., phytoplankton). The main assumption of this investigation is that benthic primary production by microphytobenthos, macrophytes, and seagrasses would decrease over this continental shelf as the result of shading by phytoplankton blooms. This assumption is supported by several empirical studies in marine and freshwater settings (e.g., Maristo 1941, Spence 1982, Meyercordt and Meyer-Reil 1999, Nelson et al. 1999). An alternative hypothesis is that shading would not limit seafloor primary production if the latter is limited by something other than light; i.e. nitrogen. Broad community changes should result from declines of biomasses or production rates of benthic primary producers if a considerable proportion of the energy used by species throughout the system originates with benthic primary production. Changes should propagate through the system when benthic primary production is decreased not only because of the degradation of food pathways, but also because of shifts in the character and distribution of food production.

The main prediction was that changes in primary production patterns and other changes related to shading (e.g., detritus deposition and DO declines) would shift the continental shelf community to a different assemblage with a proportionally greater reliance on water-column primary production and detritus deposition, and less of a reliance on benthic primary production and refuge value provided by associated biogenic structure. The modelling simulations were generally consistent with this prediction.

Biomass change (end / start)

Categories (top to bottom):
Large oceanic piscivores, Pelagic oceanic piscivores, Dolphins, Coastal sharks, Large groupers, Pelagic coastal piscivores, Benthic oceanic piscivores, Mackerel (adult), Mackerel (juvenile), Nearshore piscivores, Seabirds, Pelagic oceanic jelly eaters, Struc. assoc. coast. pisciv., Benthic coastal piscivores, Demersal coastal pisciv., Squid, Large oceanic planktivores, Rays and skates, Octopods, Benth. coast. invert. eaters, Benth. oceanic invert. eat., Dem. coast. invert. eaters, Struc. ass. coast. invert. eat., Struc. ass. coast. planktiv., Carnivorous jellyfish, Dem. oceanic invert. eaters, Lobsters, Other fishes, Pelagic oceanic planktiv., Stomatopods

Legend (left):
- Shade microphytobenthos
- Shade macroalgae
- Shade seagrasses
- Shade all three

Legend (right):
- Shade all, habitat loss
- Shade all, enrich phyto.
- Shade, habitat, enrich phyto.

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Biomass change (end / start)

Figure 6-2. Predicted biomass changes (proportional change relative to starting baseline) after the 30-year simulations for the 59 functional groups in the West Florida continental shelf ecosystem. Groups are organized by descending trophic level (from 4.7 to 1). The left panel shows the results of simulated shading of the three benthic primary producers (shading mortality equal to half the production rate). The right panel shows shading simulations with the refuge effect from biogenic habitat structure, with a concomitant enrichment of phytoplankton, and with all effects. The black line is a moving average (second period) of the predicted changes from these combined effects; it is added simply to show the general trend in the direction of biomass change at different trophic levels.

The West Florida Shelf is unique among continental shelves of North America. Historical water clarity has been so high that attached macroalgae in the region have been observed and collected at depths beyond the 200 m shelf break (Sylvia Earle, personal communication in Humm 1973; also see Littler et al. 1985). More recent data suggest that enough light reaches 75 m depths to enable substantial photosynthesis of West Florida Shelf benthic microflora. Tomas (1995) pointed out that conventionally measured estimates of overall primary production should be considerably higher to account for the benthic microflora whose contributions are likely profound, though not well known, on the West Florida Shelf. The present *Ecopath* model is among the first to account for recent high estimates of benthic microalgae in nearshore marine systems, and this could partially explain the high overall primary production estimation (6987 t ww·km^{-2}·year^{-1}) relative to previous estimates from the region when less information about benthic primary production was included (2619 t ww·km^{-2}·year^{-1} from Browder 1993 using conversions provided by Durbin and Durbin 1998 and Parsons et al. 1977). The inclusion of this previously underestimated component of primary production helps resolve a long-standing dilemma typically encountered while attempting to balance whole food web models—the apparent lack of adequate energy to support higher trophic levels. The estimate for overall primary production for the West Florida Shelf model is merely 2.7% lower than the estimate for phytoplankton primary production in the Mississippi delta bight (7182 t ww·km^{-2}·year^{-1}; from Sklar 1976 using above conversion sources). Primary production is virtually equal in these two systems if phytoplankton in the Mississippi delta bight completely inhibits benthic primary production.

Indicated community changes

The most conspicuous pattern revealed in this series of simulations is a shift in community composition away from organisms that obtain most of their energy from benthic primary production pathways, and towards organisms that obtain most of their energy from planktonic primary production. This pattern is best revealed by examining the direction of change of particular species during the final simulation, which combines shading mortality, biogenic habitat structure effects, and enhancement of plankton production (Figure 6-2, right panel). Also, the general match between the number of trophic levels represented in this food web and the full cycles of alternation in the direction of biomass change in the final simulation is reminiscent of the known alternating effects of trophic cascades in freshwater food chains (e.g., Carpenter 1988, Power 1990, Wootton and Power 1993, Carpenter and Kitchell 1996) and marine systems (e.g., Paine 1966, Estes and Palmisano 1974, Estes et al. 1974, Estes and Duggins 1995, Steinberg et al. 1995). If this pattern reflects a true trophic cascade, it is a donor-controlled cascade in a complex aquatic food web, and is thus only partially consistent with Strong's (1992) premise that most true cascades are aquatic and donor controlled and that cascades occur only in simple systems.

The simulations that specified shading mortality of benthic primary producers without concomitant increases in phytoplankton and without refuge effects of biogenic structure were valuable because they indicated the relative support provided by benthic primary producers throughout the system (Figure 6-2; left panel). These simulations indicated that 51 of 55 living groups (or 93% of living groups) in the West Florida Shelf system depend on benthic primary producers to a considerable extent, whether directly or indirectly. The lack of a predicted biomass decline in the ichthyoplankton group could be partially explained by this pooled group's lack of specified ontogenetic linkage to the various fish groups in this model iteration. Nevertheless, fish groups usually did not decline by more than 50% during these simulations so that spawning stock would presumably be maintained.

Some nearshore forage fish assemblages and higher trophic levels responded to simulated phytoplankton blooms and shading in unexpected ways (i.e., negatively rather than positively), but this paradox was resolved when *a posteriori* examinations of diet compositions revealed the dependence of these groups on benthic production pathways. For example, the considerable and apparently counterintuitive declines of 'surface pelagics' to simulated enhancement of phytoplankton and inhibition of benthic primary production is explained by the group's species composition and specified diet. Halfbeaks (*Hemirhamphidae*) and flying fishes (*Exocoetidae*) make up this group and the specified diet is 47% seagrasses, 26% small mobile epifauna, 12 % nearshore planktivores, 9% other fishes, 6% small infauna, and 1% mesozooplankton (based on halfbeak diets in Randall 1967). This implies a near exclusive reliance on benthic production, and so the direction of their response is not surprising. However, flying fish diet and biomass information were not available, and it is possible that halfbeaks occasionally consume quantities of zooplankton surpassing 1% of their diet. The indicated declines of this group would be more moderate if phytoplankton food were a larger part of its diet.

Seabirds are also specified in the *Ecopath* model as being somewhat reliant on benthic primary production; they consume a variety of demersal and benthic fish species in addition to plankton-dependent sardine, herring, and nearshore pelagics (Vidal-Hernandez and Nesbitt 2002). Adult and juvenile mackerel also rely on some demersal and benthic fishes in addition to planktivorous fishes. The alternating response of both of these species to the final two simulations (Figure 6-2) reveals the diverse production origins of their diets. Predicted responses of such species look surprising only when our immediate assumptions about a group's diet composition do not match with the diet composition specified in the model. In *Ecosim*, diet compositions do change dynamically during simulations as predators target prey at rates proportional to the prey's relative abundance. However, some level of consumption of a prey by a predator must be specified for such shifts to occur. "Apparent prey switching" by predators results from particular prey spending less time foraging (i.e., less time in the 'vulnerable' pool) as they become less abundant. This is complemented by predator 'satiation,' which is represented by decreases in feeding time at high prey encounter rates, and through direct handling time effects (C. Walters, pers. comm., 12 November 2001).

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It was surprising that biomass increased in five assumed beneficiaries of biogenic habitat refuge after the biogenic refuge effect was added to the shading simulation (i.e., after available refuge decreased with shading). The five groups were large crabs, lobsters, stomatopods, nearshore planktivores, and turtles. This initial paradox was resolved by examining changes in the predicted biomasses of the main predators of these groups. Declines in these main predators (mostly benthic and demersal fish predators) were more pronounced when the biogenic structure effect was added to the combined shading simulation. The resulting release in predation pressure on the five groups in question allowed them to increase above baseline levels despite decreases in available refugia and benthic primary production.

These opposing forces are integrated in the *Ecopath* model and the *Ecosim* simulation; the decline in predators was expressed as a relatively stronger effect than the decline in refugia (and benthic primary production). This result indicates only that these opposing forces exist. For application to lobster or crab policy development, the model should be refined to emphasize the articulation and relative strengths of protective effects of habitat and other related questions. For example, Butler et al. (1995) observed that the widespread decline of sponges in parts of Florida Bay (related to cyanobacteria-blooms) had a dramatic impact on the abundance and distribution of juvenile lobsters. Splitting lobsters into ontogenetically linked functional groups would better capture the energetic dynamics of the protective effects of sponges on juvenile lobsters, and thus the whole population, but the current West Florida Shelf model contains only one lobster group because the emphasis of the current exercise is on the whole system.

Forces other than shading can, of course, shift systems from benthic to pelagic, or otherwise considerably restructure marine communities. These include fishing impacts that can preferentially remove benthic target organisms (e.g., Overholtz et al. 1999) or benthic nontarget organisms as in trawling (e.g., Jennings et al. 2001a, Jennings et al. 2001b, Koslow et al. 2001).

Some potential consequences of benthic – pelagic shifts in community organization

Shifts from benthic to pelagic modes of production might be occurring in coastal marine ecosystems worldwide. The example that follows helps reveal specific processes of change in coastal systems relating to changes in water column transparency and benthic-pelagic shifts of production pathways, in this case related to fisheries interests. Two questions regarding to the dynamics of forage fishes and other middle and high trophic level groups can be addressed by examining a benthic portion of the West Florida Shelf food web (Figure 6-3): (1) Does the fisheries removal of shrimps and crabs increase the number of forage fishes produced through benthic pathways, or would the habitat modifications of shrimp trawling offset such benefits? (2) Can the presence of a keystone predator, such as stomatopods, lead to more forage fish being produced through benthic pathways by controlling the crustacean energy pathway (thus favoring the alternative energy pathway of forage fishes)?

The third trophic level depicted in Figure 6-3 shows the alternate pathways of benthic production through forage fishes or higher crustaceans. Flow of benthic production to forage fishes might be facilitated by the presence of stomatopods—a possible keystone predator. Intense fisheries on one of the pathways might similarly facilitate the flow of benthic production up the alternate pathway, but water quality degradation (i.e., transparency declines) could decrease the flow of benthic primary production up both pathways. However, a shift to relatively higher planktonic primary production would lead to higher detritus fallout to the benthos (not shown) thereby increasing benthic detritus pathways. Such questions can be explicitly addressed using modelling approaches such as *Ecopath with Ecosim* when linkages between benthic and pelagic components are adequately represented.
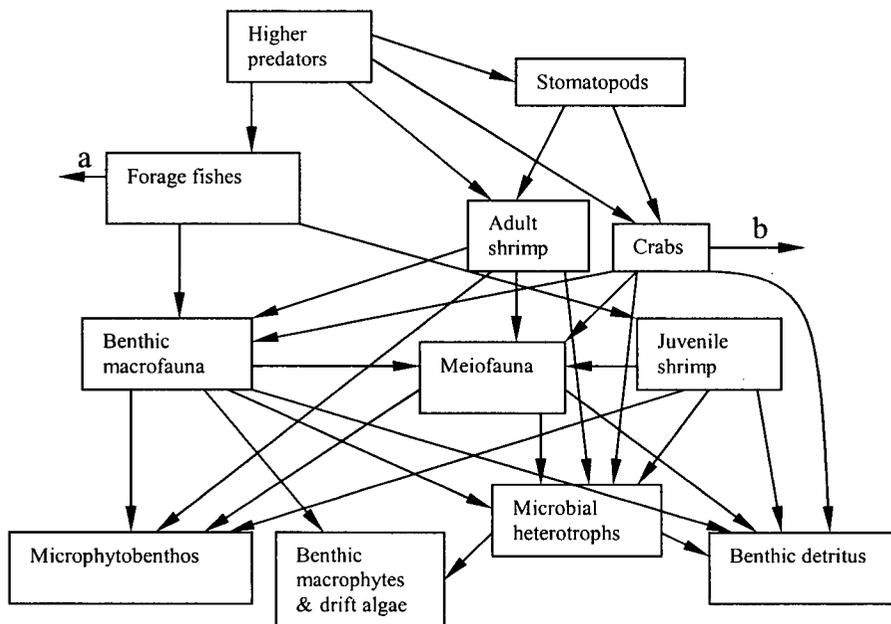
Figure 6-3. Generalized predatory interactions in a simplified benthic food web of the West Florida Shelf (expanded from Walsh's example *in* Cushing 1984). Arrow (a) represents fishes feeding on plankton and arrow (b) represents crabs feeding on clams, which eat detritus and phytoplankton. Other major components of the West Florida Shelf benthos have been excluded here for simplicity.

Notwithstanding the potential for such keystone mediation in community dynamics, seafloor shading should shift the composition of benthic communities rather than decrease the overall benthic biomass because plankton blooms should result in increased detritus deposition. Benthic primary consumers should thus shift away from herbivory and towards detritivory. Such compensation might partially explain the high resiliency of Gulf of Mexico shrimp populations to fishing pressure (Cushing 1984) because shrimp trawling can decrease the standing biomass of benthic primary producers but increase the input of detritus (e.g., discards), possibly providing a minor feedback that promotes shrimp production, especially in situations of moderate hypoxia (the direct removal of fish predators might be an even more beneficial effect on shrimp from trawling on shrimp). Moreover, trawling increases turbidity by resuspension of sediment thus further promoting shading and the shift to a detritus-based system.

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Lowered dissolved oxygen would result not just from microbial decomposition of increased organic material reaching the marine sediment, but also from decreases in benthic photosynthesis. Even extreme examples of hypoxia in marine systems, such as the "dead zone" associated with Mississippi River inputs (e.g., Malakoff 1998), might have resulted, in part, from the loss of benthic boundary layer photosynthesis related to sea floor shading.

Sources of underestimation of shading effects

The West Florida Shelf contains considerable areas of hard substrate on which benthic macroalgae can attach and grow (hard bottom is ~35% of the total shelf area; Phillips et al. 1990, Phillips and Thompson 1990). Some evidence suggests that the biomass and production of macroalgae on the West Florida Shelf as a whole are higher than the conservative estimates used in this analysis (Table 6-3). For example, Phillips and Thompson (1990) indirectly suggest that the macroalgal biomass on the overall West Florida Shelf is 45% higher than the value used here. Zieman et al. (1989) estimated that macroalgae biomass was equal to 118 t km^{-2} in Florida Bay, an area of high macroalgal biomass that does not necessarily represent this shelf as a whole. Information on macroalgae of the West Florida Shelf stands out as the most uncertain among other primary producers (notwithstanding work by Earle 1972), and underestimation of its biomass and production in this analysis would underestimate the effects of shading. Furthermore, Luning's (1990) ratio of production to biomass (P/B) that was used for macroalgae (4 year^{-1}) might be conservative.

The notion that benthic primary production could be approximately equivalent to water column primary production on the West Florida Shelf is consistent with several recent studies (e.g., Cahoon and Cooke 1992, MacIntyre et al. 1996, Miller et al. 1996) and indicates that the current analysis could greatly underestimate the impacts of shading. In some settings, sediment chlorophyll alone has been shown to exceed water column chlorophyll considerably (Cahoon et al. 1990, Nelson et al. 1999).

Is it really happening?

The trend of increasing phytoplankton production in Figure 6-1 might simply reflect an evolution of detectability from 1965 until the early 1990s, or it might reflect a chance sequence related to differences in sampling areas throughout the region. Alternatively, it could indicate widespread ecological changes on the West Florida Shelf that have gone unnoticed. El Sayed's (1972) measurements were made close to the shelf break in more oligotrophic waters than the later 'mid-shelf' samples, which could have been more influenced by riverine enrichment (Gilbes et al. 1996, Del Castillo et al. 2000). Such measurements should be compared only for similar water types (Vargo and Myers 1991). Even when considering these sources of error, the El Sayed (1972) estimate is still low relative to current measurements. The trends in Table 6-2 support the notion that water-column transparency has been declining and that those declines have been caused by phytoplankton blooms in surface waters, but just barely since R^2 values in the

present analyses are so low. These trends result from aggregation of sampling locations that shifted spatially among sampling dates throughout the Hemingway Quadrant (e.g., it is possible that a 'temporal' trend might simply represent spatial differences within the area because sites were not re-visited). However, sampling bias was minimized by the systematic sampling design, the large number of samples, and the effectively haphazard placement of the Hemingway Quadrant, which is equivalent to random placement when one cannot 'see' the system being sampled (Fager 1968).

Phytoplankton production rates per unit area are very high in the region's estuaries where nutrients are more concentrated. Livingston (1984) found that phytoplankton productivity of the Apalachicola Bay estuary system during the 1970s and 1980s ranged from 63 to 1,694 mgC $m^{-2}\cdot day^{-1}$. Eastbrook (1973 in Livingston 1984) estimated the annual phytoplankton production of the Apalachicola estuary to be 371 gC m^{-2}, which is equivalent to 15,426 $t\cdot km^{-2}\cdot year^{-1}$. Thus, phytoplankton production for the region's estuaries can be over three times higher than the phytoplankton production (per unit area) for the overall West Florida Shelf. Increases in nutrients in the waters of the greater shelf can only increase the efficacy of the shading effect explored here.

The broad shifts in benthic primary producers and the organisms they support might indeed be occurring on the West Florida Shelf, given the order-of-magnitude increases in terrestrial-origin nutrient loads in nearshore waters during the last two decades (Paul Carlson, Florida Marine Research Institute, pers. comm., 2000). A community shift from distinctly benthic-based production to one characterized by more pelagic primary production occurred in Florida Bay during the early 1990s (Hall et al. 1999, Zieman et al. 1999) when turbidity increased dramatically (Boyer et al. 1999). The results of the present analysis of the broader West Florida Shelf are consistent with these empirical findings.

The ecology of the West Florida Shelf might well hinge on basic water quality since decreases in transparency could shift the predominant energy flow pathways along a benthic to pelagic (sea floor to water column) continuum (e.g., Thayer et al. 1999). Such a change in water quality might also shift and compress low-light-adapted photosynthetic organisms into shallower zones (in cases where appropriate substrate is available).

Sears and Cooper (1979) recognized the potential importance of shading on continental shelf communities when they suggested that observed changes in the extinction depth of benthic macroalgal assemblages could be used as a bioassay for evaluating water conditions. The West Florida Shelf provides a good opportunity for applying this methodology because a unique 'deep-water' (70-100 m depth) algal nodule habitat was documented using geo-referenced video and photographs during MMS surveys during the mid 1980s (ESE et al. 1987). The question of whether microphytobenthos production or benthic primary production in general has declined over the West Florida Shelf during the last 20 years could be indirectly addressed by choosing such a measurable proxy, based on Littler et al.'s (1991) and Steller and Foster's (1995) descriptions of algal nodule habitats and their potential uses for exploration of long-term ecological changes.

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CHAPTER 7. Coral-to-algae shifts in Indonesian coral reefs: sedimentation and pollution

ABSTRACT

Corals are being replaced by algae on many tropical reefs. The percent cover of hard corals in Southwest Sulawesi's Spermonde Archipelago (Indonesia) increased with distance from watersheds while abiotic substrate decreased. Water clarity also increased with distance. Conspicuous community shifts characterized by invasion of ephemeral algae occurred seasonally at stations in both watershed blocks examined, but the shift at each block occurred in opposite seasons and involved different colonizing flora. Fleshy algae covered 36% of the reef station near the 'agricultural' watershed during the wet monsoon (they covered only 2.5% of this station during the dry monsoon). Cyanobacteria covered 25% of the reef location near the more 'urban' watershed during the *dry* monsoon (they covered only 5% of this station during the *wet* monsoon). Differences in watershed runoff characteristics at the two watershed blocks will likely explain observed differences in ephemeral flora colonization and the distribution of more enduring reef characteristics such as hard corals.

INTRODUCTION

Phase shifts on tropical reefs—generally characterized by replacement of corals by fleshy algae (e.g., Done 1992; Knowlton 1992; McCook 1999)—likely result from combinations of increased sedimentation, nutrient enrichment, fishing, disease, and oceanographic changes (Hughes 1994; Hughes and Connell 1999; McManus and Polsenberg, in press). I considered that examining community changes in Southwest Sulawesi reefs relative to distance from coastal runoff sources and season would provide useful insights into the physical mechanisms that influence these community shifts, even though modification of trophic forces (e.g., reduction of herbivores) is probably a key mediator of community shifts on coral reefs (Hay 1984; Smith et al. 2001; Belliveau and Paul 2002; Jompa and McCook 2002).

Indonesia is a principal hot spot of coral diversity (e.g., Hoeksema 1993; Wallace 1997; Roberts et al. 2002), but Indonesian reefs have degraded rapidly due to marginal socioeconomic conditions (Fauzi and Buchary 2002) and a severity of threats that was under-appreciated until recently (e.g., Edinger et al. 1998, 2000). Degradation of coral reefs is increasing worldwide due to human-caused stress and disturbance at all scales (Knowlton 2001; McClanahan 2002).

A broad literature focuses on coastal sedimentation as the major stressor to reef-building organisms (e.g., Rogers 1983, 1990; Hodgson 1989; Wolanski et al. 2003). Poor agricultural practices; deforestation; overgrazing; coastal development; and destruction of mangroves all increase sedimentation on reefs. Bossher (1991) explained that sedimentation causes reef drowning by decreasing the ratio of accretion to erosion; reducing the number, coverage, and biomass of reef builders, and exacerbating the effects of other disturbances by altering reef assemblages. High rates of sedimentation are known to retard reef development by stressing reef-building corals (Stafford-Smith 1993; Reigl 1995). Several other

studies have shown that nutrient enrichment and associated water quality degradation (e.g., transparency) can considerably modify coral reef communities as well (e.g., Wellington 1982; Dubinsky and Stambler 1996; Yentsch et al. 2002).

General declines of herbivores can also help shift coral communities (Hay 1984; Thacker et al. 2001; Belliveau and Paul 2002), but several authors have suggested that overall community changes are best explained by combined effects of nutrient enrichment and herbivore declines (e.g., McCook 1999; Stimson et al. 2001; Jompa and McCook 2002). Szmant (2002) refined this integrated view further when suggesting that observed patterns of reef degradation are best explained when effects of nutrient pollution and decreased fish abundance are combined with effects of additional stressors such as sedimentation (see also Hatcher 1997; Hughes and Connell 1999).

Although the relative contributions of the various stressors remain uncertain and inherently variable, sedimentation, eutrophication, fishing, and other agents of disturbance and stress have been increasing in the Spermonde Archipelago of Southwest Sulawesi, Indonesia, and throughout the tropics as human populations increase and resources decline (Wijsman-Best et al. 1981; Neil et al. 2002). Deterioration of the rich coral areas of Indonesia has occurred at an alarming pace due to deforestation, agriculture intensification (including pesticide and nutrient runoff), and other land use changes (Soekarno 1989; Barber 1998). Substantial ecological and hydro-geological modification is widespread throughout the mountainous and alluvial terrain (see Whitten et al. 1987), and this has led to increased erosion as well as deadly flash floods. Blast and cyanide fishing, anchor damage, coral mining, fish traps, and direct collection of reef organisms also foretell a grim outlook for Indonesian coral reefs (e.g., Wijsman-Best et al. 1981; Wilkinson 1993; Tomascik et al. 1997; Barber and Pratt 1998; Pet-Soede and Erdmann 1999).

In this study I addressed three general questions: (1) Do patterns of coral reef community structure differ consistently with distance from watersheds in Southwest Sulawesi, Indonesia? (2) Is there a relationship between sedimentation or water quality and Southwest Sulawesi reef community characteristics? (3) Do Southwest Sulawesi reef communities fluctuate between wet and dry monsoon seasons?

METHODS
Study location

The morphology and ecology of the coral cay islands in the Spermonde Archipelago of Southwest Sulawesi, Indonesia (Figure 7-1) are influenced by two alternating monsoons: a December-February wet monsoon from the Southeast Asian peninsula and a June-September dry monsoon from Australia (Umbgrove 1930; Moll 1983). The regularity of these monsoons is indicated by the Southwest Sulawesi river flow oscillations shown in Figure 7-2.
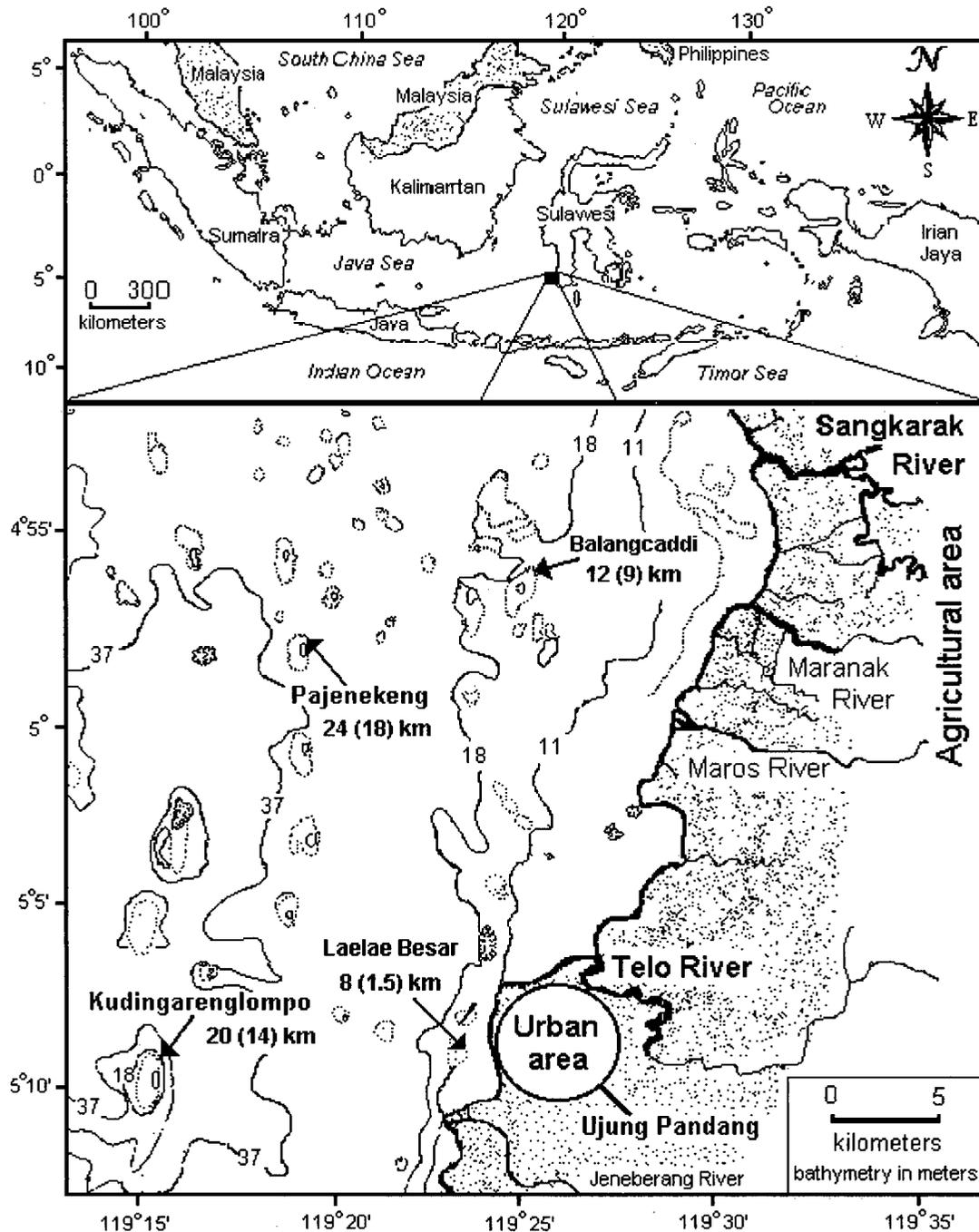
Figure 7-1. Locations of sampling stations at coral cay islands in the Spermonde Archipelago (Kepulauan Spermonde), South Sulawesi, Indonesia. Indicated kilometers are distances from chosen rivers—the Sangkarak or Telo Rivers—and nearest land (in parentheses). Detailed map is from JOG (G) SB 50-4 and SB 50-8, Ministry of Defence, United Kingdom. Broader scale map after Tomascik et al. (1997).

Reef community characteristics at separate coral cay island stations near watersheds were compared to those at island stations further from watersheds. These comprised a near island station and a

far island station—at Balangcaddi and Pajenekeng—adjacent to one watershed in the northern portion of the study area (the Sankarak River), and a corresponding near and far pair of stations—at Laelae Besar and Kudingarenglompo—adjacent to a more southern watershed area (the Telo and Jeneberang Rivers) (Figure 7-1). Reef slopes on cay islands close to rivers receive riverine sedimentation (e.g., clastics and organic material)—especially during high flow—while those further offshore receive carbonate sediment that is resuspended from adjacent reef flats. The upper reaches of both watersheds are historically influenced by deforestation in the mountains 20-30 km to the east (Barber 1998), but agricultural and urban activities influence watershed runoff to varying extents (see Introduction). Current speeds vary around each island and across the shelf, but average ~14 cm /second (Moll 1983).
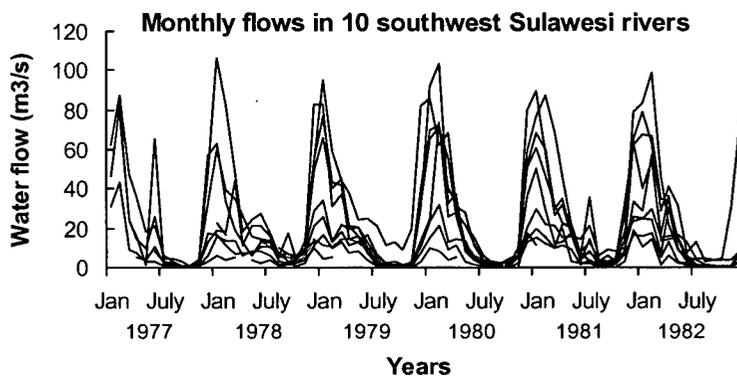
Figure 7-2. Monthly flow measurements at ten river sampling stations throughout southwest Sulawesi (1977-1982). Peak runoff occurs during the wet monsoon (December - March); lowest flows occur at the end of the dry season (September –November). Data are from RePPProT (1988); each line is the data from a single station.

Sampling design and protocol

Community structure of sessile reef organisms (percent cover, number of species, dominance), reef structural integrity (substrate penetrability, ratios of substrate types), downward flux of sediment particulate matter (DF-SPM), and water clarity (Secchi depth) were characterized at each of the four coral cay island stations. Twelve permanent sampling stations were distributed randomly along the 4 m (below MLLW) isobath of the NE facing side of each of the 4 cays by using random numbers along a 50 m transect line. This exposure direction and depth was the most comparable among cays since waves variably disturb NW and S sides during wet and dry monsoons and soft sediment predominates on direct E sides. The position of each transect was thus determined by depth and exposure direction (i.e., the northeastern-most arc of each reef's outline). Blind selection of transect positioning was ensured by surface chop by impairing visual assessment of reef details during deployment of each transect's origin. This stratum was consistently at ~40° slope, and each transect covered a large proportion of that side of each respective cay. One 0.5 m^2 photographic sample was taken at each of the 12 sampling locations along each transect using a Nikonos V underwater camera with strobe mounted on a framer made from PVC piping and fiberglass (Dodge et al. 1982). Optimum number of samples was determined during a

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pilot study as the near asymptote of a curve of cumulative number of species per sample. Photo-samples were positioned with reference to a steel reinforcement rod and the transect line so that photo-quadrats could be re-located precisely during the alternate season. Sampling was conducted on 11-12 February 1993 (near the end of the wet season) and again on 14-15 September 1993 (near the end of the subsequent dry season).

Photographic samples were analyzed by projecting each sample image onto a grid with fifty randomly selected points. This method is useful in describing species composition and cover (Foster et al. 1991; Sullivan and Chiappone 1992), but it is known to miss rare species (R. DeWreede, pers. comm., April 2003) especially when overstories are present. Underestimation of sponge biomass, for example, should be expected. The organism or substratum type intersected by each of the fifty sampling points was recorded for each of the 94 samples (12 samples x 2 distances x 2 watershed blocks x 2 monsoon seasons). Where possible, corals were identified to species by comparing to photographs in Veron (1986), but descriptors of convenience were used when confidence in species identification was limited. Sample and reference photos gave good impressions of micro-structure, but error was expected due to image resolution limits.

These four cays were chosen because they extended WSW of the two watersheds. Currents flow in that general direction for three quarters of the year (March-November; Moll 1983) but other local rivers influence these cays as currents generally flow NE during the 3-month wet season (December-February) (Moll 1983; Erftemeijer 1994; T. Tomascik, pers comm., June 1999). To address this issue, samples were analyzed based on direct distances from the coast (land) in addition to direct distances from the chosen rivers. Irregular distribution of islands led to a staggering of distances of the sampled cays from rivers and land such that the northern stations were further than the southern stations from their respective watersheds. This natural staggering enabled *a posteriori* analyses along four-point gradients of proximity to rivers (8, 12, 20, and 24 km) and land (1.5, 9, 14, and 18 km) (when replication was sacrificed). Thus, this design allows the four stations to be considered in any of three ways: (1) as near vs. far from watersheds with twofold replication as originally intended, (2) as near vs. far within each area of watershed influence, with no true replication, and (3) as 4 sampling stations along an unreplicated gradient of distance from land or rivers.

The substrate penetrability of reef locations was evaluated by recording the number of standard 'hits' with a 3 lb. hand sledge hammer necessary to drive a steel rod 0.5 m into the reef at 12 randomly-chosen locations along each transect. This measure was standardized by ensuring all hits were conducted by the same individual, and effort was taken to keep the force of the hits constant. I developed this method for the present study, and do not believe results of this penetration method can be compared to results by others. The structural state of reef locations was further evaluated by examining ratios of abiotic substrate types revealed by photographic samples.

One Secchi disk measurement was taken adjacent to each of the four transects at the end of the wet monsoon sampling (11-12 February 1993), and accuracy was assessed by repeating each measurement 3 times. Twelve sediment traps (25 cm long PVC pipe with a 2.6 cm opening diameter and sealed bottoms) were attached vertically to the twelve steel marker rods along the transects, i.e., one trap per rod along each transect on each sampling date to compare DF-SPM between reef locations and seasons. Trap openings were positioned 50 cm above the substratum (with their bottom ends 25 cm from the substratum). They were collected two weeks after deployment by sealing the tops with rubber plugs before snipping the zip tie attachments. Sediment samples were dried in the field on coffee filters (pore size 40 microns) and placed in envelopes for transport and storage. In the laboratory, sediment samples were dried further and weighed before and after removal of calcium carbonate fractions using repeated treatments with 10% hydrochloric acid. The relative organic content of the remaining non-carbonate sediment fraction was evaluated by qualitatively ranking the observed reaction strength when treated with 3% hydrogen peroxide solution into three categories of organic content: 'None', 'Medium', and 'High'. Weights of sediment fractions were presented graphically but not evaluated statistically because of unequal sample sizes resulting from the removal of some sediment tubes at Kudingarenglompo by protective locals (see also Edinger et al. 1998) and the corruption of 3 other samples during transport and drying. Resuspension and bioturbation were not explicitly assessed.

Total fish abundance was estimated at each transect during dry-season sampling using a cine-transect method. A video recording, angled at 45 degrees downward and forward was made by a diver swimming one meter above the transect line at each site.

Statistical analyses

Repeated measures analysis of variance (ANOVA) was performed on biotic categories (and abiotic substrate) using the General Linear Model (GLM) in the statistical software SPSS 10.0.5 (SPSS Inc., Chicago, Illinois). These tests encompassed the entire sampling design by simultaneously evaluating the effects of proximity to watersheds (near vs. far) (between-subject factor), monsoon season (within-subject factor), and block (North vs. South) (between-subject factor). Levene's tests and Box's tests were employed with the GLM analyses to evaluate the assumptions of homogeneity of variances and equality of covariance matrices (where appropriate), respectively. Separate repeated measures ANOVAs were performed within individual watershed blocks in cases of severe violations of the assumptions of the fully integrated tests (incorporating both watershed blocks), but where assumptions were not violated for separate tests. These separate tests simultaneously evaluated effects of proximity and season thereby sacrificed the twofold replication of each environmental unit, which was provided by the twofold repetition of the watershed blocks. Prior to these analyses, raw proportion data of each faunal and sediment-type category (i.e., occurrence / 50 sampling points) were arcsin square root transformed to change their binomial distributions to near normal distributions (Zar 1984; p. 239), as indicated by

histograms. In addition, numbers of species data were square root (x + 0.1) transformed to negate the effects of zeros and to achieve reasonable homogeneity of variances. Multivariate analysis of variance (MANOVA) was performed to simultaneously evaluate the effects of proximity to watersheds and watershed block (2 fixed factors) on three abiotic substrate categories (3 dependent variables)—rock, rubble, and sediment—using data from the sampling date with the least ephemeral algae cover at each watershed block. This MANOVA was followed by three univariate ANOVAs to evaluate the effects of proximity to watersheds and watershed block (2 fixed factors) on each substrate type (1 dependent variable). An additional univariate ANOVA was performed on the substrate penetrability data.

As a complement to this series of ANOVAs, and to aid in the interpretation of results, log-linear analyses were conducted using the backward hierarchical method to find the simplest models of main effects, or interaction effects, or both that best explained the distributions of each biotic and abiotic category tested with the ANOVAs described above. These analyses were also conducted using SPSS 10.0.5, but in this case using untransformed data.

Species-area curves were calculated as the average accumulating sum of new species from 1000 Monte Carlo iterations that randomly resampled the array of new species occurrences in the 12 photographic samples, sorting each resampling-iteration in descending order. This was performed with PopTools 2.5 (G. Hood, Pest Animal Control Research Centre, Commonwealth Scientific and Industrial Research Organization, Australia). Dominance was calculated as the total cover of the dominant taxa / the total cover of all living organisms.

Simple linear regressions were performed to compare relationships between Secchi disk extension depth and distance from land, Secchi depth and distance from rivers, light extinction coefficients (k = 1.7/Secchi depth) and distance from land, and k and distance from rivers.

RESULTS

Sedimentation and water clarity

Downward flux of suspended non-carbonate particulate matter (i.e., of riverine origin) was always higher at near-river sites than at offshore sites (Figure 7-3). These differences were as large as a factor of 49 during the wet monsoon when downward flux of non-carbonate sediment exceeded 30 mg·cm^{-2}·day^{-1} at Laelae Besar. Conversely, downward flux of carbonate sediment was always higher at offshore reef stations than at nearshore stations. Sedimentation rates were always higher during the wet monsoon than during the dry monsoon.

The organic content of suspended sediment was highest at the nearshore southern station—Laelae Besar (8 km from the Telo River; 1.5 km from Ujung Pandang city), lower at the nearshore northern station—Balangcaddi (12 km from the Sangkarak River and 9 km from land), and not detected at the offshore stations (Table 7-1). Organic content was highest during the wet monsoon at both nearshore stations.

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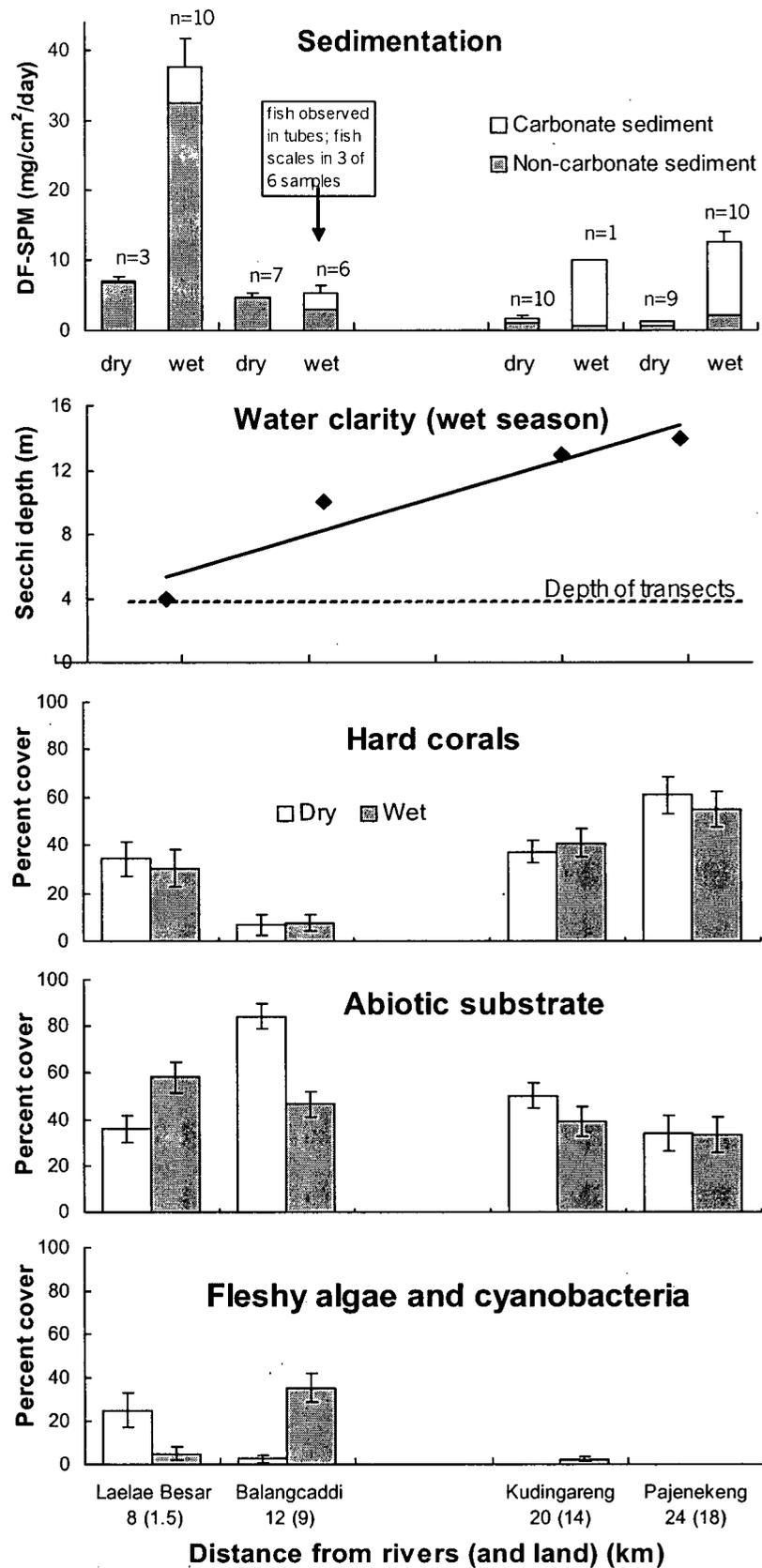
Figure 7-3. Sedimentation, water clarity, and percent cover of dominant categories at the four reef stations during both dry and wet monsoon seasons along a gradient of distance from river mouths (8, 12, 20, 24 km) and distance from land (1.5, 9, 14, 18 km). Error bars are standard error.

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Table 7-1. Relative organic content of the vertical flux of non-carbonate suspended sediment onto reefs in the study area. Proximity of transects to rivers (and land) is indicated.

Monsoon season	South cays (i.e, Telo River)		North cays (i.e., Sankarak River)	
	Laelae Besar 8 (1.5) km	Kudingarenglompo 20 (14) km	Balangcaddi 12 (9) km	Pajenekeng 24 (18) km
Dry	Medium	None	Low	None
Wet	High	None	Medium	None

Note: Organic content is ranked based on the observed degree of chemical reaction to 3% hydrogen peroxide solution.

Significant positive relationships were detected between Secchi depth and distance from both land and chosen rivers (Table 7-2; Figure 7-3). Negative relationships between k and distance from watersheds were slightly weaker. Distance from watershed is thus appears to be a good proxy for water clarity during the wet monsoon season.

Table 7-2. Relationship (simple linear regressions) between water clarity measures and distance (km) from land and chosen rivers (n = 4).

Variables	Intercept a	Slope $b \pm s.e.$	$_{adj.}R^2$	p
Secchi disk extension depth (m)				
Distance from land	3.58	0.63 ± 0.08	0.95	0.015
Distance from chosen rivers	0.91	0.59 ± 0.13	0.86	0.048
Light extinction coefficient [a]				
Distance from land	0.41	-0.02 ± 0.01	0.78	0.074
Distance from chosen rivers	0.48	-0.02 ± 0.01	0.59	0.147

a. The light extinction coefficient (k) is 1.7/Secchi depth

Community structure

Distance from watersheds had a consistently significant effect on community structure (Table 7-3; Table 7-4; Table 7-6). For example, scleractinian corals covered significantly higher proportions of the offshore stations than the nearshore stations, whereas this category did not vary significantly between seasons or watershed blocks at α = 0.05 (Table 7-3). In the northern block, percent cover of scleractinian corals was 9 times higher at the Pajenekeng station (24 km from the Sangkarak River) than at the Balangcaddi station (12 km from that river) (18 vs. 9 km from land), and the separate repeated measures ANOVA indicated this difference to be highly significant (Table 7-4).

Abiotic substrate cover was converse to that of Scleractinia, being significantly higher at nearshore stations than at offshore stations (Table 7-3). No effect of watershed block and monsoon season was detected by the integrated analysis, though the effect of season would be significant at α = 0.10. The separate repeated measures ANOVA of abiotic substrate cover at the northern station indicated significantly lowered cover of abiotic substrate during wet monsoon season sampling (Table 7-4). The seasonal difference in abiotic substrate at this station is almost completely explained by the 14 fold wet season increase in percent cover of fleshy algae (e.g., *Ulva* sp., *Enteromorpha* sp.) (Figure 7-3). Fleshy

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algae covered 36% of this location during the wet monsoon and only 2.5% during the dry monsoon (41% vs. 2.9% of the abiotic substrate; 49% vs. 3.4% of the hard abiotic substrate).

Table 7-3. Summary of integrated GLM repeated measures ANOVAs comparing nearshore stations to offshore stations and comparing dry season sampling dates to wet season sampling dates (incorporating both North and South watershed blocks; effect df = 1 and error df = 22 in all cases).

Source of variation	Mean square	F	p
Hard coral cover			
Distance	3.445	49.688	< 0.001**
Season	0.003	0.038	0.846
Distance * Season	0.001	0.938	0.930
Watershed block	0.262	3.778	0.058
Abiotic substrate cover			
Distance	1.057	13.827	0.001**
Season	0.242	3.511	0.068
Distance * Season	0.012	0.178	0.675
Watershed block	0.105	1.369	0.248
No. of hard coral species			
Distance	12.488	64.106	< 0.001**
Season	0.074	0.300	0.587
Distance * Season	0.063	0.256	0.615
Watershed block	9.695	49.770	< 0.001**
Number of sessile species †			
Distance	6.066	20.770	< 0.001**
Season	1.068	3.388	0.072
Distance * Season	0.133	0.421	0.520
Watershed block	4.275	14.636	< 0.001**

** Highly statistically significant difference;
† Levene's test indicated heteroscedasticity in dry season data.

In contrast to the northern watershed, percent cover of scleractinian corals and abiotic substrate did not differ significantly between the two southern block stations—Laelae Besar and Kudingarenglompo (Table 7-4; Figure 7-3). Fleshy green algae did not colonize the southern block, but pink cyanobacteria did cover 25% of the nearshore station during the dry monsoon sampling, almost fully explaining the 38% less space that abiotic substrate covered there at that time compared with the wet monsoon samples (Figure 7-3). This pink cyanobacteria mat covered 5 times less area during the wet monsoon season. Comparing dry vs. wet seasons, this cyanobacteria mat covered 39% vs. 8% of the abiotic substrate and 92% vs. 19% of the hard abiotic substrate.

Colonization of abiotic substrate at the north and south nearshore reef locations occurred during opposite monsoon seasons and involved different ephemeral flora (Figure 7-3). Green algae (e.g., *Ulva* sp., *Enteromorpha* sp.) colonized Balangcaddi (North) during the wet season. Pink cyanobacteria colonized Laelae Besar (South) during the dry season. Scleractinia cover was low at the nearshore north station, but it was surprisingly high at the nearshore south station, which had the lowest transparency and highest DF-SPM.

Table 7-4. Summary of separate GLM repeated measures ANOVAs comparing nearshore stations to offshore stations and comparing dry season sampling dates to wet season sampling dates (at each block separately; effect df = 1 and error df = 22 in all cases).

Source of variation	Northern block			Southern block		
	Mean square	F	p	Mean square	F	p
Hard coral cover						
Distance	5.584	78.204	< 0.001**	0.069	1.021	0.323
Season	0.003	0.047	0.830	0.000	0.004	0.952
Distance * Season	0.027	0.424	0.522	0.018	0.261	0.614
Abiotic substrate cover						
Distance	1.943	21.78	< 0.001**	0.0036	0.057	0.813
Season	0.828	9.83	0.005*	0.046	0.848	0.367
Distance * Season	0.650	7.712	0.011*	0.421	7.827	0.010*
Fleshy algae cover						
Distance	1.348	52.905	< 0.001**[††]	0.647	14.655	0.001**[†]
Season	0.878	30.477	< 0.001**[††]	0.135	2.345	0.140[†]
Distance * Season	0.878	30.477	< 0.001**[††]	0.493	8.563	0.008*[†]
No. of hard coral species						
Distance	5.371	27.307	< 0.001**[††]	7.187	37.231	< 0.001**
Season	0.005	0.017	0.896[††]	0.096	0.541	0.470
Distance * Season	0.217	0.689	0.416[††]	0.012	0.069	0.796
Number of sessile species						
Distance	167.939	603.320	< 0.001**[†]	8.990	29.403	< 0.001**
Season	2.962	7.825	0.011*[†]	0.067	0.267	0.610
Distance * Season	1.213	3.204	0.087[†]	0.343	1.363	0.256

** Highly statistically significant difference;
* Statistically significant difference;
† Cases in which Levene's test indicated heteroscedasticity in dry season data only;
†† Cases in which Levene's test indicated heteroscedasticity in wet and dry season data.

Because watershed block is used as a container for replicate environmental units (treatments) rather than as a factor (in the analyses presented in Table 7-3), a lack of significant interaction of block and distance is assumed. Stated another way, the design does not provide enough degrees of freedom to quantitatively evaluate interactions with the random effect—block (e.g., Potvin 2001). The possibility of such an interaction is, however, indicated by the comparative view of the watershed blocks afforded by the separate repeated measures ANOVAs (Table 7-4). These separate repeated measures ANOVAs indicate ecological differences between northern block and southern block sites. Another view of the role of interactive effects between and among these (potential) factors in shaping this dynamic community is afforded by the results of the log-linear analyses in which block was considered to be a fixed factor as was distance and the repeated measure 'season' (Table 7-5).

Table 7-5. Summary of log-linear analyses showing the simplest models that explain the distribution of tested biotic and abiotic categories.

Best model	Pearson χ^2	p
Hard coral cover		
Distance*Watershed block	4.22728	0.376
Abiotic substrate cover		
Distance*Watershed block*Season	0.00000	1.000
Fleshy algae cover		
Distance*Season		
Distance*Watershed block	0.00001	0.998
Season*Watershed block		
Number of hard coral species		
Distance		
Watershed block	1.46599	0.917
Number of sessile species		
Distance*Watershed block*Season	0.00000	1.000

Note: The p-value should be > 0.05 if there is a good fit between the data and the best model solution. Probabilities of 1.000 mean that the full 'saturated' model was needed to explain the data.

There were significantly more scleractinian species at offshore stations than nearshore stations, and there were significantly more at southern block stations than at northern block stations (Table 7-3). The integrated analysis indicated similar results for number of sessile species (Table 7-3), and the effects of season were near significant, but heteroscedasticity was indicated for dry season data (Levene's test; p = 0.028). In the southern block, there were significantly more hard coral species and total attached species at the offshore station than at the nearshore station (Table 7-4). A significant effect of season on number of sessile species was detected in the separate northern block analysis (Table 7-4), but dry season data were indicated to be heteroscedastic there too (Levene's test; p = 0.016).

An 'intermediate disturbance' pattern emerged in which more species of sessile organisms occurred at the station located an intermediate distance from land and river mouths—Kudingarenglompo (Figure 7-4). There, mean number of species was highest (39), mean penetration resistance was highest (19.5 hits), and mean dominance (by *Acropora* spp.) was low (0.31). At Pajenekeng, the furthest station from shore, mean number of species was relatively low (19), mean penetration resistance was relatively low (11.1 hits), and mean dominance (by *Porites compressa*) was highest (0.78). At both nearshore stations, number of species and dominance were low (<19 and <0.31 respectively), but both increased when fleshy green algae and pink cyanobacteria invaded (during opposite seasons) (Figure 7-3, Figure 7-4, Figure 7-5).
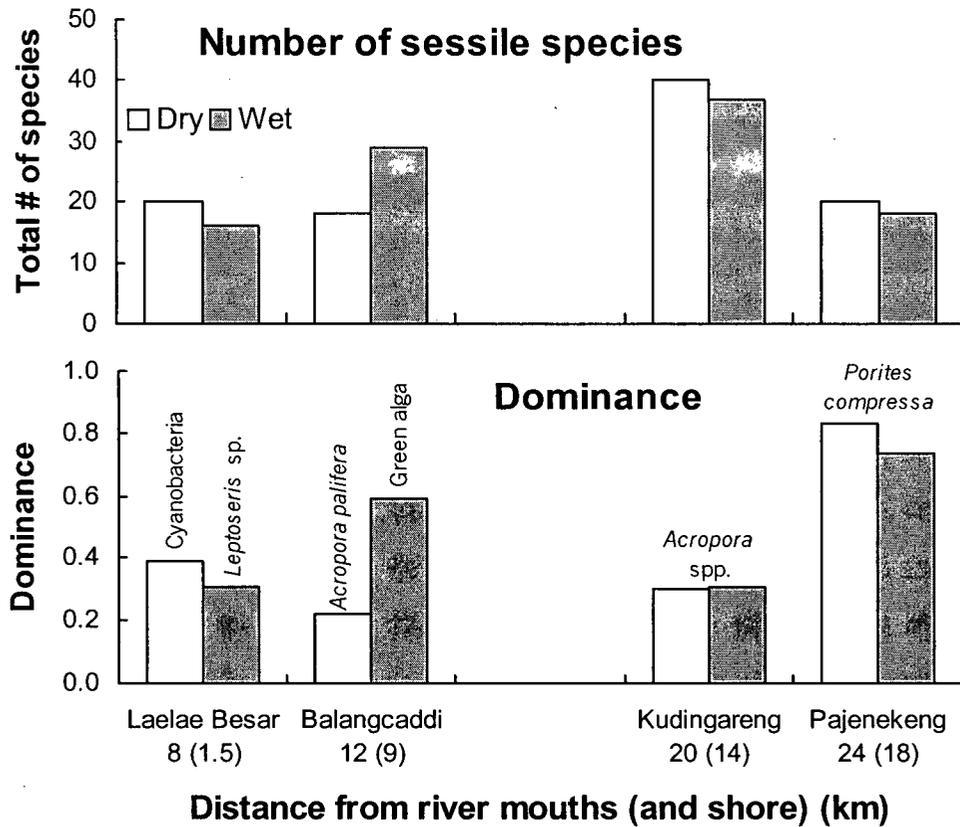
Figure 7-4. Number of species and dominance (dominant taxa cover / total organism cover) at the four stations during both wet and dry monsoon seasons along a pooled gradient of distance from rivers and land. Dominant species are indicated.

Species-area curves show differences in cumulative total number of species (of sessile organisms) at the four stations and two seasonal sampling dates (Figure 7-5). The number of sessile species at the northern nearshore reef—Balangcaddi—increased during the wet monsoon as ephemeral organisms colonized open space at that near-river station. A seasonally opposite, albeit smaller magnitide, increase occurred at the southern nearshore reef—Laelae Besar—during the opposite season when ephemeral organisms colonized there.
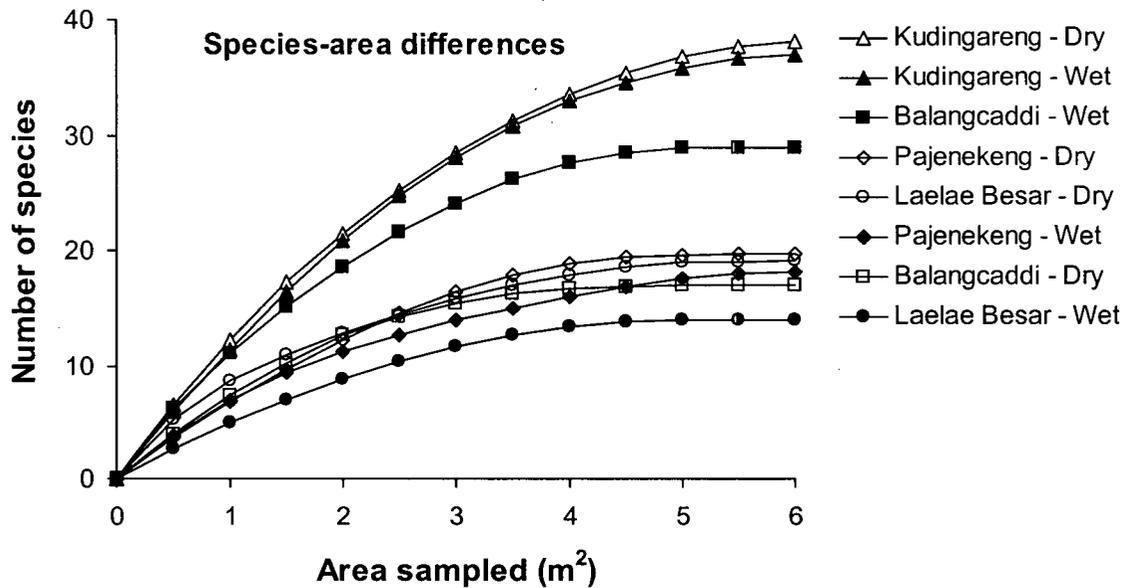
Figure 7-5. Species-area curves of sessile benthic organisms showing opposite seasonal shifts at Balangcaddi (filled and hollow squares) and Laelae Besar (filled and hollow circles). Each additional point is the mean of the accumulating sum of new species from 1000 Monte Carlo re-sampling runs of the twelve 0.5 m^2 photo quadrat samples at each station.

Percent cover of sponges was higher at the (nearshore) Balangcaddi station (means = 3.5% wet; 3.8% dry) than at the (offshore) Pajenekeng station (0.5% wet; 2.7% dry) in the northern watershed block. This pattern was reversed in the southern block with higher estimates at the (offshore) Kudingarenglompo station (7.3% wet; 5.3% dry) than at the (nearshore) Laelae Besar station (1.0% wet; 1.0% dry). The tunicate *Polycarpa aurata* was found only at the (nearshore northern) Balangcaddi station where it covered four times more area during the wet monsoon sampling (3% cover) than during dry monsoon sampling. Soft coral (Alcyonacea) were observed only in the southern block and only during the wet season. Nearshore and offshore cover did not differ (means = 2.5 and 2.7, respectively).
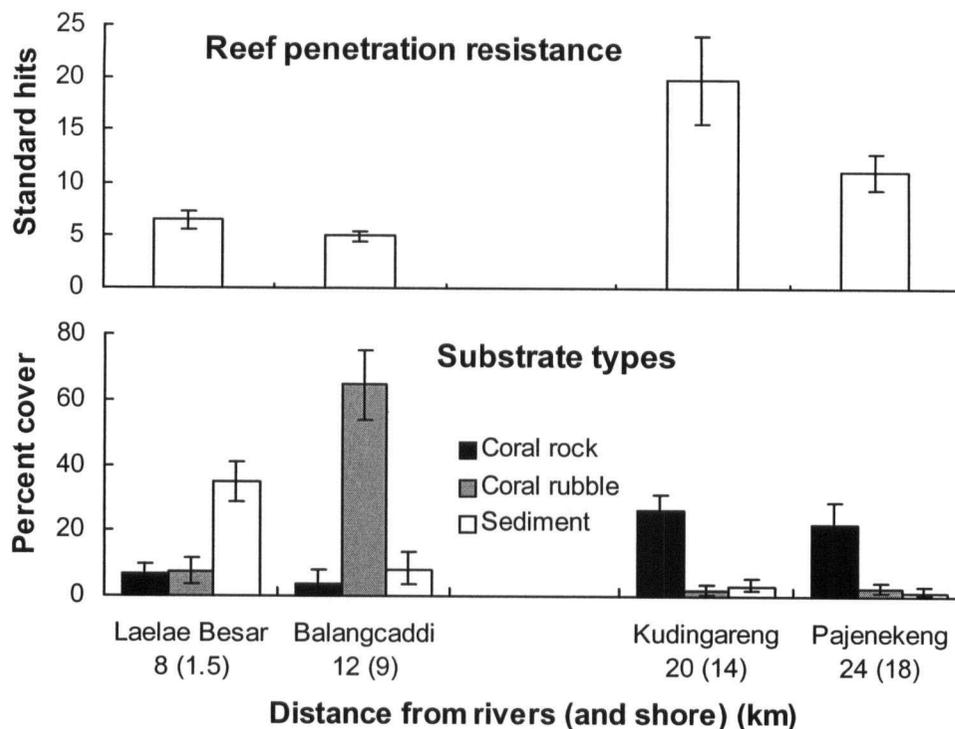
Figure 7-6. Reef substrate penetrability and types of abiotic substrate at the four reefs presented along a gradient of proximity to river mouths (and land). Error bars are standard error. Seasons of low presence of ephemeral algae were selected for display.

Fish were eight times more abundant at the offshore Kudingarenglompo station than at the nearshore Laelae Besar station during the dry season (170 vs. 21 individual fish estimated from video samples). No fish smaller than approximately 10 cm total length was observed at Laelae Besar, but many small fish were observed at Kudingarenglompo. The abundance pattern was opposite at the northern comparison where fish were 3.5 times more abundant at Balangcaddi (nearshore) than at Pajenekeng (offshore) (398 vs. 112 individual fish estimated). Overall, fishes were most abundant at the station with the least coral cover and the most fleshy algae (Balangcaddi) but they were smallest at this site, and they were found aggregated around the three-dimensional architecture of the occasional clumps of *Acropora palifera*.

Reef structure

Considerably more 'standard hits' were required to drive a steel rod 0.5 meters into offshore reefs than into nearshore reefs (Figure 7-6). The station with the highest number of species— Kudingarenglompo—had the highest penetration resistance (Figure 7-4; Figure 7-6).

Stations closer to rivers had higher ratios of unconsolidated abiotic substrate (coral rubble and sediment) indicating reef erosion and degradation, while stations away from rivers were more consolidated (more coral rock) (Figure 7-6). The station presumably exposed to the highest 'agricultural' sedimentation—Balangcaddi—had the highest proportion of coral rubble. Proximity to watersheds had a

significant overall effect on rock and sediment while watershed block did not (Table 7-6). Coral rubble was also considerably more abundant at nearshore reefs (Figure 7-6), though statistical test results for rubble were invalidated by a severe violation of the homoscedasticity assumption (Levene's test; p = 0.004). The results of the log-linear analyses of the abiotic substrate types was similar to the MANOVA results (Table 7-7).

Table 7-6. Summary of GLM integrated MANOVA exploring the effects of distance from rivers on the three categories of abiotic substrate (incorporating both North and South watershed blocks; hypothesis df = 1; error df = 44).

Source of variation	Mean square	F	p
Coral rock			
Distance	1.488	25.116	< 0.001**
Watershed block	0.036	0.614	0.438
Coral rubble †			
Distance	1.645	21.307	< 0.001**
Watershed block	1.512	19.591	< 0.001**
Sediment			
Distance	0.627	10.069	0.003*
Watershed block	0.099	1.591	0.214

Notes: This MANOVA's violation of the assumption of equality of covariance matrices (Box's test; p = 0.037) was not considered unacceptably severe.
** Highly statistically significant difference;
* Statistically significant difference.
† Levene's test indicated heteroscedasticity in the transformed rubble data.

DISCUSSION

McClanahan and Obura (1997) predicted that increased sedimentation would lead to six types of changes on Kenyan coral reefs: (1) increased algal abundance, (2) increased ascidians, sponges, and soft corals, (3) decreased hard coral cover, (4) decreased coral species and genus richness, (5) decreased diversity and increased dominance of corals, and (6) a change in coral colony size. These authors found evidence for prediction #2 only. Although limited in design and scope, the present study found support for predictions 1-4: (1) algae (or cyanobacteria) were more abundant nearshore (and fluctuated with monsoon seasons there); (2) ascidians (*Polycarpa aurata*) were found only at the nearshore Balangcaddi station (and they increased during the wet monsoon when DF-SPM was highest); sponges were more abundant at the nearshore station in the north (but the pattern was reversed in the south); no proximity pattern was detected with the sparsely distributed soft corals; (3-4) hard coral cover and both scleractinian and total sessile number of species were significantly lower at the nearshore stations in general. Ratios of number of species and dominance (5) conformed more to 'intermediate disturbance' patterns (discussed later), and (6) colony size was not measured.

Table 7-7. Summary of log-linear analyses showing the simplest models that explain the distribution of tested substrate-type categories.

Best model	Pearson chi square	p†
Coral rock		
Distance	1.26281	0.532
Coral rubble		
Distance*Watershed block	0.00000	1.000
Sediment		
Distance		
Watershed block	2.92617	0.087

Note: The factor 'Season' was not included in the rock, rubble, and sediment data (see Methods). Percent cover values are non-independent, as a high value of one category would reduce the expectation for the others, thereby reducing α for each test.

The unexpected differences in community patterns between northern and southern blocks was informative in terms of how these coral reef communities are shaped and the potential mechanisms of community adaptation to stressors. These contrasting patterns can be characterized in four ways: (1) ephemeral 'algae' colonized the northern and southern nearshore reef locations during opposite seasons; (2) coral cover was higher than expected at the nearshore southern site; (3) the relationship of coral cover to number of sessile species was opposite in the two blocks (coral cover differed with proximity in the northern block while number of sessile species did not; coral cover differed little in the southern block while number of sessile species did); and (4) the relationship of number of sessile species to dominance was similarly opposite (Figure 7-3; Figure 7-4). Several potential explanations for these differences in community patterns can be suggested: (1) the number of sampling locations is small and patterns are the result of chance alone in the context of high natural variability and scale choice; (2) downward flux of suspended particulate matter (DF-SPM) differs between the two blocks; (3) the nature of the runoff differs between the two blocks; and (4) some species can shift from autotrophy to heterotrophy in areas of lowered light and high organic enrichment. None of these explanations are mutually exclusive.

The high percent cover of fleshy algae and cyanobacteria at the nearshore stations mimics a worldwide pattern of shifts from corals to fleshy algae in areas modified by nutrients, turbidity, and sediment (see Bell 1991, 1992; Hughes 1994; McClanahan and Muthiga 1998; McCook 1999). Moreover, the Spermonde Archipelago, at least parts of it, is likely no exception to the adverse effects of sewage and other land-based pollution on coral reefs (Richmond 1993; Dubinsky and Stambler 1996; Edinger et al. 1998, 2000). In the present study, nearshore stations on the Spermonde Archipelago harboured 29% fewer species than offshore stations (at 4 m depth). These results are consistent with findings of Edinger et al.

(1998) that diversity on Indonesian reefs subject to land-based pollution was reduced by 30-50% at 3 m depth.

Jakarta Bay and other Indonesian settings have undergone structural degradation of coral communities (Tomascik et al. 1993; Tomascik et al. 1997) as well as increases in filter feeder abundance, which is considered an additional symptom of reef decline (Hallock et al. 1993; but see Hughes 1994). The finding of the filter-feeding tunicate *P. aurata* occurring only at the Balangcaddi reef (nearshore, northern block) fits this pattern, as does the finding of sponges being more abundant there, but the increase of the ascidian during the wet season is somewhat suspect since it is not known to be seasonal (T. Tomascik, pers. comm., June 1999). Aside from these two examples, the patterns of filter-feeding indicator species are ambiguous.

The seasonally-opposite colonization of macroalgae and cyanobacteria into the northern and southern nearshore reef stations might reflect site-specific differences in combinations of factors related to differences in upstream land uses or seasonally differing exposure to oceanographically induced patterns. The southern unit is exposed to concentrated urban enrichment (e.g., sewage) and the northern unit is exposed more exclusively to agricultural runoff. These differences could directly and indirectly cause the observed wet-dry opposition in community patterns through via mechanisms like those outlined below.

Open space exists at each of the nearshore reef locations, but irradiance at Laelae Besar reef (the southern nearshore reef) is perhaps too low for colonization of fleshy green algae during the wet season when it colonized Balangcaddi in the North, whereas a higher tolerance of the pink cyanobacteria (and red algae) to low light might explain the cyanobacteria bloom at Laelae Besar during the less-turbid dry season (see Dring 1981; Fiksdahl et al 1983; Camacho et al. 1996). This bloom could also be promoted by high nutrient loads at this station as the cyanobacteria shift to heterotrophic modes. Nutrients might be too limited during the dry season at Balangcaddi (in the North) to support the ephemeral green algae that invade there during the wet season. It is also possible that the grazing rate of herbivorous fishes surpasses ephemeral algae production during the season of lower production at each site. Regardless of the exact mechanism, these patterns are consistent with Thacker and Paul's (2001) finding of opposite patterns in macroalgae and cyanobacteria.

Particulate and dissolved organic matter can supply much of the nutritional requirements of corals (Sorokin 1973; Risk et al. 1994), and the tolerance of some coral species (and cyanobacteria) to seasonally diminished light conditions relates to their ability to shift from autotrophic to heterotrophic modes (e.g., Anthony 2000; Cornell 2000). Some coral species, in fact, seem to thrive on intermediate levels of higher suspended matter (e.g., *Monastrea annularis;* Tomascik and Sander 1985, 1987). Organic enrichment can thus compensate for low light in some species (e.g., *Leptoseris* sp.), though such compensatory effects differ greatly among species.

Such shifts in trophic mode and the variable heterotrophic tendencies in corals might explain why corals persist at Laelae Besar so close to Ujung Pandang's open sewers (1.5 km). Water clarity (i.e., light) is very low at this location (Figure 7-3; Table 7-1) and these colonial anthozoans likely acclimate by absorbing the highly concentrated organic material there (Tomascik and Sander 1985; Buddemeier and Smith 1999; Done 1999). Such acclimation might also explain the observation that coral reefs flourish in several other highly turbid, though enriched, settings throughout Indonesia (Tomascik 1997, p. 477). Some corals were present at Laelae Besar where downward flux of sediment was over three times greater than levels considered to be generally 'high' or 'chronic' (Rogers 1990). Still, the corals at this station might be persisting near tolerance limits (see Johannes 1975; Tomascik 1997).

The hard corals *Leptoseris* sp., *Porites lichen*, *Lobophyllia* sp., and *Goniastra favulus* are the most dominant taxa at the nearshore southern site, in addition to the pink cyanobacteria observed there (Table 7-8). A number of studies indicate that species in these coral genera, and species within Division Cyanophyta, might be tolerant to low light and enriched conditions (Table 7-9). For example, McCook (2001) found positive growth rates of *Porites lobata* on the most impacted reefs of a gradient of terrestrial influence, but Edinger et al. (2000) pointed out that positive growth rates of massive corals do not reliably indicate overall reef accretion rates.

Table 7-8. Percent cover of each of the five taxa with the highest areal dominance at each of the four sites during the wet monsoon season. Proximity of transects to rivers (and land) is indicated.

Southern block (i.e, Telo River)				Northern block (i.e., Sankarak River)			
Laelae Besar 8 (1.5) km		Kudingarenglompo 20 (14) km		Balangcaddi 12 (9) km		Pajenekeng 24 (18) km	
Species	%cov	Species	%cov	Species	%cov	Species	%cov
Leptoseris sp.	11.5	*Acropora nobilis*	11.8	fleshy green algae	31.7	*Porites compressa*	48.8
Porites lichen	7.2	dark blue sponge	5.7	*Acropora palifera*	3.5	crustose corraline	8.8
pink cyanobacteria	5.2	*Porites lobata*	4.7	crustose corraline	3.2	*Fungia* spp.	1.7
Lobophyllia sp.	3.0	crustose corraline	4.7	*Polycarpa aurata*	3.0	*Acropora vaughani*	1.3
Goniastra favulus	2.3	*Acropora divaricata*	2.8	*Codium fragile*	1.5	*Echinopora lammelosa*	1.2

Notes: During the dry monsoon, the pink cyanobacteria at Laelae Besar (1.5 km from Ujung Pandang city) *increased* five-fold (to 25% cover) and the green fleshy algae at Balangcaddi *decreased* more than an order of magnitude (to 2.5% cover).

The data provide tenuous evidence for the maintenance of diversity (and reef structural integrity) by intermediate levels of disturbance (*sensu* Connell 1978; Tanner et al. 1994) at the Kudingarenglompo station (when north and south blocks were pooled into a single proximity gradient). Kudingarenglompo rests at an intermediate position along the riverine disturbance gradient, enabling disturbance-adapted taxa such as *Acropora* to persist alongside species that would come to dominate in the absence of disturbance (Table 7-8) thus enabling more species to coexist there (Figure 7-4; Figure 7-5). The low number of species and high dominance at Pajenekeng indicates the tendency for one species to exert competitive dominance in the absence of disturbance. A conspicuous aspect of the overall pattern was the

simultaneous increases of both number of species and dominance at the culturally disturbed nearshore sites. To my knowledge, this is a novel finding. It suggests that a positive relationship between number of species and dominance might be a general indicator of degraded condition.

An intermediate disturbance mechanism might explain the lack of difference in number of sessile species between Balangcaddi and Pajenekeng in the north (Figure 7-4). Pajenekeng's position in the middle of the archipelago would place it in the zone of least overall disturbance since shoreward reefs are more impacted by riverine impacts and seaward reefs (up to ~40 km from shore) are more exposed to wave disturbance. According to the intermediate disturbance model, zones with the least and the most disturbance should have the lowest numbers of species.

However, the deeper water surrounding Kudingarenglompo is an alternate explanation for the observed high number of species at that station. Moll (1983) suggested that rivers impact Spermonde Archepelago reefs out to the ~20 m isobath. This station would thus be less exposed to riverine sedimentation than the Pajenekeng station if the extent of shelf area impacted by rivers had extended beyond the 20 m isobath during the last 20 years, but not beyond the 37 m isobath (see Figure 7-1). Indeed, de Klerk (1983) and Moll (1983) characterize Kudingarenglompo as belonging to a zone or 'strip' that is less coastally influenced than Laelae Besar, Balangcaddi, and Pajenekeng.

The finding of maximum penetration resistance at the reef at the Kudingarenglompo station suggests that intermediate levels of riverine disturbance also maximize reef structural integrity. It also suggests that the later seral stages of less-disturbed reefs are associated with structural senescence. An alternate explanation is that the highest penetration resistance might be found at the Kudingarenglompo station because it is exposed to the least riverine impacts due to protection by deeper water. Another alternative explanation is that variations in wave exposure can explain the variations substrate penetrability. I have argued that wave exposure is reasonably comparable at the NE facing sides of the four cays, but there is undoubtedly some level of wave exposure variability among sites.

The co-occurrence of maximum number of species and minimum substrate penetrability implies that the biological condition of living coral reefs is a potentially important indicator of the structural integrity of coral barriers and fringes, and visa versa. In the future, the geomorphological outlook of protective tropical coastlines as well as the biodiversity of coral reefs and their ecological values and services might be forecasted using more standardized substrate penetrability methods.

Patterns of sedimentation also indicate reef structural integrity. The shallow reef flats of these coral cays produce carbonate sediment that is generally deposited on the eastern (lee) sides of these islands. Reef inhabitants on the northeast-facing slopes are thus adapted to this historical sedimentation. Low *carbonate* sedimentation at depauperate reef platforms near coastlines is thus evidence of reef 'turn off' (Buddemeyer and Hopley 1988; Kleypas 1996). Such turnoff could result from modern expansion of nutrient and sediment plumes from coasts, but additional information about historical and present patterns of blast fishing and other destructive fishing practices (e.g., Pet-Soede and Erdmann 1999), coral mining,

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and other likely agents of degradation would aid in the interpretation of observed patterns. The human communities of Spermonde's coral cays regulate anthropogenic activities on local reefs in the context of traditional stewardship practices, but this regulation or protection varies considerably and results in a haphazard mosaic of partially protected and entirely unprotected areas.

Physical and chemical factors such as salinity, temperature, nutrients, and DOM were not measured during this study, though salinity and temperature are known to shape coral reef systems strongly (Jokiel and Coles 1990; Jokiel et al. 1993). Although sedimentation and turbidity are indicated here as potentially major agents of environmental change in the Spermonde Archipelago, tracking a broader spectrum of variables that includes *at least* nutrients and chlorophyll *a* concentrations (e.g., Tomascik and Sander 1987; van Woesik et al. 1999) would increase our understanding of Spermonde Archipelago community regulation. Regimes of sedimentation, water quality, irradiance, and biotic interactions are probably all important in shaping the observed patterns of reef community structure. Comprehensive studies should also include manipulative evaluations of the roles of nutrients and fishes (e.g., Smith et al. 2001, McClanahan et al. 2002) and other key structuring factors such as fishing practices.

Table 7-9. Evidence of tolerance to low light, pollution, and sedimentation in the most areal dominant coral genera (and cyanobacteria) at the nearshore southern site.

Species	Attribute	Study location	Source
Leptoseris papyracea	Found only in low light and abundant POM a	East Pacific and protected Costa Rica bays	Leyte-Morales et al. 2001; Jimenez et al. 2001
Porites spp.	Intermediate sedimentation tolerance	Maldini and Watamu reefs, Kenya	McClanihan and Obura 1997
Porites spp. (encrusting)	On reefs most impacted by rivers b	Whitsunday Islands, Queensland, Australia	van Woesik et al. 1999
P. porites	Ability to reject oil-sand combinations	SW coast of Curaçao, Netherlands Antilles	Bak and Elgershuizen 1976
P. astreoides; *P. porites*	Most abundant on most polluted reefs	W coast of Barbados, West Indies	Tomascik and Sander 1987
P. lobata; *P. lutea*	Ability to reject sediment	Lizard Island, Great Barrier Reef, Australia	Stafford-Smith 1993
P. sillimaniana	Resistance to adverse sedimentation effects c	Bacuit Bay, Palawan Island, Philippines	Hodgson 1989
P. lobata	Positive growth rates on impacted reefs	Nearshore islands, central Great Barrier Reef	McCook 2001
Cyanobacteria	Chromatic adaptation to low light	Irish coastal marine; Maine and Spain lakes	Dring 1981; Fiksdahl et al 1983; Camacho et al. 1996
Lobophyllia corymbosa	Relies primarily on heterotrophic feeding	Red Sea coast, Saudi Arabia	Al-Lihaibi et al. 1998
Lobophyllia pachysepta	Found at intermediate distances from river d	Whitsunday Islands, Queensland, Australia	van Woesik et al. 1999
Goniastra spp.	Three occurred at the most impacted reefs e	Whitsunday Islands, Queensland, Australia	van Woesik et al. 1999
G. retiformis	Resistant to sediment damage	Bacuit Bay, Palawan Island, Philippines	Hodgson 1989

a. POM is particulate organic matter;
b. Two other *Porites* species in this study had different distributions;
c. But *P. lutea* and *L. hemprichii* were not very resistant to sediment damage;
d. Two other *Lobophyllia* species occurred at the less impacted stations;
e. Three other *Goniastra* species had different distributions

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Global-scale changes such as rising temperatures and bleaching (Glynn 1983; Brown 1997; Berkelmans and Oliver 1999; Hughes et al. 2003), decreasing aragonite saturation (Done 1999; Kleypas et al. 1999), and turbidity caused by increased waves in back reefs (Graus and Macintyre 1998) combine with local and regional mechanisms such as coastal sedimentation, pollution, and fishing. All these factors vary with space, time, taxa, and the ontogenic stages of reef organisms, and the overall effects manifest as interactive gradients of community shifts (Rice and Hunter 1992). Corals must accrete limestone at 3-15 vertical mm per year to compensate for accelerating sea level rises (Barnes and Hughes 1982; Grigg and Epp 1989), but such compensatory growth is inhibited by this interacting suite of factors that degrade reefs and impede recovery (Smith and Buddemeier 1992; Wilkinson 1996; Pittock 1999). Anthropogenic runoff and pollution thus degrade reefs both directly and indirectly.

Design limitations

The economical nature of this exploratory study limited the power of its sampling design. The overall design featured twofold replication of environmental units through the repetition of watershed blocks. For the purposes of this design, these blocks were considered independent and each contained two distance strata (which were also sufficiently distant and separated from each other to be considered independent) and two seasonal strata. Twofold treatment replication can be sufficient if environmental units are very similar (Hurlbert 1984), but due to the special nature of such blocked designs (Potvin 2001), block x treatment interaction cannot be assessed due to the lack of replication of the fixed factor distance within blocks. Evaluation of the ecological similarity of the two watershed blocks was thus incorporated into the GLM repeated measures ANOVAs, which simultaneously evaluated proximity to watersheds, monsoon season, and watershed block. In this case, the difference indicated for the watershed block 'factor' was used as an indicator of block similarity (sensu Sokal and Rohlf 1981: p 344) to evaluate the legitimacy of the twofold replication, rather than as a treatment per se. These evaluations indicated environmental similarity of the two watershed blocks *for some of the tested categories*, while differences between these units were revealed for other tested categories (Table 7-3, Table 7-6). These two watershed blocks also differed qualitatively in terms of the seasonality and composition of community changes (e.g., Figure 7-3), and this indeed became a provocative aspect of the overall results.

Observations that the two repeated watershed blocks (and thus the replicated environmental units within them) differ quantitatively is expected since the reason for repeating the watershed block is to account for the natural variability between blocks in order to assess the variability associated with the chosen comparative strata (i.e., nearshore vs. offshore or wet vs. dry). However, relatively high variability among blocks (in some cases) might indicate additional useful ecological strata. For example, the proportions of urban and agricultural influences appear to vary among watersheds, and these differences might influence runoff character and marine community effects strongly. Notwithstanding such

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indications of potentially revealing strata, more repetition of watershed blocks (i.e., more replication of environmental units) should lead to enhanced characterization of variability and thus more revealing statistics.

For two tested groups (i.e., number of sessile species, number of scleractinian species) significant differences were detected between watershed block. This indicated that, for these two groups, the two watersheds do not exhibit adequate block similarity for the corresponding treatments (strata) within them to be used as 'good' replicates (Table 7-3). In these cases, replication was sacrificed and separate inferential statistical tests were applied to evaluate differences among sampling locations within blocks (near vs. far in either the North or South block) (Table 7-4). Inferences from these results are likewise limited to only the 'inference space' within the 15 m^2 sampling locations (50 m transects; n = 12 samples). Differences between multiple transects at a cay or a whole population of blocks, for all we can tell, might rival or surpass any differences between near and far reef stations or differences between seasons. Stated another way, sample replication within transects, in such cases, provides an inappropriate error term to inform us about riverine or proximity effects. Notwithstanding these concerns, the 50 m transects often covered most of the NE facing 'side' of the cays (at 4 m depth) and are thus somewhat representative of that entire ecological unit. The similarity of the watershed blocks could not be evaluated for sponges, algae, fleshy algae, and rod penetration because test assumptions for these groups were too severely violated.

Replication of environmental units was sacrificed again when the four sampling locations were considered to be arranged along a single gradient of distance from shore. Resulting patterns are presented with the explicit caveat that they could be the result of chance alone. They are presented here as an impetus for designing more rigorous evaluations of the dynamics of these reefs.

CONCLUSIONS

Differences in coral reef community structure and substrate penetrability corresponded with distance from land and from river mouths, in particular to general gradients of sedimentation and water clarity. Seasonal patterns were revealed in addition to contrasting patterns between the two watershed blocks, which were chosen as distinct repeated blocks, each containing the full suite of distance and season combinations. Ecological differences between these two watershed blocks might reflect between-basin differences in water quality characteristics. Explicit *a priori* distinction of urban vs. agricultural strata might be fruitful in future research designs for this region given the different patterns between watersheds observed in the present study.

The patterns revealed at the inshore reef near the northern agricultural river match at least three of the four typical symptoms of coral reef decline identified by Hallock et al. (1993), while the inshore reef station near the urban center matches only one of these criteria. This divergence from expectations is informative and requires further attention. Organic material associated with anthropogenic enrichment

(e.g., sewage) might partially compensate for other degrading agents near this urban setting in the sense that some corals can exploit the increased availability of organic material by shifting from autotrophy to heterotrophy. Nevertheless, seasonally present ephemeral flora at both near river sites indicated seasonally (riverine outflow) shifted, albeit characteristically different, states for both nearshore reef locations. Culturally intensified disturbance regimes at the nearshore sites might also be indicated by positive relationships between number of species and dominance.

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This thesis documents shifts in the community structure of four marine biological communities. Here, a 'shift' is a considerable change in the relative biomasses of a community's component parts, and a community is an assemblage of organisms in a given ecosystem. The *Ecopath with Ecosim* approach is applied here for broad scope examinations of the attributes of community structure and function that can influence and mediate shifts to very different community states. All populations and communities change, and these changes occur at a variety of rates. The character of these changes differs among spatial and temporal scales examined. Although the present approach integrates a broad spectrum of rates or change such that the interactions of fast and slow biotic components can be manifested, the approach is normally used to examine potential multi-year or decadal interactions or effects rather than seasonal or faster changes. Virtually any spatial scale can be used, though it is most useful when the boundaries of a defined ecosystem have ecological meaning and, normally, when migratory flows are minimal (unless migratory flows are well known and rigorously addressed).

Living organisms are the fundamental currencies of life for individuals and groups of individuals, which must attempt to experience maximum constancy in the availability of the living organisms that they benefit from, in order to ensure survival and prosperity. Organisms can achieve constancy of resource experience in fluctuating environments through migration and other compensatory (i.e., adaptive) mechanisms of behavior and physiology. Compensatory mechanisms are expressed as feedbacks that serve to stabilize or regulate the population or component that is imposing this compensatory force because they influence the interactions of individuals, groups, or species with surrounding biological communities and physical and chemical aspects of an environment. Such mechanisms can thus increase variability on some scales, while decreasing it on others.

Individuals and populations modify biological communities by exploiting particular components of the community as they make a living. The subsequent changes in exploited populations causes changes in the availability of resources leading to new arrangements of competition for available resources. Thus, competition occurs in the context of predation, or disturbance, or both. The re-organization of flows resulting from this combination of predatory control (or disturbance) and competition manifests as community change in the sense of simplified (or small scale) examples, but it also manifests as systemic compensation that can serve to stabilize a system (e.g., on a broader scale of time or space). Such systemic compensation assumes dynamic and adaptive exploitation strategies by species in the community as well as the presence of competitors and highly partitioned niches. Such adaptive and dynamic mechanisms might well be the key reason that complexity and stability in biological communities are, in truth, positively related (Fowler and Lindstrom 2002, Kondoh 2003).

It is an individual's, or a group's, requirement for *constancy*, and their subsequent modification of the community that thus tends to stabilize a given biological community within 'natural' bounds of

variability in the context of 'natural' disturbance regimes and other physical cycles. Here, natural means frequency, magnitude, and character of predation, disturbances, or cycles that are evolutionarily 'expected' in the sense that species are adapted to them. However, disturbances or stressors with exotic characteristics (Sousa 1984) can dramatically alter the relative biomasses of particular populations. Such reductions, removals, or modifications can, in turn, change the makeup and mixture of biological modification and feedbacks in affected communities. The resulting depletions, or ecological extinctions, of species from a community, especially those that interact strongly (Chapter 4), can lead to fundamental shifts in the structure and feedbacks in a given system. This is the reason that linear or gradual changes in imposed stressors can lead to sudden, or catastrophic, changes (Chapter 1). The resulting new regime can exhibit some inherent stability of its own because interaction strength is context dependent (sensu Power et al. 1996) because the species that profit most from the new regime naturally endeavor to exert new feedbacks that reinforce their own persistence, even if these new dominants might normally be thought of as opportunistic or fugitive species due, for example, to their potential for rapid growth and their ability to colonize open space (e.g., Chapter 3). Furthermore, because all species are at least partly opportunistic, the resources available in the new regime become 'filled up' with the 'new', or remaining, biological assemblage thus, in some cases, preventing former competitive dominants from re-establishing. While these new competitive dominants, or strong interactors, exert compensatory forces, the shift to this new state can also result in depensatory behavior of previously abundant, dominant, or even keystone species when they are at abnormally low population sizes (e.g., Sinclair et al. 1998). This scenario for shifts to alternate community states that exhibit stability depends on the existence of intrinsic mechanisms that can reinforce a new community state related to the manifested self interests of alternate dominants and the context dependencies of their interaction strengths after a community has been initially shifted by exogenous forces such as an oil spill or a fishery. Alternately, the apparent stability of the new 'domain of attraction' (e.g., Scheffer et al. 2001) could simply reflect a lag in recovery controlled by the system's slow variables (long-lived and slow growing organisms) (Carpenter 2000, Carpenter and Turner 2000), which are often the most vulnerable components of a given system to exotic stressors or disturbance.

The aforementioned theoretical concerns have transcended academic curiosity to become central issues in management and policy debates because of new revelations of dramatic structural changes in marine communities and ecosystems. Dramatic depletions of predators (e.g., Pauly et al. 1998a, Myers and Worm 2003), worldwide destruction of biogenic seafloor habitat (e.g., Dayton et al. 1995, Watling and Norse 1998), widespread adverse effects of pollution (e.g., Peterson 2001, Anderson et al. 2002), worldwide shifts and degradation of coral reefs (e.g., Done 1992, Knowlton 2001), and the effects of climate change (e.g., Scavia et al. 2002) are a few examples of the large extent that humans are modifying marine ecosystems. Although rigorous demonstration of alternate stable states of marine communities is still rare, all of these examples are reliable descriptions of large shifts in marine ecosystems. Because the

meaning of such shifts, as well as the potentials for reversal, is still very uncertain, the question of alternate stable states is of great interest.

The goal of the present thesis was to examine community shifts in four marine ecosystems with a focus on potential mechanisms that might have generated, or might maintain, those community shifts. The community trophic modeling approach *Ecopath with Ecosim,* strictly speaking, cannot be used for falsification. Rather, it is an accounting approach to pattern and process searches in biological communities. It was used here primarily to generate hypotheses, which can then be tested with empirical approaches that can be employed in the future. The exception, Chapter 7, is a field-based empirical study, but it too is a search for pattern and process that employs hypothesis testing in a sampling-based, rather than manipulative, context. Nevertheless, the *Ecopath with Ecosim* approach is empirically based— sometimes rigorously so—and it that can allow insightful evaluations of alternate possibilities and explanations.

Although the approach employed here allows only an exploration of the plausibilities of different mechanisms of shifts in marine communities, I pursued these explorations with special reference to a conceptual framework built on criteria for evaluating the existence of alternate stable states (Chapter 1). I did not, however, build a systemic approach for rigorously evaluating the existence of alternate stable states in reference to those criteria. Instead, I used them as a guideline for revaluating the plausibility of the mechanisms focused upon, and to frame how the hypotheses derived from the *Ecosim* simulations fit into broader discussions of ecosystem change and human modifications of ecological systems. I adhered to the philosophy that examination of diverse lines of evidence will maximize insights into the character of community shifts (Connell and Sousa 1983, Carpenter 2000). Such a broad approach will help us distinguish alternate stable states, persistent shifts, non-trivial boundary points, and natural fluctuations. In this light, I will summarize the findings of Chapters 2-7 and then discuss them in the context of criteria for evaluating the existence of alternate stable states.

Chapter 3, with the support of Chapter 2, indicates that the depletion of predators by unsustainable fisheries is an adequate mechanism to explain the documented emergence of *Aiptasia* sp. anemone barrens along the east side of Fernandina Island in the western Galápagos Archipelago, Ecuador. However, this finding does not preclude the very real possibility that these shifts were initiated by the severe El Niño events of the 1990s. The possibility that the two types of mechanisms—physical disturbance and trophic changes related to the removal of predators by fisheries—acted in concert to generate and maintain these anemone barrens is the subject of future research.

Chapter 4 indicated dramatic variability in interaction strengths and 'keystoneness' among species and functional groups in the *Ecopath* model of Prince William Sound, Alaska. Broad community effects differed considerably among affecting species, indicating that the removal of the strongest interactors and keystones, via an oil spill, direct exploitation, or by other means, would likely cause

considerable whole community shifts that would persist for at least as long as these strong interactors (often the most vulnerable and slow growing species) were depleted.

Chapter 5 indicated that a disturbance, such as the *Exxon Valdez* oil spill, that simultaneously impacts both slow and fast components of a biological community severely can potentially shift a community to an alternate domain of attraction (i.e., alternate stable state) because of impacts on both the biological foundations of the system and those components that regulate the community's structure. By comparison, other scenarios such as the 1964 Great Alaskan Earthquake and an *Exxon Valdez* oil spill scenario in which only some of the known impacts were specified, recovered to the pre-disturbance baselines, albeit at different rates depending on whether impacts were generally on fast or slow variables. These simulations call for continued refinement and explorations using updated effects information, which is still emerging from *Exxon Valdez* oil spill studies.

Chapter 6 indicates that intense coastal plankton blooms, and more subtle plankton increases that extend over continental shelves, can potentially cause broad shifts in the structure of whole continental shelf communities due to shading of benthic primary producers, which many organisms rely upon. It is unknown whether such shifts represent alternate stable states, but there is some evidence for reinforcing feedbacks and restructuring in such continental shelves. It might be that such broad shifts would reverse in response to reductions of coastal nutrient pollution, but coastal nutrient pollution is still generally increasing making technical questions about alternate stable states moot, at least for the time being.

Chapter 7 also describes various aspects of community shifts related to nutrient and sediment runoff, in this case in coral reef communities of the Spermonde Archipelago in Southwest Sulawesi, Indonesia. These results reveal considerable seasonal shifts in coral reef communities at which ephemeral algal and other species fluctuate and significant coral community differences with distance from rivers. Difference from rivers is associated with downward flux of riverine sedimentation on reefs and water transparency. The indicated degradation of these coral reefs is a long-term effect due to the nature of reef-building corals, but it is likely reversible in a hypothetical world in which pollution and other conspicuous coral reef community stressors were considerably reduced or stopped. However, as in the case for Chapter 6, such dramatic abatement seems unlikely, again rendering the alternate stable states question moot for the time being.

The plausibility of considerable community shifts was indicated for all three of the marine ecosystem examples to which *Ecopath with Ecosim* modeling approaches were applied. The enhanced *Exxon Valdez* oil spill scenario is the only example for which alternate stable states was indicated by these simulations, but this simulation might technically indicate *extremely* slow recovery when both fast and slow components are impacted, as the *Ecopath with Ecosim* modeling approach is based on an algorithm that should return to a global equilibrium point. Considering this, however, the results might indicate emergent behavior indicating real possibilities for the system.

An examination of overall evidence (multiple lines of evidence) for the existence of alternate stable states (Table 8-1) indicates more evidence for alternate stable states in the anemone barrens example than in the other examples. This is primarily due to the likely reinforcing feedbacks exerted by the anemones related to their likely effective consumption of settling propagules in the space they pre-empt. The rankings shown in Table 8-1 are far from definitive; more than anything, they represent a rough guide for future research in these systems.

Table 8-1. Evaluation of the four marine community examples presented in this dissertation with five criteria for evaluating the existence of alternate stable states

Example	Abrupt interfaces	Repeated shifts	Persistence	Reinforcing feedbacks	Hysteresis
Galápagos anemone barrens	Likely	Unknown	Yes	Likely	Likely
Exxon Valdez oil spill in PWS, Alaska	Likely	n/a	Unknown	Unknown	Unknown
Shading by plankton blooms over WFS	Unlikely	Unknown	Likely	Unknown	Unknown
Coral-to-algae shifts in South Sulawesi	Yes	Yes	Yes	Unknown	Unknown

Notes: The five criteria listed in this table are:

1. Abrupt interfaces or shifts between alternative community states (in time or space);
2. Repeated shifts between or among alternate community states;
3. Persistence of a given state beyond one complete population turnover;
4. Reinforcing feedback mechanisms that are intrinsic to a given community or population;
5. Discontinuity between forward and backwards shifts along an axis of stress (hysteresis).

The sixth criterion, dynamic simulations showing plausibility of shifts, is discussed in the preceding text. Repeated shifts is not an applicable category for the *Exxon Valdez* oil spill since there was only one such spill.

There is little doubt that humans have been keenly interested in, and knowledgeable about, changes in populations and communities for hundreds of thousands of years. These interests are framed on a variety of levels along a hierarchical gradient from individual through families, clans, and communities, though it is individual self interests that arguably drive most human interactions with nature (e.g., Dawkins 1976). Human interests in community change are thus inherently value-laden and subjective.

Like other non-plant species, living organisms are the fundamental currencies of life for individual humans, clans, and tribes. Also like other non-plants, humans must attempt to experience maximum constancy in the availability of the living organisms in order to ensure survival and prosperity. It is this need for biological constancy that explains the pervasiveness of persistent stability mythologies in human cultures, societies, academic communities, and our individual psyches (sensu Campbell 1972). Such mythologies likely reflect realities of nature in addition to reflecting subjective needs and desires. Likewise, contemporary mythologies are built on modern sources of knowledge, such as the scientific method, in addition to historical sources of knowledge. Individual self interests, filtered through contemporary mythologies, are the fundamental drivers of modern human endeavor.

The present exercise of using whole-community trophic modeling to examine broad community shifts in four marine ecosystems focused on the mechanisms that might generate and maintain such shifts. In every case, it produced insights into these mechanisms and a better understanding of how the

communities are structured and function. Each chapter also produced plausible explanations for shifts. These plausible explanations are hypotheses that can be evaluated further. The progress documented here will change human interactions with marine ecosystems by influencing policy and management, but also by refining scientific knowledge and influencing contemporary mythologies.

Finally, it is well worth following Carpenter's (2000, 2001) example by emphasizing that although the existence of alternate stable states in biological communities can be very difficult to demonstrate, and this is particularly true in marine ecosystems, the possibility of their existence has profound implications for policy development and management decision-making because, "It is a more costly error to conclude that alternate states are absent when they are in fact present, than to falsely conclude that they are present." It is therefore also worth paraphrasing his recommendation to reverse the conventional burden-of-proof as it relates to alternate stable states (see also Dayton et al. 1995): parties whose activities will increase the stresses on a biological community should be required to provide good evidence that those activities will not shift the system to an undesired alternate stable state, or will not substantially increase the system's vulnerability to undesirable alternate stable state shifts (in the context of existing disturbances and stochasticity). Stated another way, the onus is most logically placed on the users of living resources to show that their activities do not unreasonably erode the resiliency of whole biological communities. Moreover, future strategies for policy, management, and stewardship of biological communities should be explicitly tailored to the possibilities of non-linear dynamics, catastrophic change, cycles, and surprises (e.g., Gunderson and Holling 2002), as appropriate for each situation. The chapters presented here are examples of approaches to characterizing whole community responses to such agents and characteristics of change, and they represent preliminary steps toward developing sustainable strategies for the interaction of modern society with the challenged ecologies and economies of a naturally nonlinear and stochastic world.

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Appendix A. Diet composition matrix for the Ecopath model of the Floreana (Galápagos) rocky reef (in percent of total biomass wet weight) used in the analyses presented in Chapter2 and 3. Prey are arranged in rows and predators are arranged in columns.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 Sharks		0.1																						
2 Odontocetes																								
3 Bacalao	2	5		6	1																			
4 Birds	0.5																							
5 Sea lions	8	20																						
6 Pel predators	8.5	19.7		4	2																			
7 Non-comm pred	4	15		6		10			1															
8 Octopods	0.2	0.3			0.3																			
9 Pel planktivores	5	5		31	1																			
10 Other com pred	4	5		6	2					1														
11 Lg ben inv eat	4	5		6		10			1		1													
12 Plank reef fish	27		60	6	24.7		25	2		6								2		0.7				
13 Hexaplex											2				·									0.1
14 Sm ben inv eat	4		20	6	3		38	2										2		0.5				
15 Carniv zoops				5			1.9		45	12.3		45		14.5					0.7	1		13.1		5
16 Spiny lobster								1			0.2													
17 Slipper lobster	1							5			0.3													
18 Omniv reef fish	5.5			6		10	13	1		2	0.4						2							
19 Shrimp sm crab	1						0.5	65	2	14	23.4			6.5		3	2	0.1		10				0.1
20 Asteroids		··														1								0.1
21 Other herb fish	5	14.9		6	12	15	1.2	1			0.4							2		0.5				
22 Eucidaris	1									0.4	34.7			0.6		2	2							0.1
23 Juvenile anemones																								
24 Adult anemones																0.1		15	0.5	0.7				
25 Worms & ophioriods										0.1	1			5		3	3	2.7	5	3				1
26 Hard coral														0.1				0.1	0.1	0.7		20		0.1
27 Chitons																2.5								0.1
28 Detrit fishes	4	5		6	3																			
29 Sm gastropods											6			3		23.5	5	3.7	25	11	1			0.9
30 Sea turtles	2																							
31 Pepino																				0.1				
32 Other urchins											1			0.1										0.1
33 Parrotfishes	4	5		6		5																		
34 Marine iguana	0.9																							
35 Other cucumber	1																							0.1
36 Tripneustes	1										7					2	2							0.1
37 Lytechinus	1.1										3					2	2							0.1
38 Sm crustaceans							16.1		6.8	43				20					25.1	10		1		1
39 Filt + susp feed								20			20.6		98	15.6		30.9	33	12.7	7	21.2				0.2
40 Herb zoops							1.9		45	21.2		45		14.5	25			0.7	2		14.9			10
41 Phytoplankton									0.2			10			7				2				30	5
42 Microphytobenth														8		6		2	15	30			30	10
43 Benthic algae														9		3	5	35.2	10	5	20	50	10	1
44 Detritus							1.6						2	3.1		21	38	2	20.7	18.3	50	30	30	64.9
45 Import	5.3		20		51	50	0.8		1						68									

Appendix A. (Floreana [Galápagos] Ecopath model diet matrix continued)

	Prey \ Predator	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	Sharks																
2	Odontocetes																
3	Bacalao																
4	Birds																
5	Sea lions																
6	Pel predators																
7	Non-comm pred																
8	Octopods																
9	Pel planktivores																
10	Other com pred																
11	Lg ben inv eat																
12	Plank reef fish																
13	Hexaplex																
14	Sm ben inv eat																
15	Carniv zoops	5.5	5	10			5										
16	Spiny lobster																
17	Slipper lobster																
18	Omniv reef fish																
19	Shrimp sm crab																
20	Asteroids																
21	Other herb fish																
22	Eucidaris																
23	Juvenile anemones							8									
24	Adult anemones																
25	Worms & ophioriods					6.6		0.1									
26	Hard coral	0.1				0.8			1	0.1							
27	Chitons																
28	Detrit fishes																
29	Sm gastropods	0.1															
30	Sea turtles																
31	Pepino																
32	Other urchins																
33	Parrotfishes																
34	Marine iguana																
35	Other cucumber																
36	Tripneustes																
37	Lytechinus																
38	Sm crustaceans	0.5				0.6											
39	Filt + susp feed	2				0.2											
40	Herb zoops	5.5	10		10												
41	Phytoplankton	13	2		3							1			2	2	5
42	Microphytobenth	15	50	40	20	30		44.5	20	55					55		
43	Benthic algae	3		20	1	14.8	95		59	20	100	13	80	90	2		
44	Detritus	38.8	30	25	49	47		47.4	20	24.9		86	20	10	23	8	5
45	Import	16.5	3	5	17										18	90	90

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Appendix B. List of the 57 species in 27 families encountered during the 26 visual fish transects at Isabela and Fernandina Islands, Galapagos (total sampled area of 26,000 m^2).

Family	Species	Common name
Acanthuridae -- Surgeonfish	Acanthurus nigricans	Goldrimmed surgeonfish
	Prionurus laticlavius	Yellowtailed surgeonfish
Apogonidae -- Cardinalfish	Apogon atradorsatus	Blacktiip cardinalfish
	Apogon pacifici	Pink cardinalfish
Balistidae -- Triggerfish	Sufflamen verres	Yellow-bellied triggerfish
Blennidae -- Blennies	Ophioblennius steindachneri	Large banded blenny
	Plagiotremus azaleus	Sabertooth blenny
Branchiostegidae -- Tilefish	Caulolatilus princeps	Ocean whitefish
Chaetodontidae -- Butterflyfish	Chaetodon falcifer	Scythe butterflyfish
	Chaetodon humeralis	Threebanded butterflyfish
	Johnrandallia nigrirostris	Barberfish
Diodontidae -- Porcupinefish	Diodon holocanthus	Baloonfish
Gobiidae -- Gobies	Lythrypnus gilberti	Galapagos blue-banded goby
Haemulidae -- Grunts	Anisotremus interruptus	Yellowtail grunt
	Anisotremus scapularis	Peruvian grunt
	Haemulon scudderi	Golden-eyed grunt
	Haemulon sexfasciatum	Graybar grunt
Heterodontidae -- Bullhead sharks	Heterodontus quoyi	Horn shark
Kyphosidae -- Chubs	Girella freminvillei	Dusky chub
Labridae -- Wrasses	Bodianus diplotaenia	Streamer hogfish
	Bodianus eclancheri	Harlequin wrasse
	Halichoeres dispilus	Chameleon wrasse
	Halichoeres nicholsi	Spinster wrasse
	Semicossyphus darwini	Goldspot sheepshead
	Thalassoma lucasanum	Rainbow wrasse
Labrisomidae -- Blennies	Labrisomas dendriticus	Bravo clinid
	Malacoctenus tetranemus	Chameleon clinid
Lutjanidae -- Snappers	Lutjanus jordani	Jordan's snapper
	Lutjanus viridis	Blue striped snapper
Mugilidae -- Mullets	Mugil rammelsbergi	Yellowtail mullet
Muraenidae -- Moray eels	Muraena lentiginosa	Jewled moray
Oplegnathidae -- Beakfish	Oplegnathus insignus	Pacific beakfish
Pomacanthidae -- Angelfish	Holocanthus passer	King angelfish
Pomacentridae -- Damselfish	Abudefduf troscheli	Panamic seargeant major
	Chromis atrilobata	Brown chromis
	Microspathodon bairdi	Bumphead damselfish
	Microspathodon dorsalis	Giant damselfish
	Stegastes arcifrons	Yellow-tail damselfish
	Stegastes leucorus beebei	White-tail damselfish
Scaridae -- Parrotfish	Nicholsina denticulata	Loosetooth parrotfish
	Scarus ghobban	Blue-chin parrotfish
Scianidae -- Croaker	Pareques perissa	Glaapagos drum
Scorpoenidae -- Scorpionfish	Scorpaenodes xyris	Rainbow scorpionfish
Serranidae -- Sea Basses	Alphestes afer	Mutton hamlet
	Cratinus agassizii	Gray threadfin bass
	Dermatolepis dermatolepis	Leather bass
	Epinephelus labriformis	Flag cabrilla
	Epinephelus panamenses	Panamic graysby
	Liopropoma fasciatum	Wrasse ass bass
	Mycteroperca olfax	Bocalao
	Paralabrax albomaculatus	Comatillo
	Paranthias colonus	Gringo
	Serranus fasciatus	Barred serano
Sphyraenidae -- Barracuda	Shpyraena idiastes	Barracuda
Sygnathidae -- Seahorses	Hippocampus ingens	Pacific seahorse
Tetradontidae -- Puffer fish	Spheroides annulatus	Bullseye puffer
Tripterygiidae -- Blennies	Lepidonectes corralicola	Galapagos tripple-finned blenny

Appendix C. Refinement of the 1994-1996 Prince William Sound Ecopath model

The derivation of input parameters for the Prince William Sound Ecopath model is documented by Okey and Pauly (1999b), as is the development of the model scope and structure. Subsequent modifications are documented in the present appendix.

A. The following changes were made in June 2000:
1. Seabird and Avian raptor P/Bs were changed to the values specified in the text of Ostrand and Irons (1999) rather than according to Table 60 in the same publication. This included changing Seabird biomass to 0.011 t·km^{-2} and its P/B to 0.078 year^{-1}. The following subsequent changes were made for the purposes of thermodynamic balancing.
   a. Seabird biomass was changed was changed 0.022 t·km^{-2}.
   b. Seabird P/B was increased to 0.17 year^{-1} to account for the juvenile seabird biomass that was not initially included in the estimation (see Ostrand and Irons 1999 text).
   c. The proportion of the diet of avian raptors was changed to ease the pressure on seabirds and balance that group:
      i. Seabirds : 0.50 to 0.05
      ii. Adult salmon 0.08 to 0.48
      iii. Inshore detritus 0.28 to 0.33
2. Pollock P/B was changed from 0.707 year^{-1} to 0.709 year^{-1}.
3. Eulachon immigration was changed form 1.8 t·km^{-2}·year^{-1} to 1.9 t·km^{-2}·year^{-1}.
4. The proportion of the Seabird diet was changed in two ways:
   a. Sandlance from 0.15 to 0.13
   b. Nearshore demersals from 0.087 to 0.107
5. Nearshore omnivorous zooplankton biomass was adjusted from 0.103 t·km^{-2} to 0.105 t·km^{-2}.
6. The Salmon P/B values were changed based on information from C. Walters on survival and natural mortality, combined with the calculated PWS fishing mortality to estimate a total mortality, which is theoretically equivalent to P/B in some circumstances (Allen 1971):

Table A-1. Estimation of salmon mortality

Mortality source	Adult	Juvenile
Natural (M)	0.51	3.91
Fishing (F)	0.80	0.00
Total (Z)	1.31	3.91
Survival	0.60	0.02

7. Biomass of adult salmon was changed to from 1.034 t·km^{-2} to 3.1 t·km^{-2} to reflect that 1/4 (plus an additional 10%) rather than 1/12 adult peak salmon biomass estimate of 12.402 t·km^{-2} is

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available to organisms in PWS, assuming that more of the biomass would be available to predators even though salmon are transiting for a short duration of the year.

8. The already small Salmon predation on eulachon and sandlance was decreased from 0.5% to 1% each and the remainder was imported.

9. The small predation of Pollock on juvenile Salmon was decreased by 1% and moved to deep epibenthos.

10. Incorporated ex-vessel values from 1995 Alaska catch document.

B. The following changes were made in December 2003:

The shark group was split in to three species and an octopod group was added to the model as described in Chapter 4. Minor adjustments were then necessary to rebalance the model:

1. Salmon shark predation on dogfish and sablefish was reduced by 50% and 40%, respectively. Most of this pressure was shifted to adult salmon, with smaller amounts to arrowtooth flounder and Pacific cod.

2. Half of the rockfish consumption by salmon sharks was divided evenly between Arrowtooth flounder and Pacific cod.

3. Half of the Arrowtooth predation on rockfish was shifted to octopods.

4. Half of halibut predation on juvenile Arrowtooth was shifted to nearshore demersal fishes.

5. 40% of Pac Cod predation on Juvenile Arrowtooth was shifted to shallow large epibenthos.

6. The erroneous P/B value for porpoise was shifted from 0.24 to the more reasonable 0.15; to balance the porpoise group after this change. Predation pressure by Transient orcas on Porpoise was then lowered to 37%, the remainder being shifted to Baleen whales (10%), invertebrate-eating birds (6%), Adult salmon (to 4%), Sablefish (3%), and seabirds (1%).

All of these changes consisted of small proportions of the overall diets, so diets were changed very little. The resulting diet composition matrix is shown in Appendix D.

Literature cited in Appendix C

Allen, K. R. 1971. Relation between production and biomass. Journal of the Fisheries Research Board of Canada **28**:1573-1581.

Okey, T. A., and D. Pauly, editors. 1999. A Trophic Mass-balance Model of Alaska's Prince William Sound Ecosystem, for the Post-spill Period 1994-1996, 2nd edition. Fisheries Centre Research Report 7(4), University of British Columbia, Vancouver.

Ostrand, W. D., and D. B. Irons. 1999. Seabirds and seabird predators. *in* T. A. Okey and D. Pauly, editors. A Trophic Mass-balance Model of Alaska's Prince William Sound Ecosystem, for the Post-spill Period 1994-1996, 2nd edition. Fisheries Centre Research Report 7(4), University of British Columbia, Vancouver.

Appendix D. Diet composition matrix for the Ecopath model of the Prince William Sound (in percent of total biomass wet weight) used in the analyses presented in Chapter 4. Prey are arranged in rows and predators are arranged in columns.

#	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Transient orca																								
2	Salmon sharks																								
3	Resident orca																								
4	Sleeper sharks																								
5	Halibut	0.5	5	0.5	4.5													1							
6	Pinnipeds	38																							
7	Porpoise	37																							
8	Lingcod					0.1				0.5									1						
9	Adult atooth		1		30																				
10	Adult salmon	4	75.4	74	6	13.3	14		13.6								48								
11	Pacific cod		1.4	0.5	6	1.2	1	14					0.7		3										
12	Sablefish	3	4.5	0.5	1		1	10																	
13	Juvenile atooth.					2						3			3.9		6		2						
14	Spiny dogfish		0.4												0.1										
15	Avian raptors																								
16	Octopods				13.5					0.5					3		3								
17	Seabirds	1														5									
18	Deep demersals				2	3.8						7.9	4.8		0.5			7		16		3.1			
19	Pollock 1+		0.5	0.5	10	37.4	11.9		5.1	25.2		7.3	20.8	3.7	3			6			2				
20	Rockfish		4.8		1.5		3		3	0.5					1				2.8						
21	Baleen whales	10			1																				
22	Salmon fry 0-12					2	1		3.2		0.1				1				2.5		0.5				
23	Nshore demersal		0.5	0.5	1	3.3	23	10	27.2	9.5		8			4.1	4	6	12.7	11			0.2		4	
24	Squid		4		0.6	0.2	12	30				2.5	8	1	2			0.7	5	4.91	15.8				0.3
25	Eulachon		0.3		0.2	5.3	6		4.8	4.2	0.05	0.9	10.7	14.7	3.7	4		4.7	1	4.31			30		0.1
26	Sea otters	0.5																							
27	Deep epibenthos		0.5		0.4	14.1			4			35.8	5.1	25	2		18		15	27.5	28.8			11	0.4
28	Capelin		0.1			0.1			4.7	0.1		0.2	0.1	4	7			1	0.5	0.9	0.1		1		0.1
29	Adult herring		1.1	23.5			12	25	12.5	5	0.1	0.2	2.2	5.1	14.4							20			
30	Pollock 0									1		0.3	0.3	1	1					0.2	0.1				0.1
31	Invert-eat bird	6																							
32	Sandlance					0.1	1	1		1.5	0.05	0.2	0.1	4.3	2				11		0.6	1.1	8	1	0.5
33	Shal large epibent		0.5		0.4	2.4						4.8			14			18		2.7	10.3			11	
34	Juvenile herring				10.3	9.2	4		18.6	40.9	0.1	0.8	5.6	26.2	2			36.7	0.5	6.01	3.1	22	5.7	0.5	0.1
35	Jellies												5.4		3.4								1.1		
36	Deep sm infauna											2.8	0.4		2		2		10.5		0.3				
37	Near omni-zoo													0.1		1		1		0.2	0.3	0.3	0.1		0.3
38	Omni-zooplankto								7.7	3			6.7	14.9	21.9	1	2	6.2	2	35.1	40	49.7	16.3		96.6
39	Shal sm infauna											2.8			2		2		0.5					1	0.1
40	Meiofauna																		2						
41	Deep large infauna																10		10						
42	Shal small epibent				0.2	2.4						9.99			2	4	12	5.3	1.5		4.7		15.7	70	0.3
43	Shal lg infauna																10	1.8	5						
44	Near herbi-zoo																						0.2		0.1
45	Herbi-zooplankt								3.8									0.1		7.42	2.4		28.9	2	1.5
46	Near phytoplktn																								
47	Offshore phyto.																								
48	Macroalgae/gras																								
49	Nekton falls				4.1	2						2.5	9.1		1		3								
50	Inshore detritus															33		10.3	1						
51	Offshr detritus																	10							
52	Import				17.8	5.2					99.5	10	20												

Appendix D. (PWS Ecopath model diet matrix continued)

	Prey \ Predator	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
1	Transient orca																					
2	Salmon sharks																					
3	Resident orca																					
4	Sleeper sharks																					
5	Halibut																					
6	Pinnipeds																					
7	Porpoise																					
8	Lingcod																					
9	Adult atooth																					
10	Adult salmon																					
11	Pacific cod																					
12	Sablefish																					
13	Juvenile atooth.																					
14	Spiny dogfish																					
15	Avian raptors																					
16	Octopods																					
17	Seabirds																					
18	Deep demersals																					
19	Pollock 1+																					
20	Rockfish																					
21	Baleen whales																					
22	Salmon fry 0-12																					
23	Nshore demersal																					
24	Squid		2																			
25	Eulachon																					
26	Sea otters																					
27	Deep epibenthos		4	25																		
28	Capelin																					
29	Adult herring																					
30	Pollock 0																					
31	Invert-eat bird																					
32	Sandlance																					
33	Shal large epibent		16																			
34	Juvenile herring																					
35	Jellies																					
36	Deep sm infauna				30									4								
37	Near omni-zoo	0.3			0.3	0.2	0.2		0.1		0.1	0.1										
38	Omni-zooplankto	49.4		5	41.3	37.7	27.4		20.9		9.9	22.9	9									
39	Shal sm infauna							10		19						15						
40	Meiofauna			3													10					
41	Deep large infauna		10	5																		
42	Shal small epibent	0.1			3.4	8.3		90	6.3	79									5			
43	Shal lg infauna		70																			
44	Near herbi-zoo				0.4	0.3	0.5		0.5		0.6	0.4		0.2	0.2							
45	Herbi-zooplankt	0.2		5	54.6	53.5	71.9		72.2		89.4	66.6	9	24.8	24.8			10				
46	Near phytoplktn											0.7		75		60			35	50	100	
47	Offshore phyto.											9.3			75							100
48	Macroalgae/gras			5						1									20			
49	Nekton falls									1									0.3			
50	Inshore detritus															25	45		39.7	50		
51	Offshr detritus			20										78			45	90				
52	Import	50																				

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Appendix E. Diet composition matrix for the Ecopath model of the West Florida [continental] Shelf (in percent of total biomass wet weight) used in the analyses presented in Chapter 6. Prey are arranged in rows and predators are arranged in columns.

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Dolphins	0.02																							
2	Seabirds																								
3	Turtles	0.02																							
4	Manatees																								
5	LgOcePisc					1					0.2														
6	LgOcePlank										0.1														
7	Coastalsharks					1		2			0.7														
8	Rays/skates					1.2		15																	
9	PelOcePisc					7		0.04		7	0.02														
10	PelCoasPisc	1.69	0.2			8.5		2.5			1	1													
11	MackerelAdul					5.7		0.35		1	0.3														
12	MackerelJuv	1.51	0.2			5.7		0.35		2	0.46														
13	Sardine/Herring	5.32	24.4	0.72		7.3		3.74		10	15	44.6	40.8		0.1	1.6		1.68	0.6						
14	PelOceJelly/eaters		0.2			9.2		3		10	7.61				0.1										
15	PelOcePlanktivores	1.63	5			9.6	11.7	2.99		11	6.22	11.2	22.2		0.1	1									
16	DemOceInvert/eaters										0.59										9.98				
17	DemCoasPisc		9.87								0.02	1.16					1				9.98				
18	DemCoasInvert/eaters		14.2			1.5		3.02			8.07	2.91	14.6				4	0.43					8.85	0.02	
19	DemCoasOmniv	20.8	9.87			5.2					5.61						2	0.1					5.42		
20	BentOcePisc																				0.1	0.1			
21	BentOceInvert/eaters					0.1		0.34			0.21										20	4.75			
22	BentCoasPisc					1.5		4.03			0.02		2.13						0.1		5	1	0.02		
23	BentCoasInvert/eaters	0.09	13.4			1.6		2.21	4.5		0.3							2.5	0.6		15	2.05	0.02		
24	SurfacePelagics	1.51	0.2			9.8					0.91	9.42													
25	StrucAssCoasPisc					1.4		3.11			0.03	2.28							0.13						
26	LgGroupers					0.5		2.41			0.01														
27	StrucAssCoasInvert/eaters		1.12			1.1		3.66			6.21	3.42	4.46				2.27		0.12				5.76	10	
28	StrucAssCoasOmniv	1.08				1.3		0.74	2.3		5.4						1.97	1.95	0.04						
29	StrucAssCoasPlank																								
30	NearshAssPisc	0.18	3.15			0.4		1.11			0.01														
31	Mullets	2.3	11.9								0.44	1.28													
32	NearshPlanktivores	13.1	6.21	0.72				2.06	2.3		18.4	12	10			1		20	5.18				13.3	0.02	12
33	Other fishes	7.66				3.3		9.03	1.5	10		3.42		5.8		3.6	2.2	5.22		1.11	9.98		7.21	7.14	9.13
34	Squid	40.1				12.3	6.48	8.9	10.2	28.5	7.4	5.6	5.81			1.4	6	0.12					7		
35	Adult Shrimps	0.01				0.5		1	1	0.5	1	1.6		0.1		0.05	1	1	4	1	1	4	1	8	
36	Lobsters	0.07				0.01		0.2	0.2										0.01					0.01	
37	Large Crabs	0.07		23		1.5		3	10		1	0.03		0.1			4		3	1	3	3	3	2	
38	Octopods	0.07				1.6		4.9	2									1							
39	Stomatopods								0.5		0.36						1.97		1.3	0.4		3.99	1	1	
40	Echinoderms/Large	0.07					4.86	1.8	15.8								5.48		8.55	4.7		9.98	6.4	8	
41	Bivalves	0.11		21.5				4	12										0.3			2	2	8.4	
42	Sessile epibenthos			22.6				4.22						1.7			4		8.37	30.3		0.6		7	
43	Small infauna							1.2	14.9		0.3			1.7			43.9	0.61	13.7	7.8	9	26.9	13.8	17	5.82
44	Small mobile epifauna							1.5	17		4.3	0.1		5		6.8	35.4	15.5	32	15.3	17	29.9	12.9	35.2	25.5
45	Meiofauna													3.2					0.28	0.03					
46	Small Copepods					23.5								32.4		12		2.6	0.01						
47	Other Mesozooplankton					23.5				5	5.03			20.8		26.5	4.98	4.62	1.91			2.8	0.04		0.78
48	CarnivZooplank	1.11				0.1	23.5			5	1.7			6	58.7	29.9	0.21	4.5	1.11			8.29	0.11	5.7	
49	Ichthyoplankton					0.1				10					1				0.5						
50	CarnivJellyfish			10			4.86									40									
51	Microbial Heterotrophs																								
52	Macroalgae		10.8	100							0.02			2.85				0.11	0.63	12.5		2.8			
53	Microphytobenthos		10.8					1.3	1.55		0.01			0.2				0.21	0.11	5				0.44	
54	Phytoplankton																								
55	Sea grasses					1.76								9.01		16.2									46.7
56	Dead carcasses	1.51						6.59																	
57	Sediment Detritus													2.63				0.05	2.88	17.9			0.04		
58	Watercolumn Detritus													8.48											
59	Drift Macrophytes																								
60	Import							3.99										35							

Appendix E. (West Florida Shelf model diet matrix continued)

#	Prey \ Predator	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
1	Dolphins																											
2	Seabirds																											
3	Turtles		0.05																									
4	Manatees																											
5	LgOcePisc																											
6	LgOcePlank																											
7	Coastalsharks																											
8	Rays/skates		1.65																									
9	PelOcePisc	0.26	0.47																									
10	PelCoasPisc	0.46	0.72				2.5																					
11	MackerelAdul		0.06																									
12	MackerelJuv		0.06																									
13	Sardine/Herring	5.8	5.8	0.9			3.75				0.5																	
14	PelOceJelly/eaters										5.01																	
15	PelOcePlanktivores	3.8	1.5								0.5																	
16	DemOceInvert/eaters						2.5																					
17	DemCoasPisc																											
18	DemCoasInvert/eaters	2.04	4.2				9.51								8.1	1												
19	DemCoasOmniv	0.42	6.57	0.7			1.75																					
20	BentOcePisc	0.1	2.34	0.05																								
21	BentOceInvert/eaters	0.91	3.1	0.24																								
22	BentCoasPisc	0.75	2.27	0.1																								
23	BentCoasInvert/eaters	3.84	2.2	0.45			1.5								20	2												
24	SurfacePelagics	1																										
25	StrucAssCoasPisc	1	2.41										1															
26	LgGroupers		0.08																									
27	StrucAssCoasInvert/eaters	13.4	8.57	0.05																								
28	StrucAssCoasOmniv	7.35	4.72	0.74									1															
29	StrucAssCoasPlank	4.4	6.24										1															
30	NearshAssPisc																											
31	Mullets		3.6				5.5						1															
32	NearshPlanktivores	2.6	2.54	1.27			9.51				5.01																	
33	Other fishes	1.67	0.36	3.59	0.62	1.98	26.3			0.1																		
34	Squid	6	6.3	3.11			10			1	0.1	0.8				6												
35	Adult Shrimps	3	2	5	0.01	0.1	1		0.1			0.4		1			0.1	10										
36	Lobsters	0.05	0.2	0.1						0.01							0.1											
37	Large Crabs	15	15	3	0.01	0.1	9			0.1				18.7	0.5		0.5	3										
38	Octopods	3.27	10	0.7													0.1											
39	Stomatopods	1	2	0.9								0.03																
40	Echinoderms/Large	2.11	1.5	10	0.1	0.35					5	0.6		22.7	4.1	5.6	1		1									
41	Bivalves										16			18	36.4	23.5		11	1									
42	Sessile epibenthos		1.5	16.5	21.4	1.59					14	8.21	5.69	15.3	12		10.2		1.01									
43	Small infauna	5			17	3	8.21				2	19.6	3.69	14.9	15.7	15	4.9		0.1		4							
44	Small mobile epifauna	10.7	2	22	5.57	16.5	13	0.5	9	29.7	14.8	23.2	2	1.9	10	18	2		2	1	1							
45	Meiofauna		0.09						1		2	12.4		2.9	1		3.1	1	3	10	7	1						
46	Small Copepods	1.8		1.52					34.4	4	2								0.1				2	12	12	35	20	
47	Other Mesozooplankton	2.22		2.55	0.67	35.2			35.5	4	33.1								0.1					1	10	25	47	
48	CarnivZooplank			4	1.86	16.1	3.9		8.4	18.6	32.9														1	4	10	
49	Ichthyoplankton		0.15							1	0.1															0.2	1	
50	CarnivJellyfish										2								0.1									
51	Microbial Heterotrophs													21.7	10.5	20	10.1	10	30.1	15	19	35	13	40	64	5	23	
52	Macroalgae				53.9		0.25	5		2		0.3	3.69			1	12.2				12							
53	Microphytobenthos							1					10		3.8	6	9.9	12	4	9	8	20	4	5		5		0.5
54	Phytoplankton							0.5	3.12								2.8	23	23.2	22	10		80	37	10	15		0.5
55	Sea grasses			0.29	0.73					1							4.7				5		5					
56	Dead carcasses								1	1.5		3.1		0.9	3.3		2		1		5							0.7
57	Sediment Detritus			12.1			3			2		21.3		7		6	11.3	41	17.3	32	7	44		1		5		44.8
58	Watercolumn Detritus								5.04								6.7	13	18	5	7		1	4	2.8	5		50
59	Drift Macrophytes								2.52						0.8		18.1				5	15						3.5
60	Import							90																				