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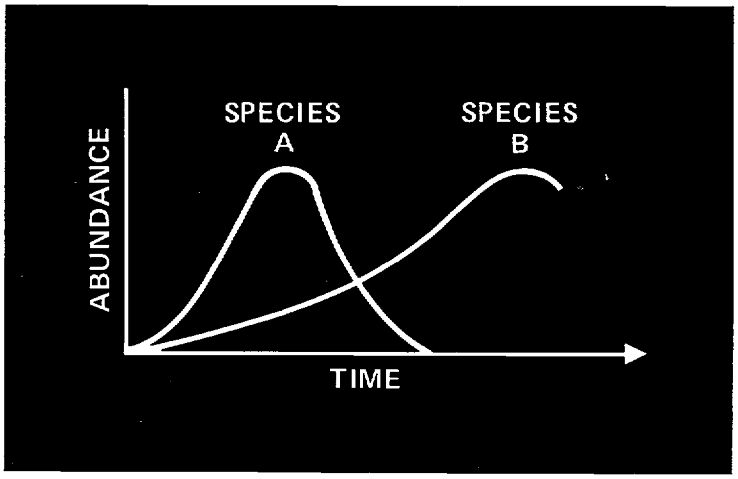
OCS Study
MMS 88-0034

REVIEW OF RECOVERY AND RECOLONIZATION OF HARD SUBSTRATE COMMUNITIES OF THE OUTER CONTINENTAL SHELF

FINAL REPORT 1988



MMS
U.S. Department of the Interior
Minerals Management Service
Pacific OCS Region

OCS STUDY
MMS 88-0034

BIOLOGICAL RECONNAISSANCE OF SELECTED BENTHIC HABITATS WITHIN THREE CALIFORNIA OCS PLANNING AREAS

FINAL REPORT ON

REVIEW OF RECOVERY AND RECOLONIZATION OF HARD SUBSTRATE COMMUNITIES OF THE OUTER CONTINENTAL SHELF

June 1988

Edited by

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This study is supported by

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1340 West Sixth Street
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Under

Contract No. 14-12-0001-30388

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CHAPTER 1. INTRODUCTION

1.1 PURPOSE AND OBJECTIVES

The Minerals Management Service (MMS) program to conduct a "Biological Reconnaissance of Selected Benthic Habitats within Three California OCS Planning Areas" is designed to increase the knowledge of the marine benthic habitats within the Northern, Central, and Southern California OCS (Outer Continental Shelf) Planning Areas (Figure 1-1). The general program includes a field survey conducted in November/December 1987 of selected hard substrate and soft substrate habitats from approximately 50 m to 500 m depth (165 ft to 1650 ft), laboratory and data analysis, and report characterization of the biological communities, particularly as related to differences in geographic range (e.g., latitude), bottom depth, and substrate type. The study sites are located in areas that potentially will be included in planned oil and gas lease sales in the three California OCS planning areas, beginning in 1989, and for which there was little or no information on the biological communities. The results from this study will aid the MMS in making environmental assessments and management decisions associated with potential leasing and oil and gas exploration and development activities.

As part of the overall study, this report on "Review of Recovery and Recolonization of Hard Substrate Communities of the Outer Continental Shelf" provides an analysis of relevant existing literature to assess recovery rates and recolonization patterns of hard substrate communities located in the OCS. Definitions of the terms recovery and recolonization and associated terms including recruitment and succession are presented in Section 1.2 and further detailed in Chapter 2. Major objectives of the report are to review relevant recovery studies, pertinent life history information, and data gaps; to make recommendations for future studies including field sampling methodologies; and to discuss the relevance and applicability of recovery/recolonization studies in the decisionmaking process for-oil and gas activities. The recommendations for future studies are particularly relevant to potential MMS programs such as the "Patterns of Succession in Deep Water Hard Substrate Communities Potentially Disturbed by OCS Oil and Gas Activities," as listed in the MMS Draft Environmental Studies Plan for Fiscal Year 1989.

The primary focus of this report is on benthic invertebrate communities of the Ocs. The role and importance of fish in recovery/recolonization processes and the significance of oil and gas development activities to fish communities and fisheries species are beyond the scope of the present study. However, these topics are the subject of other potential MMS programs listed in the FY89 Studies Plan including "Effects of an OCS Oil and Gas Production Platform on Rocky Reef Fishes and Fisheries", "Fisheries Ecology of California Offshore Oil and Gas Platforms", and "Survey of Commercially Important Fishes in Rocky Reef Habitats off Washington and Oregon."

Potential effects of OCS development on hard substrate communities can be assessed based on three primary factors: (1) the sensitivity of the community, expressed in terms of the ability and time for recovery; (2) the local or regional abundance (e.g., common or rare) of community and/or substrate types;

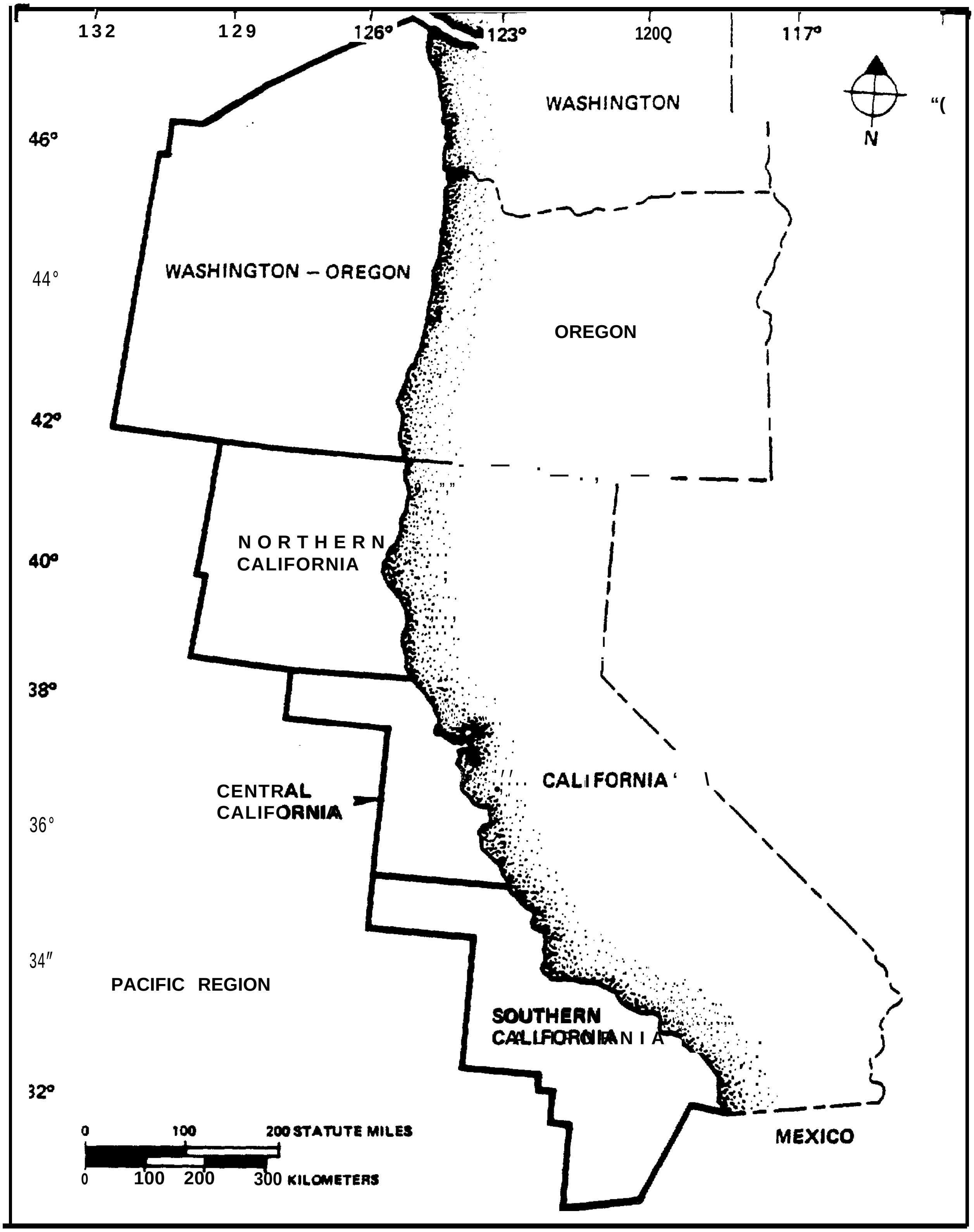

FIGURE 1-1. MMS NORTHERN, CENTRAL, ANO SOUTHERN CALIFORNIA PLANNING AREAS

and (3) the predicted extent of disturbance from oil and gas development activities. Knowledge of each factor is important to predict the significance of potential impacts,

The sensitivity of hard substrate communities is addressed partly by the present study and the ongoing MMS California Monitoring Program (CAMP); however, there are numerous gaps in our current knowledge of the life histories of many key taxa. In general, the most sensitive communities are predicted to be those characterized by numerous long-lived (> five years), slow-growing (> five years to reproductive maturity) organisms, including many sponges, anemones, and corals, having larvae with short range (few meters) dispersal abilities. These communities are typical of many high relief (> 1-3 m) hard substrate features of the California OCS; the communities appear to be most diverse in areas where there is little sediment cover (SAIC, 1986). The associated organisms would be most sensitive to disturbance if they are not located near or downcurrent from source populations that could contribute (e.g., from adult immigration and larval dispersal) to recolonization and recovery.

Less sensitive hard substrate communities are predicted to be those characterized by fast-growing organisms having larvae with long range dispersal, thereby representing a greater potential for recovery. These communities are typical of many low relief (e.g. , < 1 m) hard substrate features of the California OCS. These features commonly appear to be covered with a thin (millimeters) to thick (centimeters or greater) sediment veneer, presumably from greater sedimentation and/or sediment movement, and therefore appear to represent more variable, marginal habitat for the associated organisms.

The local or regional extent of OCS hard substrate communities can be estimated partly from indirect methods such as side scan sonar and precision bathymetric surveys , which can provide a conservative estimate of the amount of hard substrate available for colonization by organisms. However, as evidenced by the results from numerous reconnaissance surveys (e.g. , SAIC, 1986 and the present November/December 1987 survey) of suspected hard substrate features, many of the low relief features are covered partly or completely by sediments, which in many instances are deep enough (e.g., > 1 m) to support well developed soft substrate communities. These results indicate that the actual extent of hard substrate communities may be significantly less in some areas than can be estimated using indirect methods alone, and emphasizes the importance of ground- truth surveys (e.g., ROVs; manned submersibles, or camera drops) to verify these assumptions. MMS, Pacific OCS Region, currently is computerizing the locations of known or suspected hard substrate features to provide estimates of the percentage of hard substrate in various OCS regions (G. Brewer and J. Lane, MMS, pers. comm.). Once sufficient information is known on the types and sensitivities of hard communities and the extent of exposed substrate, these data can be integrated with models of the types and extent of potential effects from oil and gas development activities to enhance decisionmaking capabilities on local and regional scales.

Where data or information are available, this report focuses on the biological communities of the California OCS; however, relevant studies from other OCS regions are incorporated as appropriate. In particular, the information on ecological theories and models is representative of scientific thought that has evolved from worldwide studies including marine, freshwater, and some terrestrial work. Information on recovery and recolonization studies, including sources of disturbance, focuses on marine regions of North America, with additional emphasis on the California OCS. The life history information primarily represents a summary of California OCS taxa with extrapolation from other geographic regions only to fill data gaps.

The report is organized into five major chapters: an introduction and overview of ecological theory on recovery/recolonization and succession of marine benthic communities (Chapter 1); an expanded discussion of these processes, primarily available from intertidal and shallow subtidal studies with extrapolation to deeper water hard substrate communities as appropriate (Chapter 2); sources of disturbance to these communities, including natural and man-induced effects (Chapter 3); review of relevant studies on recovery/recolonization including experimental and field surveys and a summarization of life history information such as larval dispersal and selectivity, adult longevity and growth rates, and biological interactions for selected taxa (Chapter 4); and recommendations for future studies, including identification of data gaps, proposed studies, and the relevance and applicability of recovery and recolonization studies in decisionmaking processes (Chapter 5).

1.2 OVERVIEW OF THEORETICAL FRAMEWORK

This section presents an overview of the models and theories used to describe the recovery and recolonization of hard substrate communities following disturbances. Detailed discussions of these models and theories are presented in Chapter 2 and have been the subject of numerous review papers dealing with these processes (e.g., Connell, 1975, 1985; Connell and Slatyer, 1977; Connell and Keough, 1985; Crisp, 1974; Dayton, 1984; Sousa, 1985; Underwood and Denley, 1984).

Disturbance is a general term referring to any process which removes all or part of the community of organisms living on the substratum. Disturbances can result from natural biological processes (such as predation), physical processes (such as shear stresses generated by storm waves), or from various anthropogenic causes. After a disturbance, a cleared or partially open space, referred to as a patch, can be recolonized and undergo recovery. Two possible ways of viewing recovery and recolonization are from the species (Figure 1-2) and community (Figure 1-3) perspectives. From the standpoint of individual species (Figure 1-2), propagules are the primary means of colonizing patches (effects of patch size and alternative colonization mechanisms are detailed in Chapter 2), Propagules, the larvae of animals or the spores of plants, are the primary means used by benthic organisms for dispersal and colonization of new habitats. The initial step in the transition from the plankton to the benthic habitat is referred to as settlement, defined by Connell (1985) as "the point [in time] when an individual first takes up permanent residence on the substratum." Recruitment refers to those juveniles which have survived for a period of time after settlement. This is an operational definition, which depends on the period of time chosen. The "bottleneck" effect, represented diagrammatically in Figure 1-2 as a sharp decrease in the number of organisms at the transitions to settlement and recruitment, emphasizes the fact that only a subset of the total number of individuals pass on to subsequent stages. Different physical and biological processes may operate at each bottleneck (e.g., the widths of the bottlenecks may be a function of the type of substratum, presence of

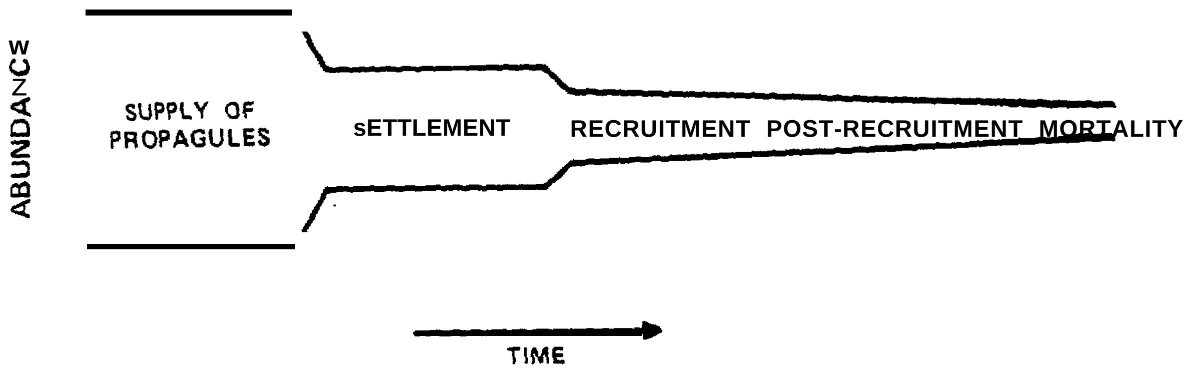

FIGURE 1-2. MODEL OF SINGLE SPECIES RECOVERY/RECOLONIZATION FOLLOWING A DISTURBANCE.

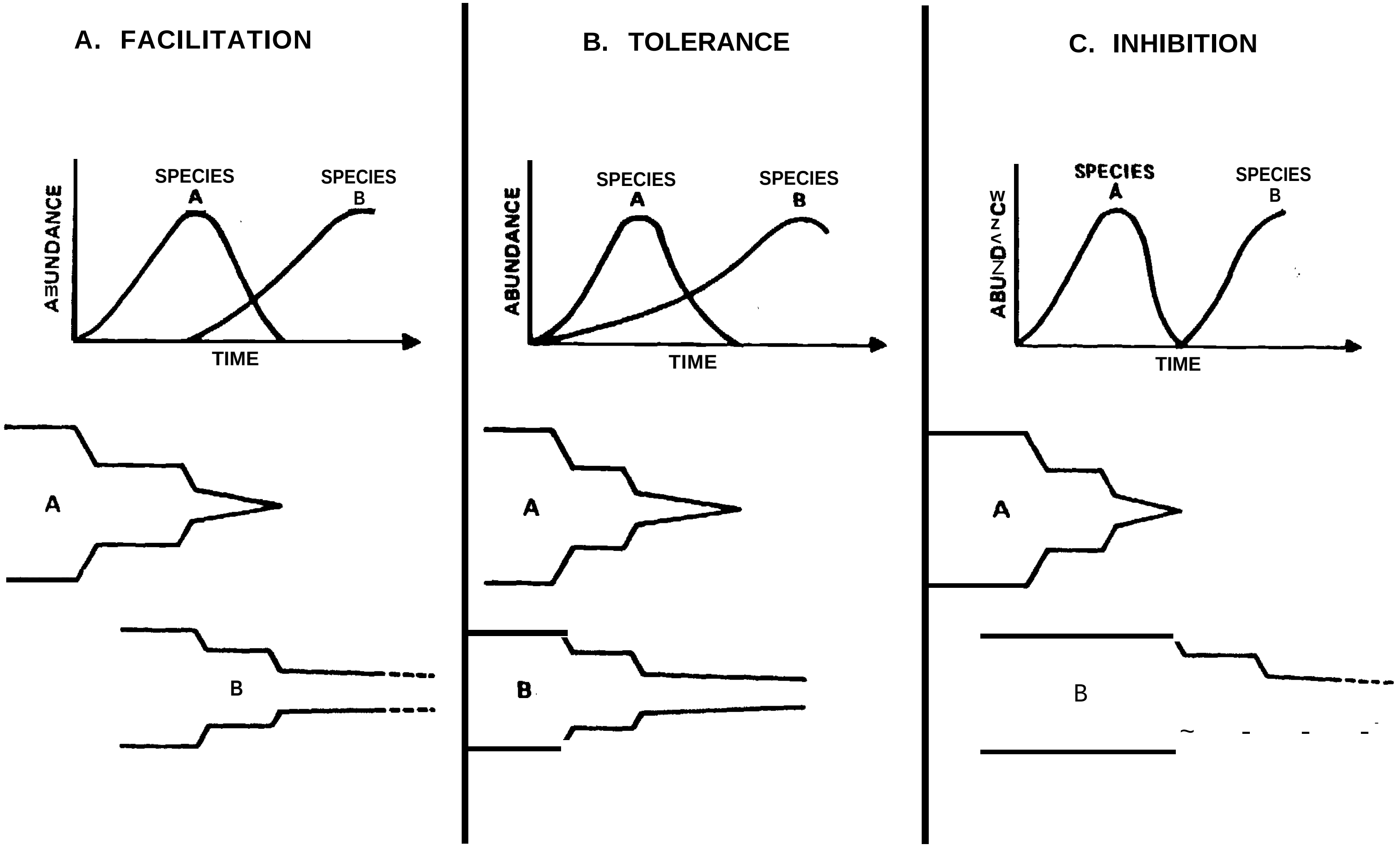

FIGURE 1-3. THREE MODELS OF BIOLOGICAL COMMUNITY SUCCESSION FOLLOWING A DISTURBANCE (MODIFIED FROM CONNELL AND SLATYER, 1977). See Text for Discussion.

competitors or predators, etc.). These processes are discussed in more detail in Chapter 2. After successful recruitment, the number of organisms usually continues to decrease over time due to various causes (e.g., predation and competition), which generally are included in the generic category of "post-recruitment mortality,."

From the community viewpoint (Figure 1-3), many species of organisms potentially can colonize a patch; furthermore, after the disturbance the characteristics of the biological community may change over time as recovery proceeds. The process of change in a community following a disturbance that creates a patch of open space is called succession. The changes in the community can refer to biomass, productivity, species diversity, or species composition. Recent usage (e.g., Connell and Slatyer, 1977) focuses on changes in the species composition of communities over time. Connell and Slatyer (1977) review the history of studies of succession in a variety of environments and present three models into which most of the results fit. It is important to note that they only considered changes in species composition that occurred "in the absence of significant trends in the physical regime"; that is, the disturbance that created a patch represented a temporary change in the normal physical/chemical environment, not a permanent change. To date, this latter possibility has not been considered in any model of succession.

In all three models, the initial event is a disturbance which creates a patch. In the first model (Figure 1-3A), the facilitation model, this patch can only be colonized initially by certain "early succession" or opportunistic species (represented in the figure by Species A). These early colonists then modify the environment so that it becomes less suitable for continued colonization by other "early succession" species but more suitable for the recruitment of "late succession" species (represented in the figure by Species B). The growth of the later succession propagules is facilitated by the environmental modifications produced by the earlier succession species, which are eliminated in time. This sequence of replacement continues until the resident species no longer facilitate the colonization and growth of other species, At this stage, further changes in the species composition of the community are possible only if another disturbance occurs.

In the second model, the tolerance model (Figure 1-3B), the patch can be colonized by the propagules of any species that arrive after the patch is created and that can survive in the environment as an adult (represented in the figure by Species A and B). These early colonists then modify the environment so that it becomes less suitable for continued colonization by "early succession" species, but now this environmental modification has little effect on the recruitment of "late succession" species. The later succession propagules grow to maturity and are unaffected by the continued presence of early succession species; in time, these latter species are eliminated. This sequence continues until no propagules are able (e.g., from space limitation) to colonize and grow in the presence of the resident community. At this stage, further change in the species composition of the community is possible only if another disturbance occurs.

In the third model, the inhibition model (Figure 1-3C), the initial colonization of the patch proceeds in a similar manner as the tolerance model. However, now the early colonists, represented in the figure by Species A, modify the environment so that it becomes less suitable for continued colonization by the propagules of any species. As long as individuals of the early colonist species persist, they exclude or inhibit colonists of all species. Further change in the species composition of the community is possible only if another disturbance occurs.

The succession of benthic communities, as defined by the three models, is obviously a complex process. At any point in time, the outcome of succession reflects the interaction of numerous factors including patch size and type, current/boundary layer flow, larval selectivity and abundance (e.g., seasonal variability) , biological interactions, and the frequency of disturbance (e.g. , Connell and Keough, 1985). Studies of recovery/recolonization (i.e., succession) require an operational definition of that point in time when recovery following a disturbance is complete. In the extreme case, complete recovery from a disturbance could imply that the community has returned to its pre-disturbance state for all parameters such as species composition, species diversity, abundance of organisms, and the age structure of the populations. However, based on many recent studies (e.g. , Paine and Levin, 1981; Sebens, 1986) which define benthic communities as consisting of a mosaic of patches that vary in size, age, species composition, and are each the result of a prior disturbance (the spatio-temporal mosaic model of Johnson, 1972), a less rigorous definition is more practical. Under this scenario, it is more appropriate to think of recovery as being complete when the community in a disturbed area exhibits variation that is within the range of variation seen in communities from undisturbed, control areas (Boesch et al., 1987). Using this definition, the time to recovery can" provide an important direct measure of the severity of a disturbance.

Connell and Keough (1985) conclude that given a knowledge of disturbance regimes and the sizes and types of patches produced, general predictions can be made about the types of organisms likely to predominate in the recovery/ recolonization process. However, as more detailed information is available on species and community level responses and life history traits, this will enable predictive/probabilistic models to be improved substantially. In particular, even general models of subtidal hard substrate community structure are limited by the paucity of data on community dynamics (Witman, 1987).

An important goal of this report is to summarize relevant studies and current ecological theory on recovery and recolonization of subtidal hard substrate communities. However, to be most applicable to MMS decisionmaking needs for potential oil and gas development, this information must be related, to the extent practical, to the types of species, communities, and disturbances (natural and anthropogenic) that are characteristic of the California OCS. To accomplish this, subsequent chapters characterize these hard substrate habitats in terms of the types of disturbances and resultant patch sizes and types that are known or predicted. This information then is integrated with information on life history traits and strategies of associated organisms to assess/predict their potential for recovery and recolonization. Finally, data gaps on the above topics, which are significant for the great majority of deep water hard substrate taxa, are summarized; and suggested studies and recommendations are presented. The following chapter expands upon the ecological theories and models to provide a framework against which the hard substrate communities of the California OCS can be evaluated.

CHAPTER 2. ECOLOGICAL THEORY ON RECOVERY/RECOLONIZATION

Numerous empirically based models have been developed to describe the processes which occur during the recovery and recolonization of hard substrate communities. Most of the data used to formulate these models are from studies conducted in the intertidal, primarily because it is relatively accessible for study. However, the applicability of these theories and models to deeper subtidal habitats is important to assess since there is some evidence that processes on subtidal hard substrates may be somewhat different (Connell and Keough, 1985; Dayton, 1984).

Six factors appear to influence the recovery/recolonization process in marine systems: (1) the type and size of the patch; (2) seasonal fluctuations in abundances of propagules; (3) water movement (including boundary layer flow and currents and storm surge) ; (4) selectivity of propagules for substratum characteristics during settlement; (5) biological interactions occurring among the organisms colonizing patches; and (6) frequency of disturbances of the substratum. These six factors are reviewed in Section 2.1, with particular emphasis on benthic macroinvertebrate communities. A summary of key theories and processes is presented in Section 2.2. In subsequent chapters these theories are related to deep water, hard substrate communities, particularly those of the California OCS.

2.1 FACTORS INFLUENCING RECOVERY/RECOLONIZATION

2.1.1 Type and Size of Patch

The type of patch created by a disturbance will affect significantly the mode of recolonization. Sousa (1985) and Connell and Keough (1985) distinguished Type 1 and Type 2 patches. Type 1 patches are those that are created within a larger, occupied site; they are surrounded by an "undisturbed" community. Type 2 patches are isolated from occupied sites; generally, they are larger than Type 1 patches and are created by large-scale disturbances. An example of a Type 1 patch is a portion of a subtidal hard bottom community that is damaged by anchor dragging. A Type 2 patch could result from the uncovering of a patch reef that previously was disturbed (covered) by encroachment of bottom sediments, or from the overturning of a boulder (e.g. , by an anchor or storm).

Organisms living on hard substrates employ three basic mechanisms for colonizing new surfaces: (1) release of planktonic propagules which have the potential for long-range or short-range dispersal, (2) vegetative growth along the margins of colonial species, or (3) immigration by adults of forms which have some mobility (e.g. , certain species of anemones and crinoids).

Edge effects, may be particularly important. A useful measure of the "edge" is the ratio of the perimeter of the patch to its area. For patches with a large ratio, recolonization by lateral movement of adults or vegetative growth will be relatively more important than for patches with a small ratio. Furthermore, larger Type 1 patches will be more effectively colonized by colonial forms with indeterminate growth patterns (e.g., encrusting sponges and ectoprocts). Colonial forms can exert a strong influence on recolonization and recovery of Type 1 patches. They can do this by rapidly filling in space (usually by asexual reproduction or short-lived larvae), by preying on propagules of other species attempting to settle from the plankton, or by modifying various physical parameters of the patch, such as patterns of water flow and sedimentation.

Type 2 patches generally are colonized most effectively by planktonic propagules. Therefore, for Type 2 patches water currents and boundary layer flow structure, availability of propagules from the plankton, and processes affecting settlement behavior become more important. However, long-range recolonization by adults of some species such as the anemone Metridium (Wahl, 1985) also may be important.

2.1.2 Availability of Propagules in the Plankton

The species and abundance of propagules available as potential colonists will depend on the reproductive rates and spawning seasons of the adult source populations, large-scale patterns of water flow which disperse propagules or concentrate them in different habitats, and conditions in the plankton such as food supply and predation by planktivorous fish and invertebrates. These factors result in strong seasonal differences in propagule availability (e.g., Peckol and Searles, 1983). While all these factors may be important, they have not been examined in as much detail as processes affecting settlement and recruitment after the propagules have arrived in a cleared patch.

The inclusion of all processes operating on propagules while in the plankton into a "black box" arises at least in part from logistical difficulties. At this time, a thorough understanding of the causes of the differences of numbers of recruits from site to site and year to year is lacking (Connell, 1985). Underwood and Denley (1984) have expressed the opinion that the vagaries of propagule supply are at the root of the "considerable variations in intensity and outcome of processes" in rocky intertidal communities. Seasonal differences in the availability of propagules from potential colonizing species can have a dramatic effect on the succession of intertidal patches cleared at different times of the year (e.g., reviewed in Foster et al., 1986; Kinnetics, et al., 1986). These factors and post-settlement events including biological interactions (e.g., competition and predation), and the frequency and type of additional disturbance define the recovery/recolonization pattern of a patch. Similar mechanisms would be expected to influence strongly the successional patterns of subtidal hard bottom communities.

Although communities generally are recognized as being comprised of a mosaic of patches, there are common or repeated species and characteristics that allow us to define community types within a geographic range and, in many instances, zones of species or assemblages which occur over a specified depth range. Patterns of zonation are evident in rocky intertidal and temperate subtidal hard bottom communities (Witman, 1987). Although numerous studies (e.g. , Connell, 1961, Dayton, 1971 ; and Denley and Underwood, 1979) have defined many of the physical and biological factors that determine zonation in the intertidal, little is known of the subtidal mechanisms (Witman, 1987), particularly for deep water hard bottom communities.

2.1.3 Water Movement

Water movement, including boundary layer flow and larger scale effects from currents and storm surge, can have a significant effect on the settlement and recruitment of larvae and the distribution of adult populations of hard substrate organisms. Boundary layer flow refers to the region of reduced flow near the surface of a solid object (e.g., a rock or an organism) in moving fluid. The boundary layer forms because of friction. This frictional drag is passed on to the next layer of the flow, slowing it from the free-stream velocity, or subsequent flow layers. The velocity gradient which results from the frictional loss of energy in the boundary layer generates shear forces whose magnitudes depend on the magnitude of the velocity gradient. These shear forces may have important consequences on the settlement success of propagules attempting to attach to the surface. Crisp (1955) was one of the first to recognize the subtle processes of boundary layer flow and conducted a series of classic experiments showing that optimal boundary layer conditions existed for maximal settlement of barnacle cyprids. If flow and shear stress in the boundary layer was too high or too low, settlement was reduced.

Many of the data on settlement and recruitment patterns of hard-substrate organisms have come from field experiments utilizing artificially created patches on natural substrates or settling plates. While the value of controlled experimentation is well known (e.g., Connell, 1975; Paine, 1977), the renewed appreciation of boundary layer flow processes requires that we examine critically the results of previous experimental investigations of recolonization and plan new experimental designs appropriately. An example of the importance of boundary layers is presented in Keen (1987), in which she showed that settlement patterns of a scyphozoan larva depended on the position on the surface of settling plates. The central areas of the plates had the highest abundances, which can be explained by considering the growth of organisms on a surface immersed in a flow. As the organisms grow from the leading edge of the surface, shear stresses within the boundary layer will decrease. Given Crisp's (1955) early studies of settlement in barnacle cyprids, it is predictable that the propagules of different species may have different preferences for settlement sites in relation to the structure of flow in the boundary layer.

Organism growth effects on boundary layers may also offer at least a partial explanation for the effects of patch size on recolonization and recovery processes (e.g., Osman, 1977; Sousa, 1985). The traditional explanation has been that large patches will be expected to receive a greater proportion of available propagules, and this will lead to differences in the species composition of the initial colonists and differences in the community during recovery. An alternative explanation for the patch size phenomenon is that the structure of the boundary layer will also differ for patches of different sizes.

In addition to boundary layer effects on larval recruitment, numerous studies have documented the effects of water motion including currents and storm surge on the distribution and survival of adult populations (Grigg, 1977; Sartori, 1980; Koehl, 1977; Lissner, 1983; Witman and Suchanek, 1984; and Witman, 1987). Extreme water flows can dislodge adults, affect predation and grazing (Kitching et al., 1966), and enhance the feeding of filter feeding organisms such as gorgonians. The California OCS region, particularly off the northern and central coast, experiences episodes of strong bottom currents in excess of one knot (SAIC, 1986; present November/December 1987 survey). The effects of these types of flows on adult and larval forms in the region has not been measured directly; however, it is likely to be a significant factor influencing settlement, feeding, and potential disturbance from the movement of bottom sediments.

2.1.4 Processes Affecting Larval Settlement Behavior

Initial settlement rates vary considerably in space and time (Connell, 1985) Settlement is less often measured than recruitment since settling propagules are typically very . small in size and would need to be censused frequently at the appropriate spatial scale to avoid missing those which settle out but then become detached or die. It is generally much easier to quantify the abundances of organisms after they have reached a larger size. The disadvantages are that the time factor is less well constrained and that no information is provided either on the bottlenecks at the planktonic/benthic transition or on the differences between settlement and post-settlement factors affecting the development of the community (see Figures 1-2 and 1-3).

Numerous studies (e.g., reviewed by Crisp, 1974; Scheltema, 1974) on the behavior of larvae in the laboratory showed a high degree of choice among microsites on the substrate. The larvae of hard-substrate epifauna have a variety of sensory organs to aid them in finding the appropriate habitat in which to settle. Larvae react to cues such as light direction, light intensity, gravity, exposure to water flow, surface contact, texture and contour of the surface, pressure, and chemical substances released by adults of the same species or other organisms such as bacteria and algae (Crisp, 1974).

Settlement rates also are affected by surface texture. Generally, larvae settle more readily on rough surfaces. Irregularities and surface contour affect settlement of both hard substrate (Crisp, 1974) and soft substrate (Eckman, 1979; Gallagher, et al., 1983) benthic larvae. “Texture”, “roughness”, and “irregularities” are largely subjective terms that usually are not defined in a marine r that would permit their incorporation into models of recolonization of patches, but their potential importance has been shown in many laboratory and field studies. One approach that may prove important is to express these terms in the context of a roughness Reynolds number, which might provide a quantitative basis for describing settlement as a function of the small-scale spatial structures on surfaces.

Larvae also respond to surface films and chemical cues (Raimondi, 1988). In seawater, inert surfaces adsorb high molecular weight dissolved compounds and become rapidly colonized by bacteria (e.g., Kirchman et al., 1982). Most invertebrate larvae settle more rapidly on such “filmed” surfaces. The extracellular products of the bacteria may be more important as a settling cue than the bacteria themselves. Chemical settlement cues also are produced by adults of some species (e.g., Crisp, 1974). These chemical cues lead to gregarious settlement patterns, which can be advantageous for reproductive purposes of sessile organisms. The disruption of surface films or elimination of chemical cues from adults that could result from disturbance thus may affect the rates of recolonization of patches. Of added importance, especially from the perspective of oil and gas exploration and development, is whether the presence of high molecular-weight aromatic hydrocarbons or metals in drilling muds might affect the ability of propagules to perceive surface-associated chemical cues important for their settlement success. Interference from petroleum hydrocarbon exposure with chemoreception by larvae and the potential effects on behavior, including settlement, is suggested by Blumer (1969) and the National Academy of Sciences (1985). However, many potential effects should be moderated significantly in deep water habitats due to the small percentage (e.g., < 5%)

which is estimated to reach the bottom from most spills (Boehm et al. , 1982), Potential hydrocarbon effects are discussed in greater detail in Section 3.3.

2.1.5 Post Settlement Processes Within Patches

After propagules have settled on a substratum, a variety of biological and physical processes can affect the further development of the community. A useful framework in which to discuss these processes are the successional models of Connell and Slatyer (1977), as summarized in Figure 1-3. All the models assume that early colonists modify the environment so that it is unsuitable for continued recruitment of their own species. This assumption would not hold for colonial forms colonizing vegetatively, but may be true for planktonic propagules in some cases. The succession models make different predictions about how community structure changes with time. In the facilitation model, later colonists can only recruit successfully after the early colonists have suitably modified the environmental conditions. In the tolerance model, environmental modifications by the early colonists have no effect on the recruitment of later colonists. Later colonists are species which may have been present initially but grow slowly, so that their presence is only obvious after some time has elapsed, or they may have arrived later. The sequence of species in the tolerance model is controlled by their life history characteristics. Later colonists can recruit successfully because they can tolerate lower levels of resources (e.g., space and food availability) than early colonists. In the inhibition model, later colonists cannot recruit while the early colonists are present. The later colonists appear in the community ' as succession proceeds" due to their longer life spans, allowing them to build up their populations as the early colonists die off. Both the size and type of patch will be important in determining the primary model that is followed.

Another distinction among the models is the cause of death of the early colonists . In the facilitation and tolerance models they are outcompeted by the later colonists. Competition for space among hard substrate organisms can be manifested as the overgrowth, undercutting, or crushing of one species by another, or chemical interactions (Sebens, 1986). However, as reviewed in Sebens (1986) the overall patterns of recovery and recolonization are a complex product of competition, other biological interactions including predation (e.g., Paine and Vadas, 1969; Dayton, 1971; Menge, 1976; Lubchenco, 1978), and physical disturbance (e.g., Paine and Levin, 1981), as well as random and non-random events associated with larval selectivity and availability. In the inhibition model, the early colonists die naturally or because they are susceptible to predation or localized physical disturbances, such as can result from adverse effects of water motion (discussed in Section 2.1.3) including sediment movement/encroachment.

Evidence for the facilitation model comes largely from those studies (e.g. , Sheer, 1945; Kirchman et al., 1982) showing that surfaces must be conditioned, often by microbial films, before recolonization proceeds. Other studies have documented secondary settlement on biogenic structures provided by early colonists (e.g., Bayne, 1965; Seed, 1969) . In light of recent studies on soft substrate communities that facilitation may be mediated by biogenous structures (Eckman, 1979; Gallagher, et al., 1983), and the developing methodology for quantifying boundary layer processes (Newell and Jumars, 1984), the relative role of facilitation via alterations of boundary layer flows by early colonists in the succession of hard substrate communities may need reassessment. Notable in this respect is the study of Okamura (1985), in which the feeding rate of colonies of an encrusting bryozoan was enhanced when actively feeding colonies were located upstream. This example demonstrates that post-recruitment mortality can be influenced by feeding ability.

However, despite some evidence for the facilitation model, many species which colonize hard substrates appear to inhibit colonization by other species. Early colonists can inhibit the recruitment of later colonists by preempting space, by feeding on or killing propagules as they invade from the plankton, and by altering the local physical environment. All of these inhibitory influences are expected to be maximal in small Type 1 patches, particularly when the surrounding community is composed mainly of species with indeterminate growth (e.g., sheet and moundlike sponges that are able to extend quickly into the disturbed patch; Connell and Keough, 1985). Studies based on development of communities on settling plates, which mimic Type 2 patches on a small scale, also indicate that inhibition is a major structuring mechanism during recolonization and recovery. Dean and Hurd (1980) presented evidence for both facilitation and inhibition during the development of an estuarine fouling community, but inhibition was much more prevalent. Sousa (1979) found that all species of algae in the rocky intertidal habitat he studied inhibited the invasion of other species. Grosberg (1981) demonstrated that settling larvae of a variety of species avoided substrates that were already colonized by the juveniles of a competitively dominant ascidian; these results imply that some larvae can distinguish and avoid substrates where post-settlement processes would be unfavorable.

2.1.6 Frequency of Disturbances

Successional sequences can be interrupted by further disturbances, therefore the frequency of disturbances is an integral component of models of recolonization and recovery (e.g. , Paine and Levin, 1981; Sousa, 1984). In these models the disturbances do not represent fundamental changes in the physical nature of the habitat, but rather the loss of existing organisms from the substrate. The frequency of disturbance also determines whether the effects of the disturbance will result in the natural selection of adaptive responses within the population. In general, if 1/(frequency of disturbance) is less than the generation time of a species, then individuals of that species will on average experience a disturbance during their lifetime. There is evidence that the life histories of some species have evolved to take advantage of predictable disturbances (e.g., Paine, 1979; Suchanek, 1981). Conversely, if I\(frequency of disturbance) is greater than the generation time of a species, then populations will not show an adaptive response. Disturbances in this case constitute catastrophic events that result in acute changes in population structure and dynamics, but do not cause directed changes in the genome.

The frequency of disturbances also will affect within-patch dynamics, especially the species diversity of the community in a patch (Paine and Levin, 1981) . Diversity can be used as one measure of the recovery stage of a community. There are many definitions and formulae of species diversity, but the common denominator is that diversity expresses both the numbers of species present in a community (species richness) and the evenness with which individuals are distributed among all the species (Hurlbert, 1971). According to the intermediate disturbance hypothesis (e.g., Connell, 1978; Sousa, 1979), intermediate frequencies of disturbance will lead to the highest diversity in a community. The reasoning is that if disturbances are too frequent, only good colonizers will have the ability to persist in the environment and diversity will be low. At very low frequencies of disturbance, diversity will also be low because one or a few competitively dominant species will take over all available space (e.g., Paine, 1966, 1974; Connell, 1978). Intermediate frequencies of disturbance prevent competitive monopolization by one or a few species and maintain the greatest diversity in the community.

In an important extension of the intermediate disturbance hypothesis, Huston (1979) suggested that a more practical approach to the question of diversity was to compare the rates at which differences in the competitive abilities of species were expressed, rather than the competitive abilities per se. Even though one species in the assemblage potentially may be the superior competitor, that species will be slower to emerge as the dominant if the population sizes of all competing species also are increasing slowly. Conversely, a marginally superior species will dominate more quickly if all species are increasing rapidly. If competitive equilibrium is prevented by disturbances, then diversity among the competitors will be affected by the rate of competitive displacement, which in turn is related to the growth rates of the competing species. Thus, Huston (1979) combined the intermediate disturbance hypothesis with the concept of rate of competitive displacement to explain how diversity varied in communities. Both physical and biological parameters are directly included in the model.

These models of how the diversity of the community changes in response to disturbance assume that the outcomes of competitive interactions are consistent and asymmetrical, that is, one of the pair of competing species always wins. Based on the results of studies on rocky intertidal communities, this appears to be a reasonable assumption. However, in subtidal hard substrate environments there appears to be an unusually high incidence of symmetrical competitive interactions among colonial organisms; an average of 50% of the competitive interactions listed by Connell and Keough (1985; Table 5) are symmetrical. Therefore, diversity may not decline with time following the creation of a patch, and in the absence of further disturbance, to the same extent it does in intertidal habitats. In these subtidal areas, succession would not lead to the predictable equilibrium communities that are the final step in the models of Connell and Slatyer (1977). Peckol and Searles (1983) also suggested that, in comparison to the rocky intertidal, processes regulating community composition in the subtidal do not always act in a predictable fashion. This lack of consistent patterns of community development has been attributed to seasonal patterns of dispersal of propagules, recruitment, and survival. While these are certainly reasonable explanations, the symmetry of competitive interactions found in subtidal organisms represents an additional explanation. At this time, however, there is little information available to test these theories.

2.2 SUMMARY OF ECOLOGICAL THEORIES AND MODELS RELATED TO OCS HARD SUBSTRATE COMMUNITIES

This section provides a summary of theories and models presented in Section 2.1, with particular reference to California OCS communities. Key elements are summarized in Figures 2-1 and 2-2, which present a hypothetical sequence of disturbance and subsequent recovery and recolonization of two common community types , associated with high relief and low relief hard substrate features (e.g., SAIC, 1986), . of the California OCS. These figures are not exhaustive "models", but draw together earlier (Chapter 2) conclusions with information on general life history strategies of hard substrate organisms (Chapter 4).

Working definitions of key terms as applied in this report include:

Low relief, hard substrate	0 to 1 m of vertical relief above adjacent soft substrate
High relief, hard substrate	> 1 m of vertical relief above adjacent soft substrate
Short-lived (organisms)	zero to one year
Moderate life span (organisms)	> one to five years
Long-lived (organisms)	> five years
Fast growth (to sexual maturity)/recovery	< one year
Moderate growth (to sexual maturity)/ recovery	one to five years
Slow growth (to sexual maturity)/recovery	> five years

Figure 2-1 represents a high relief (> 1 m) hard substrate community that has been disturbed by anchor dragging. The community is comprised of a complex association of long-lived, slow growing, vasiform sponges; encrusting sponges, bryozoans, and urochordates; relatively long lived anemones and cup corals with short- lived (short dispersal) larvae; fast growing, "opportunistic" taxa with long- lived (long dispersal) larvae such as hydroids and erect bryozoans; and motile predators/scavengers such as sea stars and some ophiuroids with long-lived larvae. The disturbance from anchor dragging is assumed to have produced a Type 1 patch in the middle of the community, and resulted in the removal of some individuals of each species type. Recolonization of this type 1 patch will be a product of numerous factors including:

- Vegetative growth by species (e.g., encrusting sponges) that were outside of the margin of disturbance, (this re-growth can be initiated quickly and will be largely dependent on growth rates);
- Asexual reproduction (such as budding off of new individuals) by species (e.g., some anemones) that were outside of the margin of disturbance (may be initiated quickly);
- Settlement of larvae from opportunistic, fast growing species (species and settlement rates will be determined by larval availability and selectivity) ;

- Settlement of short-lived larvae from adjacent undisturbed areas (species and settlement rates also will be determined by larval availability and selectivity);

- Settlement of long-lived larvae (e.g., from distant source populations) from slower growing species such as vase sponges and sea stars (species and settlement rates also will be dependent on larval availability and selectivity); and

- Immigration of motile adults from adjacent undisturbed areas (rates will be influenced by feeding/foraging habits and food availability).

Post-settlement recolonization and recovery processes will be influenced by numerous biological interactions, particularly as related to inhibitory influences (e.g., direct or chemical aggression) whereby later colonists are inhibited by the activities of early colonists. This result appears to be particularly likely in a Type 1 patch where regrowth from the margins can be accomplished by early colonists such as encrusting sponges (including sheet-like and mound-like forms). Interactions , such as those defined by the facilitation and tolerance models where early colonists are outcompeted by later colonists , probably are less likely to be the primary methods of succession. However, this needs to confirmed by additional direct experimentation. In the absence of additional disturbance, recovery of the community will be a complex response determined by the outcome of biological interactions and their influence on growth rates of individual organisms. Insufficient information exists to make detailed predictions concerning the overall time to recovery. However, minimum recovery times can be estimated for key taxa based on growth rates from laboratory and field studies. In general, slower growing, longer lived taxa, such as some vase sponges, may require years to decades to achieve regrowth, particularly for species with low natural densities and long-lived larvae. Taxa such as some anemones which are relatively slow growing, but which may have nearby source populations for larvae, may require a few years, while adults of other slow growing but motile organisms (e.g. , seastars) may recolonize an area almost immediately via immigration. Finally, fast growing, opportunistic taxa may colonize the area almost immediately to days to months depending on larval availability. Therefore, complete recovery, in terms of replacement of most taxa may require many years to achieve. However, if the recovery is viewed as the time required for a disturbed community to exhibit variation (diversity) that is within the bounds of variation seen in undisturbed, control areas (e.g., Boesch et al., 1987), the complete replacement of each species, particularly rare species, may not be a practical endpoint. Under this scenario, communities would require relatively shorter times for "recovery". The appropriateness of this moderate definition of recovery to impact assessment and decisionmaking by MMS will need to be addressed by further experimental studies.

Figure 2-2 represents an isolated, low relief (≤ 1 m) hard substrate area that has been uncovered following previous sediment encroachment. This area represents a typical Type 2 patch that is characteristic of many hard substrate features of the central and northern California OCS (e.g., SAIC, 1986; present November/ December 1987 survey). The normal community is comprised of fast growing, opportunistic taxa with long-lived (long dispersal) larvae such as

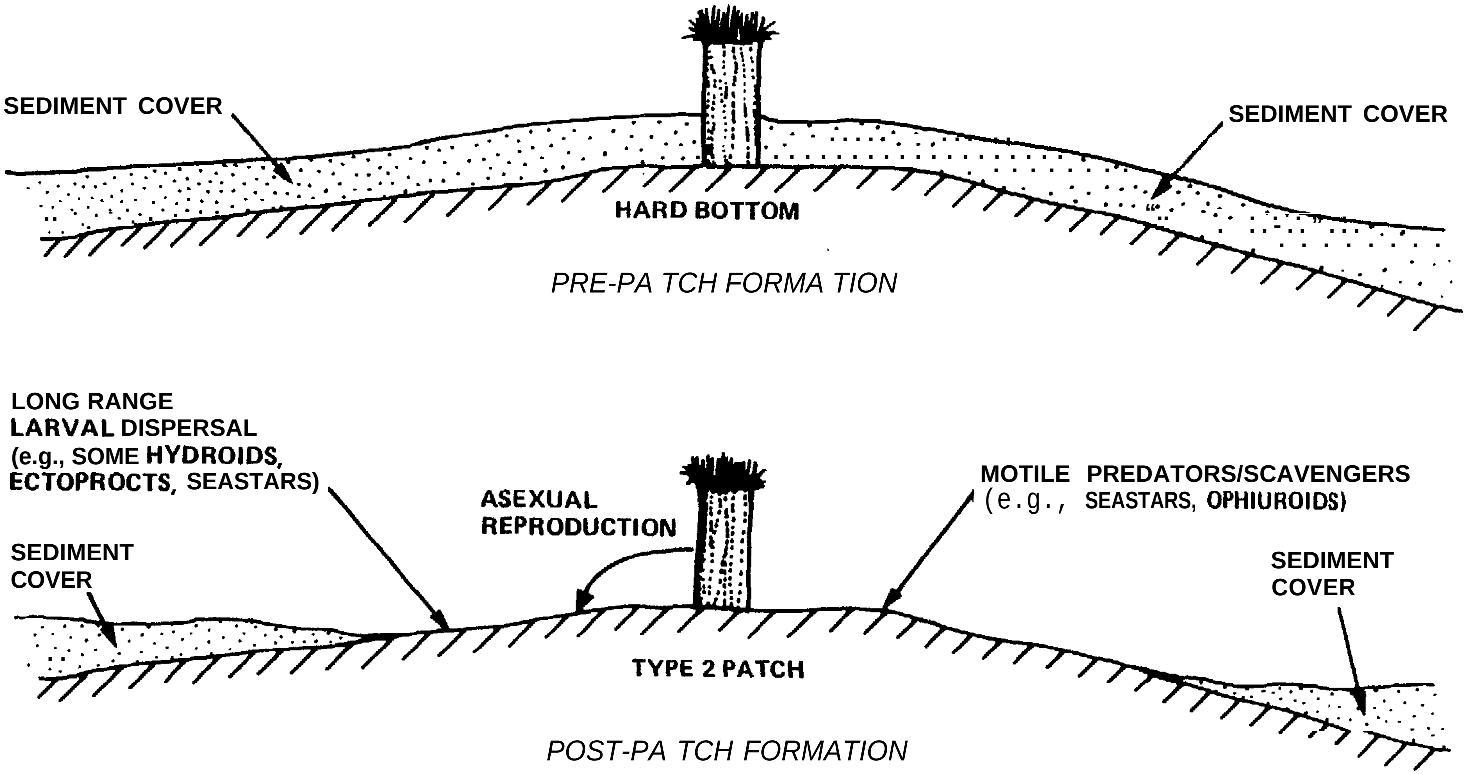

FIGURE 2-2. EXAMPLE OF HYPOTHETICAL RECOVERY AND RECOLONIZATION OF A TYPE 2 PATCH CREATED BY THE UNCOVERING OF AN OUTCROP THAT PERIODICALLY IS DISTURBED BY SEDIMENT BURIAL: LOW RELIEF HARD SUBSTRATE COMMUNITY OF THE CALIFORNIA OCS

disturbances will have a significant effect on the recovery and recolonization process (e.g., Sebens, 1986). Understanding the nature and potential occurrence of different disturbances is therefore critical to studying/predicting the responses of the communities to these changes. The following chapter addresses some sources of disturbances that are likely to be significant to the hard substrate communities of the California OCS, with particular emphasis on anchoring disturbances and potential effects from sediment encroachment/ increased turbidity.

CHAPTER 3. SOURCES OF DISTURBANCE

This chapter reviews potential sources of disturbance to hard substrate communities of the outer continental shelf, with an emphasis on anchoring impacts and effects of sedimentation including sediment encroachment and increased turbidity. A variety of physical and biological mechanisms can create disturbances that result in open spaces along the hard substrate. These open spaces may range from millimeters (e.g., due to grazing and elimination of individual organisms) to kilometers (e.g., due to burial of large, low relief outcrops by sediments) . However, in order to provide information that is most relevant to oil- and gas-related assessments, which can be addressed practically by experimental field studies, this discussion focuses on physical disturbances (anchoring and sedimentation) that may create spaces on the scale of meters to kilometers, generally Type 1 and Type 2 patches (see Chapter 2).

Discussions of anchoring and sedimentation effects are presented in Sections 3.1 and 3.2, respectively. Effects such as patch formation from chemical contaminants (petroleum hydrocarbons and trace metals) associated with some oil and gas activities generally do not produce large-scale disturbances to deep water communities. Those effects which might occur typically are more widespread for hydrocarbons (e.g. , produced from blowouts or subsurface seeps) than for trace metals. An extensive review of toxicity effects, particularly from drilling muds and cuttings, is provided in Neff (1987). A summary of potential hydrocarbon effects on deep water hard substrate communities is presented in Section 3.3.

Anchoring impacts can be a direct result of oil and gas exploration and development activities. Impacts from anchoring include the disruption (e.g., breakage and dislodgement) of organisms and the hard substrate. Such impacts do not have any common parallels among those caused by natural disturbances, although some fishing activities such as trawling and dredging may cause disturbance of soft substrate '(e.g., Butman et al. , 1988) and hard substrate habitats, In contrast, impacts from sedimentation can occur naturally or can be due to human activities including disposal of drilling muds and cuttings and dredged material. However, in addition to direct effects of sedimentation, such as burial and smothering of some organisms, which may be similar for both natural and anthropogenic inputs (Cimberg et al., 1981), there can be additional concern for chronic toxicity to organisms from discharge of contaminated sediments. Adequate knowledge of natural disturbances and the role they play in structuring biological communities is critical to distinguish these potential impacts from man-induced disturbances.

There is conclusive evidence from studies conducted in a wide range of environments that natural disturbances play a major role in structuring biological communities. Study areas have included temperate forests (Sprugel, 1976; Sprugel and Bormann, 1981; Heinselman, 1981; Henry and Swan, 1974), tropical forests (Connell, 1978, 1979; Eggeling, 1947; Jones, 1956), tropical coral reefs (Connell, 1978), and temperate freshwater habitats (McAuliffe, 1984; Siegfried and Knight, 1977) . The evidence is particularly compelling for marine communities on rocky intertidal substrates (e.g. Dayton, 1971; Connell, 1978; Paine and Levin, 1981; Sousa, 1979; Taylor and Littler, 1982; Seapy and Littler, 1982; Dethier, 1984; for reviews see Sousa, 1984, 1985; and Connell and Keough, 1985), and shallow subtidal hard bottom areas (Foster, 1982; Dayton severity. Bottom-scarring patterns from oil and gas activities (e.g., anchoring) in some developed areas off California can be observed in sonar records (Lissner and Benech, pers. ohs.), and apparent dragging patterns from fishing activities also have been observed over broad areas of the shelf (Butman et al., 1988).

The significance of these effects on a biological community will depend on the severity and the frequency of the disturbance; continued disturbance from physical (or biological) factors can delay the recovery process "indefinitely at an intermediate stage" (Sebens, 1986). Boesch et al., 1987 summarize that general recovery of soft substrate communities from small-scale disturbances can range from weeks, in shallow water temperate areas, to years in deeper water shelf and slope environments. Hard substrate communities, particularly those which include many slow-growing species, are expected to require several years (see Chapter 2 Summary and Chapter 4 discussion). Assuming only a single disturbance event, the types of impacts that might result from anchor dragging through a hard substrate community are crushing and dislodgement of organisms and breakage/overturning of the substrate. This disturbance generally will produce a Type 1 patch (see Chapter 2; e.g., Figure 2-1) in which the space or patch that is created by the removal of organisms or overturning of rocks is located within a larger, undisturbed site. Recolonization and recovery of this patch will occur based on the outcome of numerous biological and physical processes, including larval availability and selectivity, and competitive interactions as summarized in Figures 1-1 and 1-2 and Chapter 2.

Several studies have documented that significant damage to hard substrate communities can result from anchoring activities, although none of these represented a closely controlled experimental design with long-term monitoring of before versus after impact conditions. For example, studies conducted on the Flower Garden Banks (Gulf of Mexico) by Texas A & M University (1976, 1979, 1981) and the Southwest Florida shelf by Environmental Science and Engineering, Inc. et al. (1987) suggested that anchoring effects, particularly from small boat traffic, can have a significant impact on shallow water hard substrate communities. In these examples, particular concern was expressed for slow-growing, long-lived species such as some sponges and corals. Environmental Science and Engineering, Inc. et al. (1987) further suggested that effects last longer in areas of higher relief areas due to the greater diversity of the communities found in such areas. Texas A & M (1981) documented two anchoring events by oil tankers on the East Flower Garden, and although no postevent sampling was conducted, based on qualitative observations they surmised that substantial damage occurred to the reef community. Studies by Ecomar (1978) on Tanner Bank (southern California) probably represent the most direct observational surveys of before-versus-after anchoring effects. They concluded that anchor and chain damage to the hard substrate community from an exploratory drilling platform was relatively minor and caused damage to less than 0.02% of the area encompassed by the anchoring system. However, at areas directly impacted by the anchors and the lower portion of the anchor chain, there was significant, although localized, damage that included crushing of rock substrate and the associated organisms (Ecomar, 1978; S. Benech, pers. comm.) The greatest potential for additional damage from these types of anchoring operations would occur from anchor and chain dragging associated with anchor slippage or multiple attempted sets of an anchor. Anchor slippage and dragging appears to be more common in low relief hard substrate areas because the anchor cannot dig into or "hang-up" on the bottom as readily as on soft sediments or high relief areas, respectively (S. Benech, pers. comm.).

It is expected that some abrasion and breakage would occur to hard substrate communities that are located within anchoring or dragging paths, although the specific nature of the damage and the time to recovery probably will vary substantially from site to site. Experimental studies that simulate anchoring impacts through the partial removal (e.g., scraping) of the community and then follow the recovery process would allow specific conclusions to be made in selected habitat types; however, these types of studies have not been conducted to date. Suggestions for studies that could be performed in deep water hard substrate areas are presented in Chapter 5.

3.2 SEDIMENTATION EFFECTS

Sedimentation effects on deep water communities can result from natural sources such as the movement and encroachment of sediments due to bottom currents (e.g., Environmental Science and Engineering, Inc. and LGL Research Associates, 1986; Hollister et al., 1984) or increased turbidity (e.g., Texas A & M, 1981). Effects of sediment encroachment can include burial and smothering of hard substrate organisms and destruction of the habitat. Increased turbidity can cause reduced feeding efficiency and clogging of filter-feeding structures and can also decrease success of larval settlement (e.g., Grigg, 1975; Benech et al., 1980; Sartori, 1980). The disposal of drilling muds and cuttings potentially may have similar," although much more localized, impacts; but they may be associated with chronic toxicity effects on marine organisms (e.g. , Neff, 1987; Butman et al., 1988).

The scale of potential sedimentation effects is a primary factor that appears to distinguish natural from anthropogenic sources. Natural movements of large quantities of bottom sediments which periodically cover and uncover broad, low relief hard substrate areas of the Southwest Florida shelf are documented in Environmental Science and Engineering, Inc. and LGL Research Associates (1986) and Continental Shelf Associates (1987). A primary mechanism for this sediment movement appears to be episodic storms. Although these studies were conducted at relatively shallow shelf depths (generally < 50 m), there appears to be a striking parallel between these results and general impressions of the effects of sedimentation on low relief hard substrate communities of the California OCS (SAIC, 1986; present November/December 1987 survey). Large, sessile invertebrates including sponges, gorgonians, and corals have been observed projecting through sediment layers in the Southwest Florida studies; while large anemones and some gorgonians and sponges similarly have been observed on many low relief outcrops off the coast of California. In both examples a presumed explanation for these occurrences is that the organisms first settled during a period when the hard substrate was exposed, then grew to a sufficient size to resist burial, and persisted when sediment encroachment occurred. Direct evidence of sediment encroachment in the deep water hard substrate areas has yet to be demonstrated; however, there are numerous examples of strong bottom currents (e.g., > 1 knot) and high levels of near-bottom turbidity at depths greater than '200 m (SAIC, 1986; present November/December 1987 survey). As a direct example of potential deep water sediment movement, Komar et al. (1972) noted sediment resuspension from extreme surface waves off the Oregon coast at depths as great as 204 m. Important data on the frequency of strong bottom currents, high-turbidity events, and potential examples of sediment encroachment on low relief outcrops may be obtained during subsequent years of the MMS California Monitoring Program (CAMP).

The space created by the retreat of sediments from a low relief outcrop is equivalent to a Type 2 patch in which the patch generally is isolated from colonized, undisturbed sites (e.g. , Figure 2-2) . In contrast to a Type 1 patch (such as may be created by anchor dragging and which is located within a larger, colonized site) recovery and recolonization of a Type 2 patch will rely more on larval recruitment and adult immigration than on vegetative growth or short range larval dispersal (see Chapter 2). However, recovery of the patch also will be determined by the result of numerous physical and biological interactions. Recovery, particularly in an environment typified by frequent disturbances (e.g., sediment encroachment), may be arrested at an intermediate stage (sensu Sebens, 1986) and might be characterized by species which are relatively tolerant of these conditions. However, drilling and discharge of muds and cuttings from multi-well production platforms may last several years.

In contrast to natural sources of sedimentation, the input of anthropogenic sources associated with oil and gas development are expected to be of relatively short duration (e.g., less than six months for platform installation) and much more localized in effect (reviewed in Neff, 1987). In general, the greatest potential impacts from burial or smothering of hard substrate organisms by drilling muds and cuttings would be in low-energy environments where the hard substrate feature was located within a few hundred meters of the discharge. In this example, the drill cuttings in particular could form a relatively resistant mound near the platform. Evidence from studies of these types of mounds indicates that a somewhat unique fauna, as compared with premound conditions, may develop that would be characterized by many motile predators such as sea stars and crabs (reviewed in Boesch and Robilliard, 1987). In higher energy environments the discharges are dispersed more broadly (e.g., a few thousand meters or more for drilling muds) with corresponding reduced effects on benthic communities. The presence of oil and gas platforms and mounds from the disposal of drill cuttings can have the effect of an artificial reef and may promote diverse, although localized, hard substrate communities (e.g., reviewed in MBC, 1987). Potential effects to deep water hard substrate communities as a result of discharges of drilling muds and cuttings would be reduced substantially by the siting of drilling activities at least several hundred meters from any outcrops (e.g., Boesch and Robilliard, 1987; Neff, 1987),

The potential for chronic toxicity effects to marine organisms from exposure to drilling muds is reviewed extensively in Neff (1987); however, information on effects to deep water hard substrate organisms is generally lacking. Important data on the effects to selected species will be available from the MMS California Monitoring Program.

3.3 HYDROCARBON EFFECTS

Chronic or episodic exposure of organisms to petroleum hydrocarbons represents a potential source of disturbance to benthic communities. Biological impacts, representing a wide variety of behavioral, toxicological, physiological, pathological, and genetic responses, have been observed near the sites of accidental oil spills, near sites of natural oil seeps, and from the results of laboratory and mesocosm experiments. However, much of the data on biological effects to benthic organisms pertain to soft substrate, shallow subtidal or intertidal species and communities; whereas, effects to deeper water benthic communities are more speculative. Biological responses to petroleum hydrocarbon exposure have been reviewed in detail and summarized by National Academy of Sciences (1985) and by Spies (1987). Information pertaining to deeper water benthic communities is discussed briefly in this section.

The relative lack of data for deeper water communities reflects the difficulty associated with studying these communities and the paucity of information needed to characterize natural variability. Potential effects to these communities will be moderated by changes (e.g., weathering) which occur to spilled oil during its transport to deeper benthic environments. Several mechanisms for transporting spilled hydrocarbons to deep offshore areas exist, including adsorption onto suspended particulate material, mixing of oil with nearshore sediments and its subsequent current-induced transport, ingestion of particulate oil by zooplankton and its incorporation into fast-sinking fecal pellets, and encrustation of weathered oil/tar particles by organisms (e.g., barnacles) which decreases buoyancy sufficiently to promote sinking (Jordan and Payne, 1980; Boehm, 1987). It is notable, however, that these mechanisms typically account for the removal and sedimentation of only a small fraction of the spilled oil. Thus, even for subsea releases of oil, such as the Ixtoc blowout, only a small percentage of the oil (e.g., < 5%) is estimated to impact the benthos (Boehm et al., 1982). Additionally, the relatively long time required to transport the oil to the deep subtidal areas suggests that significant physical/chemical weathering will occur, which acts to remove the more labile and toxic mono - and diaromatic compounds (Payne et al. , 1987). Discharges of relatively unweathered oil from subsurface seeps or discharges from municipal or industrial effluents, represent a greater potential for affecting deep water benthic communities. Regardless, it is evident that the extent of disturbances caused by hydrocarbon exposures are related to the amount as well as the composition (whole crude or refined product and the degree of weathering) of the hydrocarbon contaminants.

The concentration of the toxic hydrocarbon components, the duration of the exposure, the sensitivity of the affected species, and the stability of the community all determine the extent of the disturbance (Spies, 1987). However, Spies (1987) speculated that the magnitude of a disturbance to the benthic communities could be predicted based on the concentrations of the dissolved aromatic compounds present in the interstitial or bottom boundary layer waters. Areas with high hydrocarbon concentrations in interstitial waters are characterized by depauperate benthic communities; whereas, areas affected by hydrocarbon inputs but with low dissolved concentrations may represent enriched environments that support high species abundances, similar to a Pearson-Rosenberg response (Spies et al., 1987). This relationship appears to be valid for , communities existing near submarine seeps (Spies et al. , 1980), although too few data are available to extend the relationship to areas impacted by deposition of spilled or discharged oil.

A wide range in tolerances to hydrocarbon exposures is apparent between different phyla and different developmental life stages (National Academy of Sciences, 1985). In general, attached or sedentary organisms with low reproductive rates will exhibit more significant changes than species with higher fecundity and greater potential for larval dispersal (Mann and Clark, 1978). Based on population-level studies, many species including corals, bivalves, and decapods can exhibit marked, long-term (years) impacts from such disturbances; whereas, many annelids, gastropod, and copepods do not appear to exhibit long-term impacts. During previous studies under real or simulated spill conditions in subarctic environments, the echinoderms *Strongylocentrotus droebachiensis* and *Ophiopholis aculeata* exhibited some uptake of lower molecular weight aromatic hydrocarbons (Carstens and Sendstad, 1979), and the annelid *Acanthostephieia behrengiensis* did not recolonize sediments which had been experimentally oiled (Atlas et al., 1978). In tropical environments, exposures of hermatypic corals to chronic oiling have impacted reproductive systems negatively (Loya and Rinkevich, 1979). Too few data are available to extend these observations to temperate, deeper water communities. It has been suggested that intertidal communities are less susceptible to impacts than pelagic or offshore benthic communities, perhaps because intertidal organisms are better adapted than the subtidal benthos to varying degrees of environmental stress. Additionally, feeding modes may affect rates of hydrocarbon bioaccumulation (Roesijadi et al., 1978). Detrital feeders generally do not exhibit magnification of hydrocarbons when exposed to oiled sediments (Anderson and Malins, 1978). Infaunal suspension feeders may be more susceptible to uptake of hydrocarbons associated with interstitial waters as opposed to uptake of particulate hydrocarbons. Retention times for hydrocarbons in tissues depend on the presence of degradative enzymes and the chemical characteristics of the bioaccumulated compounds (e.g. , the degree of alkyl substitution and numbers of aromatic rings) . Data on the effects of spilled oil on shallow (e.g. , < 50 m depth) subtidal hard substrate communities are mostly observational and do not suggest significant impacts except in some cases (e.g. , Torrey Canyon spill) which involved the heavy use of dispersants (National Academy of Sciences, 1985). Potential effects on deep water hard substrate communities also are predicted to be relatively minor.

Effects of hydrocarbon exposure on behavioral responses are poorly understood, but they may be the most sensitive type of organism response (National Academy of Sciences, 1985). For example, some effects on larval settling, feeding, reproduction, and substrate recognition have been observed under laboratory conditions at concentrations as low as 10 parts per billion (National Academy of Sciences, 1985). However, under real spill conditions these effects to natural communities are difficult to distinguish from other related disturbances such as smothering, toxicity, and physical disturbances during oil cleanup,

In summary, a wide range of benthic community responses to petroleum hydrocarbon exposures have been reported. The recovery rates for affected communities will depend on the magnitude of contamination and the self-cleaning ability of the environment. However, even in a recolonized area, the composition of the community may exhibit some alterations from prespill conditions due to shifts in dominance which reflect tolerances to contaminants and larval dispersal and settling rates of potential colonists.

CHAPTER 4. STUDIES ON RECOVERY/RECOLONIZATION RATES AND PATTERNS

This chapter provides a review of selected literature on recovery and recolonization of hard substrate communities (Section 4.1) and integrates these studies with information on life history and recruitment strategies of representative benthic invertebrate taxa of the California OCS (Section 4.2). The focus of Section 4.1 is to address selected studies that provide empirical data on the mechanisms that influence recovery and recolonization and which are topically representative of the theories and models discussed in Chapter 2. The life history information discussed in Section 4.2 is based largely on a summarization of the extensive data presented in Table 4.1. Taxa are included in the table based on either their known occurrence in the California OCS communities or their potential similarity (in terms of life history characteristics) to California OCS taxa, and the availability of data. The list of taxa is not exhaustive and is intended only to provide representative information on the range of life history strategies expected for benthic invertebrates of this region.

4.1 SUMMARY OF SELECTED STUDIES ON RECOVERY/RECOLONIZATION

Responses of natural assemblages or communities to disturbances will depend on the nature of the disturbance, the types and sizes of patches that are created, and the importance of processes such as competition and predation. On one end of the disturbance spectrum are chronic, small disturbances such as grazing on part of a colonial organism that damages but does not kill the colony. Recovery from such disturbances are accomplished by regrowth and repair. As the intensity and severity of the disturbances increase to levels at which individuals or colonies are killed, recovery involves not only regrowth, but some form of recolonization,

The relative importance of growth, immigration, and recruitment in this process will depend on the area and severity of the disturbance and the nature of the patches created. In the case of Type 1 patches, recovery may be largely influenced by the composition of sessile species bordering the patch (e.g., Figures 2-1 and 4-1). For Type 2 patches, distance to source populations, substrate area, and height above soft substrates will be important features affecting rates of recolonization (e.g. , Figures 2-2 and 4-l). The recovery process in both Type 1 and Type 2 patches also will be influenced by local abundances of predators and scavengers, and by the kinds of species that contribute to the regional pool of planktonic propagules (Connell and Keough, 1985). The models, such as those on inhibition, facilitation, and tolerance (Figure 1-3), that define possible mechanisms of recovery/succession are general in nature; however, the testing of these assumptions through experimental studies may result in refined numerical models.

A variety of physical and biological mechanisms can produce patches of open space on hard substrates (e.g., Connell and Keough, 1985, Table 4). Physical mechanisms include turbulence from waves and currents and burial by sediment movement (Littler et al., 1983). In intertidal or shallow subtidal areas, storm waves can create patches by dislodging organisms from the substrate (Paine and Levin, 1981), crushing surfaces with water-borne objects such as logs (Dayton, 1971; Dethier, 1984), overturning moveable substrates such as

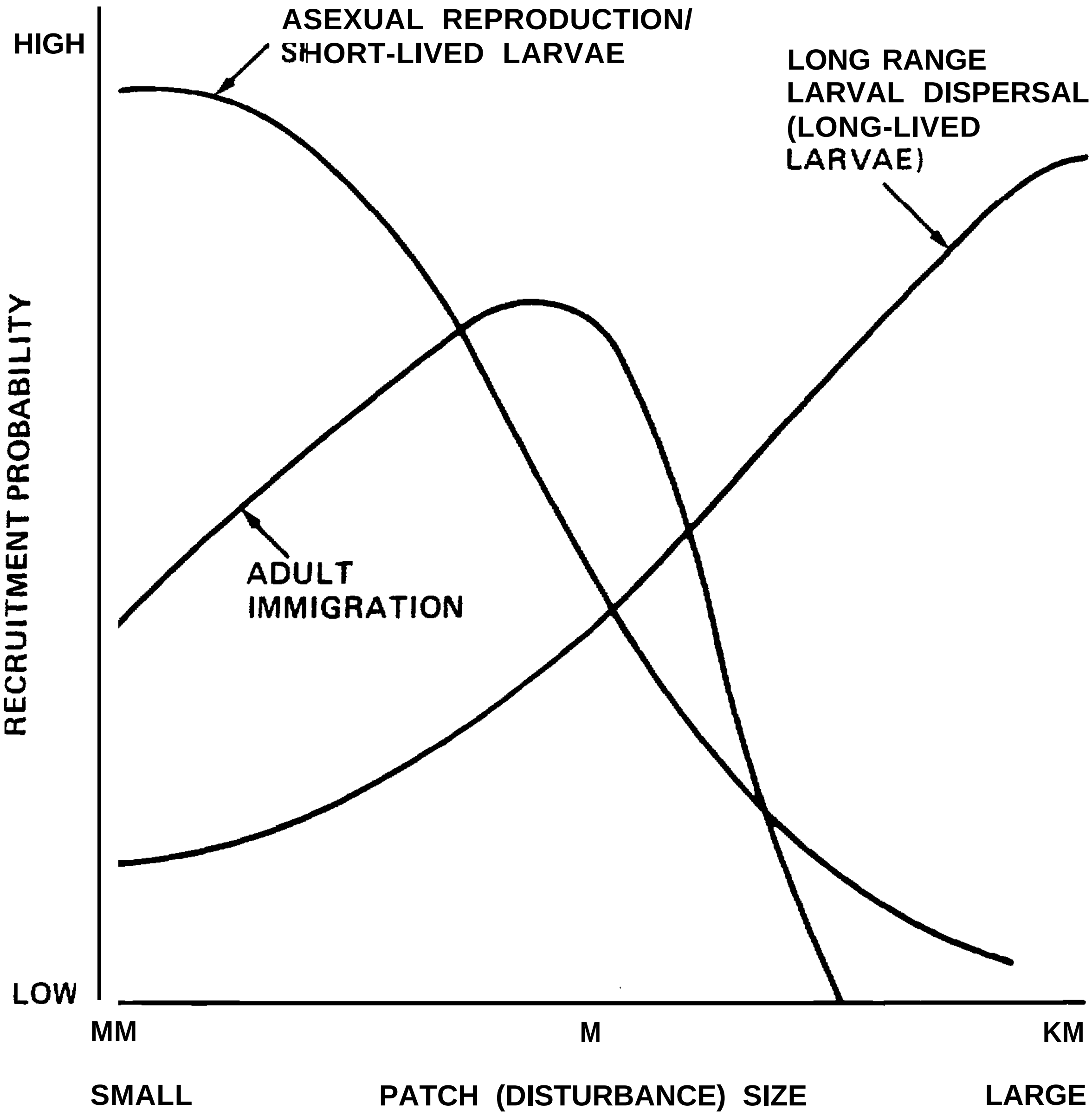

FIGURE 4-1. SUMMARY OF RECRUITMENT PROBABILITY AS A FUNCTION OF PATCH SIZE AND COLONIZATION STRATEGY

boulders (Sousa, 1979a,b), breaking the substrate and exposing bare rock (Ebeling et al. , 1985), or by burial or scouring of organisms by sediment (Seapy and Littler, 1982; Robbs, 1982; Littler et al., 1983). Biological activities that have been shown to clear space include predation (Ebert, 1977; Karlson, 1978; Ebeling et al., 1985), senescence (Kay and Keough, 1981) and disease (Ayling, 1981; Palumbi and Jackson, 1985).

As is evident from Chapter 2, a variety of factors can potentially affect the recolonization and recovery of patches. In this section, attention is centered on several key experimental studies that focused on these factors. The strength of experimentally focused studies is that one or more independent variables, such as time since patch creation or patch size, can be controlled. Ideally, this ability to control at least some of the factors affecting recolonization and recovery results in minimizing the variation in the biological communities and allows a greater degree of confidence when attempting to define causal mechanisms . Numerous survey- oriented, before-vs-after studies have been conducted to examine the effects of a disturbance. However, they generally are not appropriate in a formal assessment of recovery/recolonization since the magnitude of the disturbance usually is not known with enough certainty to make firm conclusions. For example, Kirby-Smith and Ustach (1985) compared still-camera and television transects of hard substrate communities at 27-35 m depth on the continental shelf off North Carolina taken in 1981 with data collected 41 days after Hurricane Diana passed over the area in 1984. A storm of such magnitude would be expected to generate strong near-bottom currents from shoaling waves, but the survey data was inconclusive on how much sediment might have been resuspended or how much erosion of rock ledges had occurred. Given the limitations of the data, only general statements about changes in the biological communities could be made. No significant differences could be attributed to the hurricane.

Experimental studies allow more control over the magnitude of the disturbance (the independent variable), but their design also must be evaluated carefully. For example, unanticipated effects of some types of experimental manipulations have plagued interpretation of results (e.g., the controversy over caging artifacts; Hulberg and Oliver, 1980) , A more subtle problem is the danger of reverting to circular reasoning (Peters, 1976) when attempting to test some of the models outlined in Chapter 2. Since the models are based largely on empirical results from a variety of habitats it is inappropriate to use results from similarly designed experiments to test the models. The most useful models and experimental tests allow predictions and extrapolations beyond the data used to formulate the models.

The majority of key studies of disturbance in marine hard substrate communities have been conducted in intertidal and shallow subtidal habitats. In deeper OCS waters, the sources of disturbance (particularly physical disturbance) potentially are different, at least in their frequency and severity, from those documented for shallow waters (see Chapter 3). This will be related to decreased wave energy in these deeper habitats (e.g., Sverdrup et al, 1942; Gross, 1972). In contrast, biological disturbances may be similar to those observed in shallow rocky habitats, but pertinent data are not available.

However, for the purposes of this discussion, it is perhaps less important to distinguish the source of the disturbance than its result. For example, if two disturbed patches are approximately the same size and shape and are surrounded by similar organisms, it would make little difference that one was created by log damage and the other by intense predation. Therefore, the focus of this discussion is to relate observed patterns of recolonization and recovery to measurable attributes of patches and their environment. Selected studies of recolonization and recovery are addressed for the two primary kinds of patches: Type 1 and Type 2 (see Chapter 2 for a definiton of patch types).

Other factors which will probably influence rates of colonization are the size and shape of the patches and their proximity to potential colonists. Type 1 patches will be affected by the growth form and physical structure of the individuals or colonies surrounding them. Colonization rates are also likely to be affected by the growth forms of initial colonists from the borders of the patch (Type 1 patches) or from the plankton (Type 1 and Type 2 patches). While size also affects the pattern of colonization of Type 2 patches (Connell and Keough, 1985; Sousa, 1985), it is usually not important unless very large patches are considered that are created by catastrophes such as landslides (Connell and Keough, 1985; Gulliksen, 1980) or lava flows (Grigg and Maragos, 1974).

4.1.1 Type 1 Patches

Clearings, such as might be created by an anchor disturbance (e.g., Figure 2-l), generally are surrounded by adults of the same species that were removed. The recovery patterns generally will be a function of the attributes of those same adults. If the dominant species are colonial, recovery probably will occur rapidly by the vegetative growth of bordering colonies, and there will be little change in species composition or dominance (Figure 4-l). Many sheet-like forms appear particularly well-adapted to colonize these types of patches (Ayling, 1983). Some sponges produce a thin extension that quickly covers the newly opened space, This portion of the colony is then thickened by the addition of tissue. Kay and Keough (1981) also found that experimental clearings adjacent to sheet-like sponges were almost always recolonized by the vegetative growth of those sponge colonies. Any recruits from the plankton were generally overgrown before they could become established.

Recovery of the patch will be slower if the dominant species are solitary forms. In some cases, however, there may be a rapid but brief decline in the patch size caused by the movement of surrounding individuals. One might expect that solitary species with some power of movement, such as the anemone, <u>Metridium</u>, might move to fill the space, (although asexual budding is probably more important for this species). More sessile individuals along the periphery of the patch may "lean in" and take up space (Paine and Levin, 1981). Generally, however, solitary species will colonize most effectively by means of larvae. If the community is dominated by species whose larvae only disperse a short distance, then the patch probably will be closed in a relatively short time, again with little change in species composition or dominance. Cup corals (Gerrodette, 1981), hydrocorals (Ostarello, 1976), and octocorals (Sebens, 1983) may be in this category.

On the other hand, if the community dominants are solitary forms which disperse as long-lived planktonic larvae or are very slow-growing colonial forms, the pattern of recolonization and recovery may be very different. In this case colonization will be a more stochastic process and will very likely involve different species than were originally present. As a result, recovery (that is a return to the original condition) may take several years (Figure 4-l).

Jackson (1979) predicted that sheet-like colonial species would tend to be less abundant in habitats. where the rates of sedimentation are high. This prediction is supported by the observation that with increasing depth and sedimentation there appears to be a shift from encrusting, sheet-like species to erect species (e.g., Freeland et al., 1980). If in general the more erect species tend to grow more slowly, deep water communities made up of colonial forms may be more similar to communities of solitary species in their response to disturbance. Therefore, the recovery of small Type 1 patches would be predicted to be slower in deep water. However, it would be unlikely for a disturbance, such as that from anchor dragging, to clear a hard substrate patch completely. If the dominant members of the disturbed community are colonial forms such as sponges, bryozoans, and tunicates, they may be able to grow back from fragments and reclaim space (Kay and Keough, 1981; Palumbi and Jackson, 1982; Ayling, 1983) .

The surviving species surrounding Type 1 patches also can affect colonization by inhibiting or enhancing recruitment by the same or different species outside of the patch. Most of the studies that provide evidence for these effects were done in the intertidal and deal with algal species (Foster, et al. , 1986). Lubchenco (1980) demonstrated that surviving holdfasts of the red alga Chondrus crispus inhibited the recruitment of the brown alga, Fucus distichus, while Foster (1982) showed that survivors of experimental clearings in the low intertidal inhibited the colonization of a middle intertidal red alga, Iridea flaccida. Sousa's (1979a,b) studies in an intertidal boulder field showed similar inhibition processes. His work was particularly interesting because it showed that inhibition of colonization occurred regardless of the successional "stage" of the survivors surrounding Type 1 patches. Ulva spp., a species of green algae that is commonly regarded as an early successional or "fugitive" species , inhibited colonization as effectively as the species of red algae (Gigartina leptorhyncos and Gelidium coulteri) that tend to appear much later in successional sequences. It is probably generally the case that early plant or animal colonists inhibit the recruitment of later arrivals (Sousa, 1985). In subtidal habitats, colonial species usually outcompete solitary forms (Osman, 1977; Jackson, 1977), and hence are more likely to dominate patches where they are present.

There is some evidence that the size of Type 1 patches is a less important determinant of recolonization events than the position of the patch relative to surrounding organisms. Kay and Keough (1981) found that a small patch located next to a slow-growing species was more likely to be colonized from the plankton than a large patch adjacent to fast-growing, sheet-like sponges. Similar patterns have been found for Type 1 patches in the intertidal (Sousa, 1984; Paine and Levin, 1981). For both small and large Type 1 patches, larvae from colonies or individuals surrounding the clearing will not be favored over those of outside species unless they are demersal or spend a very short time in the plankton.

4.1.2 Type 2 Patches: Habitat Islands

Most Type 2 patches represent relative "islands" of hard substrate physically separated by soft sediments (e.g., Figure 2-2). These islands can range from rock outcrops to cobbles and boulders or plant or animal surfaces such as mollusc shells. When these surfaces are cleared, recolonization will mostly be by means of planktonic larvae. Sousa (1985) argued that the probability of an organism colonizing a Type 2 patch from the plankton will generally be small because they occupy a small portion of space available for colonization. If this is true, one would expect the colonists of small Type 2 patches to have propagules capable of long-range dispersal. This prediction seems to be confirmed by two studies of small Type 2 patches consisting of the shells of the bivalve <u>Pinna,</u> which are anchored in soft sediments in the shallow subtidal. Kay and Keough (1981) found that these patches were dominated either by solitary or colonial forms with determinate growth. In contrast to these small Type 2 patches, Type 1 patches on nearby pier pilings were dominated by sheet-forming colonial species with indeterminate growth. Keough (1984) showed experimentally that colonial species forming indeterminate sheets were more common on Type 1 than Type 2 patches and more common on large than small Type 2 patches. Solitary serpulids and bryozoans with determinate growth forms showed the opposite trends. However, a significant question that remains is whether the solitary forms and determinant growers were better dispersers than the indeterminate sheet-like colonies. The growth forms of the colonists will influence rates of patch closure and subsequent colonization. There are likely to be differences among large areas in the dominant growth form related to such factors as current and sedimentation regimes. Kay and Keough (1981) demonstrated such regional differences in the growth forms of colonists. Study sites in a region characterized by relatively high abundance of fine sediments tended to have a higher proportion of colonists with solitary growth form than sites in regions where the sediments were coarser.

The relationship of these general patterns of recovery described for Type 1 and Type 2 patches to the life history strategies of representative hard substrate species is presented in Section 4.2.1. This initial summary is based on a presently limited database of deep water hard substrate communities and processes. However, some basic predictions can be made such as those summarized in Figures 2-1 and 2-2.

4.2 SUMMARY OF LIFE HISTORY STRATEGIES OF CALIFORNIA OCS BENTHIC INVERTEBRATES

The Pacific coast of North America supports an abundant and diverse marine biota inhabiting a wide variety of habitats. While some species in these communities, particularly in the intertidal, have been scientifically investigated for nearly a century, there is a lack of knowledge about the natural history of many common species. Even for well-studied taxa, the level of biological understanding limits predictions concerning the recovery and recolonization of a community following a perturbation. Knowledge is particularly limited on the rates and patterns of recovery of deep water (e.g. , >50 m depth) species and communities . To date, most of the studies have been conducted on species that have depth distributions extending farther inshore and/or that because of "submergence," are found in shallower waters to the north. However, many of these studies are further complicated by the unrefined taxonomy of many groups of organisms (e.g. , sponges) . Consequently, the discussion in this section relies heavily on intertidal and shallow subtidal studies of known species to infer/ predict details about the biology of the deep water hard substrate communities of the California OCS.

This section focuses on nine major phyla commonly observed during MMS OCS studies : Porifera, Cnidaria, Bryozoa, Brachiopoda, Echinodermata, Chordata-Urochordata, Mollusca, Annelida, and Arthropoda. For each phylum, information is presented on specific taxa and/or genera that are representative of the common life history strategies within that phylum; the list is not intended to be exhaustive, Selection criteria for representative taxa were based on frequency of occurrence in MMS surveys, including SAIC (1986), Battelle (1988), and the present November/December 1987 survey conducted off central and northern California, and on available literature on the various species or genera. Generalizations about representative families or genera serve as a guideline for broader community discussions. However, in some cases the biology of a particular species is well known and provides detailed information from which generalized strategies within a phylum may be deduced. For example, in the discussion on Cnidaria the ahermatypic corals are represented by two species, *Balanophyllia elegans* and *Lophelia californica*, that probably are broadly representative of many other coral species for which there is little or no information. It was assumed that general life history features of one species of coral are similar to other species of the same general type. Thus , whereas the biology of *L. californica* is essentially unknown, the Atlantic species *L. pertusa* has been well studied, and its life history information is utilized to make generalizations about the genus *Lophelia*. Using this approach, generalized life history features for each of these phyla are summarized in Tables 4-1A through 4-11. Common names are included in the table for those taxa that have widely accepted, “standardized” common names, such as “orange puffball sponge” for *Tethya aurantia*. References from which information is summarized for each taxon are coded numerically, corresponding to the reference list presented in Chapter 6, and listed in parentheses under the taxonomic names in Table 4-1. The general format of Table 4-1 is modeled after Vesco and Gillard (1980), who summarized life history information of intertidal and shallow subtidal organisms of the Pacific Coast.

The discussion includes an overview of life history characteristics including potential rates and patterns of recovery where they are known or can be estimated reasonably (Section 4.2.1) followed by a more detailed presentation of each phylum (Section 4.2.2). The overview consists of a summary and integration of the discussions of the various phyla and focuses, to the extent practical, on the deep water (from approximately 50 m to 500 m deep) hard substrate communities of the California OCS, with comparisons as appropriate to species and communities from other geographic areas.

4.2.1 Overview of Life History Characteristics

4.2.1.1 *Feeding Types*. Deep water hard substrate communities generally are removed from most direct sources of primary production; food resources are, therefore, conveyed to these communities by three major pathways: "detrital rain" from production in surface waters; entrapment of drift algae and kelp; and zooplankton and nekton in the near bottom waters. Community composition

TABLE 4-1A. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS*

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
PORIFERA (sponges) (8,9,11,13,29,30,31,43,44,49,140, 141)			Sexual reproduction includes both int. and ext. fertilization-some brood; release flagellated larvae which last from hours to a few days, then becoming crawling larvae and undergoing metamorphosis. Asexual reproduction including fragmentation, budding, and formation of gemmules and pseudolarvae	
Calcarea (13)			Generally limited dispersal	Sessile
Clathrina spp (70)	Filter feeder	Fast growth; small annual species		Sessile
Leucandra heathi (spiny vase sponge) (9,43)	Filter feeder	Small vasiform; fast growth		Sessile
Leucetta losangelensis (9)	Filter feeder	Large amorphous, encrusting sponge; fast growth- -one to two years		Sessile
Demospongiae (13,119,120)				
Geodia mesotrianena (31)	Filter feeder	Large subglobular; slow growth		Sessile
Haliclona spp (13,43,44,120)	Filter feeder	Encrusting; small, fast growing; some annual species		Sessile
Mycale spp (29,43, 120)	Filter feeder	Erect, encrusting; large-to-small; lives at least eight years for some species	Generally limited dispersal	Sessile

TABLE 4-1A. SUNMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES cHARACTERISTIC! OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE Communities OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION DISPERSAL RECRUITMENT	MOTILITY
Suberites ficus (10,43,72)	Filter feeder	Subglobular, medium size	Generally limited dispersal	Sessile
Tethya aurantia (orange puffball sponge) (9,43)	Filter feeder	Hemispherical, large size; lives at least two years in aquaria	Generally limited dispersal	Sessile
Hexactinellida (glass sponges) (13,29)		Glass sponges characteristically are slow growers and long lived, up to 100s of years		
Aphrocallistes vastus	Filter feeder	Large cylindrical	Generally limited dispersal	Sessile
Staurocalyptus solidus	Filter feeder	Massive vasiform	Generally limited dispersal	Sessile

TABLE 4-1A. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
PORIFERA	Sponges are preyed on by nudibranchs, chitons, sea stars, and fishes. Contain many chemicals to deter grazing and predation	Sponges provide habitat for numerous organisms, e.g., amphipods, crabs, polychaetes, ophiuroids		
Calcarea				
Clathrina spp.			Rapid recovery once larvae have colonized	*C. blanca* reported to 820m, S. Calif to Baja, CA; *C. californica* to 100m
Leucandra heathi			Rapid?	Central Calif. to 111m
Leucetta losangelensis			longer for large size	Pt. Conception to Baja, CA to 110m
Demospongiae			Some annual species, larvae attach within 24 hours in some species. Rapid recovery once larvae settles; other larger species would require years or decades to regrow	
Geodia mesotrianena				Alaska to Baja, CA to 370m
Haliclona spp.				World wide encrusting sponge
Mycale spp.				Worldwide encrusting sponge

TABLE 4-1A. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGRAPHY NOTES
Suberites ficus		Generally found on hermit crab shells		Alaska to San Diego to 80m
Tethya aurantia				British Columbia to Mexico to 440 m ,
Hexactinellida			Slow recovery	
Aphrocallistes vastus				California waters at depths greater than 150-200 m
Staurocalyptus solidus				

TABLE 4-1B. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
CNIDARIA (anemones, corals, sea fans, etc.) (11,18,60,67,86,121)				
Hydrozoa . Hydroida (hydroids) (18,27,48,99)		Branching growth form; short lived; rapid growth rate		Once planula settle they become permanently attached
Abietinaria spp.	Passive filter feeding planktivore		Generally no free medusa stage; longer lived swimming planula larvae (hours to weeks)	
Aglaophenia spp. (ostrich-plume hydroid)	Passive filter feeding planktivore	May live several years.	Short lived (hours) crawling larvae - limited dispersal	
Plumularia spp.	Passive filter feeding planktivore		Longer lived swimming planula larvae	
Hydrozoa - Stylasterina (hydrocoral)				
Allopora spp. (106,107)	Passive filter feeding planktivore	Slow growth, long lived once established; few colonies survive first year. Colonies 30 cm height at least 20 years old	Retained tiny medusae produce gametes and brood larvae. Demersal larvae settle within 1 day; limited dispersal	Once established, permanently attached

TABLE 4-1B. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
CNIDARIA				
Hydrozoa - Hydroida (hydroids)	Early colonizers and initial competitive dominants. Preyed on by fishes, nudibranchs, and flatworms; nematocysts deter some predators	Provide heterogeneous habitat for numerous species, e.g., amphipods and pycnogonids	Recovery can be rapid-weeks to months	Hydroids generally have wide distributions, many being found worldwide
Abietinaria spp.				
Aglaophenia spp.				*A. struthionides*, Alaska to San Diego to 160 m
Plumularia spp.				
Hydrozoa - Stylasterina (hydrocoral)				
Allopora spp.	No observed predators; young colonies killed by being overgrown or by sedimentation	Provides hard substrate for hydroids, barnacles, and amphipods	Recovery would probably require many years	S.E. Alaska to Baja, CA; subtidal to over 100 m. Stylasterines are both tropical and temperate.

TABLE 4-1B. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
Anthozoa - Gorgonacea (sea fans) (57,58,67)				
Muricea spp. (56,57,58)	Passive filter feeding planktivore	Upright, branching, grow to large size; slow growth - -5-10 years to reach sexual maturity in M. californica	Sexes separate; longlived larvae (-30 days for broad dispersal)	Once established permanently attached
"Lophogorgia" spp	Large, passive filter feeding planktivore			
Anthozoa - Actiniaria (anemones) (50,98,139)				
Actinostola spp (122)	Passive carnivore	Long lived	Sexual reprod.; int. fertilization; larvae brooded; large larvae released, planktonic for months- -unusual for group	Limited mobility; may detach and move in response to predators.
Metridium senile (plumose anemone) (16,20,47,117,118,133,148)	Passive filter feeding zooplanktivore	Long lived, medium fast growth?	Sexual reprod.; ext. fertilization; planula larvae planktonic days to weeks. Asexual reprod. --pedal laceration	Limited mobility, pedal crawling; adults apparently can detach and drift or roll to new locations
Urticina (= Tealia) spp. (34,81,134)	Passive carnivore	U. crassicornis - 10 mm dia./first year; long lived to 100 yr?; slow growth	Ext. fertilization; demersal, longlived larvae, 10-30 days; broad dispersal - some Altantic species brood Larvae-direct development.	Usually attached, some pedal crawling; limited mobility; may detach and roll

TABLE 4-1B. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAxA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
Anthozoa - Corallimopharia				Detach and roll?
Corynactis californica (strawberry anemone) (19,20,61,96)	Suspension feeding macro zooplantivore	Small anemone; rapid growth?; long lived	Sexual reprod., planula larvae for broad dispersal. Asexual reprod. by fission, no dispersal	Permanently attached
Anthozoa - Madreporaria (ahermatypic coral)				
Lophelia spp (152)	Passive suspension feeding omnivore and zooplantivore	Forms branching "heads" through budding; 6mm/year slow growth - long lived	Successful larval recruitment appears rare; breakage of colonies and dispersal important for colonizing new areas; larval preference to settle on worm tubes?	Permanently attached-broken pieces may recolonize new areas
Balanophyllia elegans (orange cup coral) (46,53)		Solitary coral; long lived, slow growth rate	Short lived planula larvae, limited dispersal; tolerance for sediments unknown	Permanently attached; broken individuals not likely to recolonize/attach

TABLE 4-1B. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
Anthozoa - Gorgonacea (sea fans)	Preyed on by gastropod and nudibranchs. May be indicators of environmental stability? Nematocyst and chemical defenses may deter predators	Provides diverse epibiotic habitat for anemones, sponges, echinoderms, crustacea, bryozoans, etc.	Larvae of sane species may be able to settle and establish colonies through a thin sediment layer?? Recovery would probably require years	Widely distributedon the continental shelf; taxonomy poorly known
Muricea spp				
"Lophogorgia" spp				
Anthozoa - Actiniaria (anemones)		Copepods and some shrimps commonly associated with anemones		
Actinostola spp.			Broad larvae disperal recolonization rapid; regrowth slow	World wide, deepwater genus
Metridium senile	"Catch" tentacles for inter/intraspecific aggression; acontia for interspecific defense. Preyed on by nudibranchs and asteroids	Crustacea have been observed on Metridium columns. Some Epitonium gastropods feed on anemones	Potential for rapid recovery by adult migration; longer recovery via larval recruitment (years)	Maybe 3 species, widely distributed temperate and cold water to over 150m
Urticina (=Tealia) spp	Some asteroids, e.g., (Dermasterias) feed on small U. piscivora; large Urticina feed on asteroids		Potential for rapid recovery by adult migration; longer recovery via larval recruitment (years)	World wide temperate and cold water genus

TABLE 4-1B. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
Anthozoa - Corallimopharia				
Corynactis californica	Forms clonal sheets; overgrows encrusting forms		Probably needs clean substrate for larval recruitment; rapid recovery once colonized	N. Calif to Baja, CA to 65m
Anthozoa - Madreporaria (ahermatypic coral)				
Lophelia spp	Tend to grow over other low growth forms.	Provides diverse habitat for crustacea, echinoderms	Requires clean substrate for larval settlement; recolonization from fragmented colonies may be quicker	Distribution poorly known; to 1000m
Balanophyllia elegans			Dispersal very limited; years to recover.	Calif to Alaska subtidal to - 100m

TABLE 4-1C. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TANA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
BRACHIOPODA (lamp shells) (26,56,69,92,93)				
Terebratalia transversal (90, 108)	Active and passive filter feeder; protozoan and micro zooplant i vore	Moderate growth rate, 10 inn/first year, 25 inn/2nd year; live a few years	Sexes separate; free swimming nonfeeding larvae (fen hours to days); limited dispersal	Permanent 1 y at t ached
Laqueus .californicus.	Active and passive filter feeder; protozoan and micro zooplant ivore		Egg brooding known for some species	Permanent 1 y attached

TABLE 4-1C. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OF REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
BRACHIOPODA (lamp shells)				
Terebratalia transversal	Preyed on by crabs and asteroids	Shells provide hard substrate for other organisms; often heavily encrusted	Limited dispersal once established; recovery in a few years.	Alaska to Baja, CA to 1800m
Laqueus californicus				Alaska to S. Calif to 400m

TABLE 4-ID. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
ECHINODERMATA (seastars, sea urchins, sea cucumbers, feather stars, etc.) (11,68,136)				
Crinoidea (sea lilies, feather stars) (68)				
<u>Florometra serratissima</u>	Passive filter/ suspension feeder; ciliary mucus feeder; protozoan and micro zooplantivore	Long lived	Sexes separate; ext. fertilization; larva short lived-limited dispersal; Regeneration of body parts common	Attached by cirri -creeping rate , [illegible] 40m/hr, some individuals may "swim"
Holothuroidea-Aspidochirotida (sea cucumbers) (68, 159)				
<u>Parastichopus californicus</u> (California sea cucumber) (90,159,189)	Sediment detritivore		Sexes separate, ext. fertilization; free pelagic swimming larvae [7-13 weeks); broad dispersal; regeneration well -developed	Mobile
Holothuroidea-Dendrochirotida (159)				
<u>Cucumaria</u> spp (22,45, 128, 135)	Passive suspension feeders; phyto and zooplanktivore	Some species take 4 years to become sexual mature; probably long lived and slow growth	Sexes generally separate; indirect and direct development	Slightly mobile/ sedentary habit
<u>Psolus</u> spp				

TABLE 4-1D. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OF REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
ECHINODERMATA				
Crinoidea				
Florometra serratissima	Preyed on by some gastropods	May provide habitat for ophiuroids and polychaetes	Limited larval dispersal once established; recovery in a few years. Adult immigration may be imprtant to colonize new areas	Alaska to Baja Calif to 1000m
Holothuroidea-Aspidochirotida				
Parastichopus californicus	Preyed on by asteroids e.g., *Pycnopodia* and *Solaster*, and the gastropod *Pleurobranchaea*	Small crabs and polychaetes (*Arctone* sp.)	Quick recovery; species able to utilize soft and hard substrates for larval recruitment and adult immigration; larval settlement and growth would require a few years	Alaska to Mexico to 200m
Holothuroidea-Dendrochirotida				
Cucumaria spp.	Chemical defense to deter predators		A few years, once colonized	Alaska to Calif to 200m
Psolus spp.		Overgrown by some encrusting forma		Difficult to collect; deeper water species poorly known
Asteroidea	Seastars once grown, have few predators other than some gastropods and other seastara. Many prey species exhibit strong avoidance/escape reactions to asteroids	Some scaleworms and gastropods are found associated with starfish	Immigration of adults could provide for rapid recovery; larval recruitment and growth would require a few years	
Henricia spp.			Limited dispersal once established; recovery in a few years.	Alaska to Baja Calif to 650m

TABLE 4-ID. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGRAPHY NOTES
<u>Mediaster aequalis</u>				Alaska to Baja, CA to 275m on rock, sand and mud
<u>Stylasterias</u> spp.				Alaska to Calif to 600m
<u>Solaster</u> spp				Alaska to Calif to 400m
<u>Pycnopodia helianthoides</u>	King crabs may prey on juveniles of this species			Alaska to S. Calif to 435m on rock, sand, and mud
Ophuroidea (brittle stars)				
<u>Amphipholis squamata</u>	Preyed on by fishes		Rapid recovery once recruited to an area; may raft to new areas on debris, floatsam	Worldwide to 823m
<u>Ophiothrix spiculata</u>	Preyed on by sea stars, fishes, crabs			Central Calif to Peru to 2000m
<u>Ophiopholis aculeata</u>	Preyed on by fish	Often associated with encrusting organisms	Recovery by recruitment probably a few years	Alaska to Santa Barbara to 732m
<u>Gorgonocephalus eucnemis</u>		<u>Gersemia</u> sp., an alcyonarian soft coral, may serve as a nursery host for juveniles	Adult immigration can provide for relatively rapid recovery; colonization to areas without adults may be difficult or impossible; very long recovery may be required	Widely distributed Atlantic and Pacific to 2000m;
Echinoidea				
<u>Strongylocentrotus</u> spp.	preyed on by sea stars, fish, and otters (shallow)	Polychaetes, isopods, amphipods	Adult immigration possible; few years via larvae recruitment	Alaska/British Columbia to Baja, CA to 160m

TABLE 4-1E. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
ARTHROPODA (crabs, barnacles, etc.) (1,11)				
Cirripedia (barnacles) (80,101,121)		Growth generally rapid		Once larvae settle permanently attached
Arcoscalpellum californicum (101)	Active filter and suspension feeder	Probably live less than one or two years	Hermaphroditic; nauplii larvae, cyprid larvae; long time in plankton	
Conopea galeata (101)	Active filter and suspension feeder		Hermaphroditic with complimental males; planktonic larvae	
Balanus spp. (101)	Active filter and suspension feeder	Many annual ap-sties; some live up to 10 years	Hermaphroditic; nauplii larvae; cyprid larvae; broad dispersal	
Amphipoda				
Caprella spp.	Omnivorous, opportunistic	Short lived, rapid growth	Sexes separate; females brood; direct development; adults and juveniles can swim or drift to new areas	Generally cling to substrate or epibiotic; can crawl and swim

TABLE 4-1E. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OF REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
ARTHROPODA				
Cirripedia				
Arcoscalpellum californicum	Preyed on by sea stars; often settles on worm tubes	Often overgrown by ectoprocts and hydroids		Monterey to San Diego to 200m
Conopea galeata		Obligate commensal on gorgonians	Cyprid larvae settle directly on the gorgonian where it has been denuded of tissue by predators	Monterey to Central America to 90m
Balanus spp.	Preyed on by sea stars and gastropods	Can provide hard substrate for encrusting organisms		B. pacificus--Monterey to Mexico to 75m B. nubilus--Alaska to La Jolla, CA to 90m
Amphipoda				
Caprella spp.	Preyed on by fish	Cling to hydroids, bryozoans, and algae, but can be mobile and swim or crawl	Rapid recovery by drifting of juveniles to new areas	Broad distributions along the Pacific coast to 100m

TABLE 4-1E. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
Decapoda - Brachyura (crabs) (52)			Egg brawling in general and sane planktonic larval phase	
Cancer spp. (incl. rock and market, dungeness, crab) (52,54,85,116,149)	Active omnivore and scavengers	May live to 8 years; sexual maturity at 1-1/2 to 2 yeara; legal size = 3- 1/2 to 4 years old (_C. magister_)	Sexes separate; long lived; planktonic larvae (3-5 months); broad dispersal	Mobile
Loxorhynchus spp. (masking and sheep crab) (52)	Active omnivore and scavenger	Long lived; slow growth		Generally slow moving
Galathea californiensis			Large number of small eggs; probably broad dispersal	Possibly prefers sedentary habit
Paralithodes spp. (incl. king crab) (12)	Omnivore, carnivore	Slow growth live 14-20 years	Larvae planktonic -2 months; broad dispersal	Motile
Paramola faxona				Motile

TABLE 4-1E. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGRAPHY NOTES
Decapoda - Brachyura				
Cancer spp.	Preyed on by fish, octopus, otters (shallow)		Several yeara to recover	C. magister--Alaska to Santa Barbara to 350m
Loxorhynchus spp.		Carapace heavily encrusted and decorated	Several years to recover	Humboldt to Baja, CA to 103m
Galathea californiensis			A few years to recover	In California 100 to 4000m
Paralithodes spp.	Preyed on by fishes and octopuses	Carapace often heavily encrusted	Needs years to recover	In California to 400m
Paramola faxons		Carries sponge and/or anemone; on leg, holds over carapace - defensive or decorative?		California to 130-370m

TABLE 4-IF. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
MOLLUSCA (snails, chitons, octopus, etc.) (3)				
Gastropoda - Prosobranchia (marine snails) (14)				
Ceratostoma foliatum (leafy hornmouth) (3, 14,55, 137)	Predator on barnacles and sessile gastropods	8 to 15 mm/year; slow growth; live to 16 years; growth ceases around age 4	Eggs laid on rocks; 4 months to develop into juvenile snails; limited dispersal	Motile
Fusitriton oregonensis (Oregon triton) (155)	Carnivore, scavenger	Slow growth	Eggs cases laid on rock; limited dispersal	Motile
Gastropod - Opisthobranchia (nudibranchs) (14,15,82,87,95)				
Aeolidia papillosa (shag - rug nudibranch) (14,15,127,138,151)	Predator on anemones	Probably lives a few years?	Egg cases laid on hard substrate; limited dispersal	Motile
Dendronotus spp. (14,95,125,154)	Predators on hydroids, bryozoa, anemones	Some species live only 1 year, others longer lived	Egg cases laid on substrate; most have planktonic larvae	Motile
Cephalopoda (octopus and squid) (78)				
octopus spp. (51,115)	Predator on crustacea, mollusca, fish	Live up to 4 or 5 years	Sexes separate; eggs brooded, takes a few months to develop; young are pelagic for a few weeks	Motile

TABLE 4-IF. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
Polyplacophora (chitons) (59,136,121)				
Lepidozona spp. (59)	Rock grazer	Live a few years	Sexes separate; usually ext. fertilization usually; a few species brood eggs; veliger larvae for a few hours--limited dispersal	Motile but sedentary habits
Placiphorella velata (59,9?)	Rock grazer; carnivore on small crustaceans and worms	Lives a few years?	Brood eggs; veliger larvae, lasts hours; limited dispersal	

TABLE 4-IF. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OF REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
MOLLUSCA				
Gastropoda - Prosobranchia			Recovery rapid by adult immigration	
Ceratostoma foliatum		Shells become overgrown with organisms	Recovery would take years from recruitment of juveniles	Alaska to San Diego to 65m
Fusitriton oregonensis		May harbor *Terebratalia* at apex of shell. Shell often overgrown with organisms	Recovery would take years from recruitment	Alaska to California to 1000m
Gastropoda - Opisthobranchia	Nudibranchs often utilize nematocysts from prey for defense against predation			
Aeolidia papillosa			Adult immigration, rapid recovery; larval recruitment would take a few years	Atlantic and Pacific to 760m
Dendronotus spp.			Rapid recovery	*D. subramosus* --Washington to Baja, CA to 120m; *D. iris* --Alaska to Baja to 200m
Cephalopoda				
Octopus spp.	Preyed on by fish	Mesozoan parasites	Adult immigration rapid recovery - larval recruitment - years	*O. dofleini* --N. Pacific to S. California to 500m *O. rubescens* --Alaska to Baja, CA to 200m
Polyplacophora				
Lepidozona spp.			Limited dispersal; a few years once established	Common off California to 100m
Placiphorella velata				Alaska to Baja, CA to over 100m

TABLE 4-1G. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
ANNELIDA (segmented worms) "Errantia" - free living (35,62,63,71,132,160)				
Polynoidae				
Halosydna, Harmothoe spp. (160)	Jawed; carnivorous; eversible pharynges	Slow growing; may live several years?	Ext. fertilization; separate sexes; planktonic larvae; brooding for late phase planktonic or demersal larvae	Motile, discretely motile
Phyllodocidae				
Eulalia, Phyllodoce spp.	Eversible pharynges; carnivores to deposit feeders	Generally smaller annual species? fast growing	Demersal eggs, planktonic larvae; reproduce via surface swarming of adults in some species	Motile
Syllidae				
Exogone, Syllis spp.	Jawed omnivores	Generally small, annual species	Hermaphroditic; asexual budding; broad dispersal for planktonic larvae	Motile
"Sedentaria" - tube dwellers non- calcareous tubes				
Chaetopteridae				
Phyllochaetopterus prolifica (160)	Active and passive filter feeding surface deposit feeding	Large species, slower growth; longer lived		Sessile, discretely motile

TABLE 4-1G. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
Sabellariidae				
Sabellaria cementarium (160)	Passive filter feeder	Large; slow growing, long lived species	Prolonged planktonic larvae (months); broad dispersal	Sessile; discretely motile
Sabellidae				
Eudistylia polymorpha (feather-duster worm) *Sabella crassicornis* (160)	Filter feeder	Large; slow growing, annual to longer lived species	Hermaphroditic short-lived planktonic larvae; limited dispersal; asexual fission	Sessile; discretely motile
"Sedentaria" calcareous tube builder			Short-lived planktonic larvae phase limited dispersal, asexual fission and regeneration	
Serpulidae (142)				
Serpula vermicularis (plume worm) (160)	Filter feeder	Smaller, faster growing species.	Short-lived planktonic larvae phase limited dispersal, asexual fission and regeneration	Sessile; discretely motile
Spirorbidae "*Spirorbis*" (160)	Filter feeder	Short lived, usually less than a year; in S. Calif. successive generations in as little as 33 days	Hermaphroditic; generally brood eggs, releases larvae	Sessile; discretely motile

TABLE 4-1G. SUMNARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OF REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
ANNELIDA		Commensal with other polychaete sea stars and gastropod shells	Polychaetes generally would recover rapidly; longer lived species with limited dispersal would need a few years to recover	
"Errantia". Free living				
Polynoidae				
Halosydna, Harmothoe spp.				Alaska to Baja, CA to 500m; soft and hard substrate
Phyllodocidae				
Eulalia, Phyllodoce spp.				California to 200m; soft and hard substrate
Syllidae				
Exogone, Syllis spp.				Alaska to Baja, CA to 200m
"Sedentaria". tube dwellers non-calcareous tubes				
Chaetopteridae				
Phyllochaetopterus prolifica		Scale worms found in tubes, tube clusters provide habitat for encrusting organisms and may provide nursery habitats for juvenile starfish		British Columbia to Baja, CA to 450m; hard and soft substrates

TABLE 4-1G. SUNMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGRAPHY NOTES
Sabellariidae				
Sabellaria cementarium				Alaska to S. California to 80m
Sabellidae				
Eudistylia polymorpha	Fish predation on anterior portion of worms; regenerate new parts	Tubes colonized by encrusting organisms		Alaska to S. California to 450m
Sabella crassicornis "Sedentaria" calcareous tube dweller		Tubes colonized by encrusting organisma		Alaska to S. California to 200m
Serpulidae				
Serpula vermicularis		Tubes colonized by encrusting organisms		Alaska to San Diego to 100m
Spirorbidae "Spirorbis"		Tubas colonized by encrusting organisms	Rapid recovery; early colonizer	Alaska to Baja, CA to 200m

TABLE 4-1H. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
ECTOPROCTA (bryozoa or moss animals) (5,33,69,74,79,126,129,130,131, 136)		Colonist growth forms, either sheet-like encrusting or upright branching forms. Generally short lived, rapidly overgrown by other species; early colonizers	Sexual reproduction for new colonies; asexual reproduction to increase colony size. Many different types of larvae all swim or move about providing for broad dispersal	
Ctenostomata (105,153)				Sessile
Alcyonidium mammillatum	Active impact suspension feeder			
Cyclostomata (105)				
Diaperoecia californica (southern staghorn bryozoan)	Active impact suspension feeder	Large upright growth; one of the longer lived species		Sessile

TABLE 4-1H. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
Tubulipora spp.	Active impact suspension feeder			Sessile
Cheilostomata (103,104)			Cheilostomata are generally considered hermaphroditic, but cross fertilize; brooding in scare species; several types of larvae- -some short-lived, others having longer planktonic phases	
Thalamoporella californica	Active impact suspension feeder	Upright branching growth forms		Sessile
Hippodiplosia insculpta (fluted bryozoan) (102)	Active impact suspension feeder	Large colonies		Sessile
Holoporella brunnea	Active impact suspension feeder	Thick encrusting form to 10 mm		Sessile
Phidolopora pacifica (lacy bryozoan)	Active impact suspension feeder	Upright colonies to 10 cm high		Sessile

TABLE 4-1H. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OF REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
ECTOPROCTA				
	Most ectoprocts are overgrown by later succession species		Rapid recovery for most species, weeks to months for small encrusting forms; 1 to 2 years for larger growth forms	
Ctenostomata				
Alcyonidium mammillatum				Alaska to Baja, CA to 200m
Cyclostomata				
Diaperoecia californica				British Columbia to Costa Rica to 165m
Tubulipora spp.		often grow on mollusc shells		I. tuba-- British Columbia to Mexico to 700m I. pacifica-- British Columbia to Mexico to 300m
Cheilostomata				
Thalamoporella californica				Central California to Columbia to 145m
Hippodiplosia insculpta		Commonly epizoic		Alaska to Mexico to 780m
Holoporella brunnea	Preyed on by a flatworm, Hoploplana			Alaska to Mexico to 600 m
Phidolopora pacifica	Preyed on by starfish			British Columbia to Peru to 200m

TABLE 4-11. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
CHORDATA - UROCHORDATA (tunicates or sea squirts) (2,36,37,65,66,73,123,124,145, 146,147,157)				
Aplousobranchia (all colonial, mostly compound)		Rapid growth; short lived, basal portions may over winter	Sexual reproduction; few eggs brooded; produce swimming, nonfeeding tadpole larvae: settlement within minutes to hours	Sessile
Aplidium californicum (2)	Filter feeder			Sessile
Polyclinum planum (elephant ear tunicate) (2)	Filter feeder			

TABLE 4-11. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OF REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
CHORDATA - UROCHORDATA				
Aplousobranchia (all colonial, mostly compound)		Colonized by amphipod, bivalves, copepods	Early colonizers; rapid recolonization during reproductive season; do not tolerate siltation	
Aplidium californicum				British Columbia to Baja, CA to 85m
Polyclinum planum				California to 50m

TABLE 4-11. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OR REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	FEEDING/ TROPHIC	GROWTH/LONGEVITY	REPRODUCTION/DISPERSAL/RECRUITMENT	MOTILITY
Didemnum carnulentum (2)	Filter feeders	Grow to a diameter of several inches in 1-2 months at La Jolla, CA		Sessile
cystodytes lobatus (lobed tunicate) (2,76)	Filter feeders			Sessile
Phlebobranchia (mostly solitary forms, a few social species) (7s,77)		Most live 1 year or less; in tropical areas live for months; in subartic areas lives for years	Most spawn their eggs, a few are brooders; tadpole larvae are smaller and numerous (life of hour to days); dispersal may be widespread	Sessile
Ciona intestinalis (2)	Filter feeders			Sessile
Ascidia paratropa (2)	Filter feeders			Sessile
Chelyosoma productum (2,156)	Filter feeders			
Stolidobranchia (nearly all solitary, a few compound forms) (100,158)		Generally larger and longer lived	Both brooders and spawners in this order; tadpole larvae live for 1 to 2 days; good dispersal	Sessile
Styela montereyensis (stalked tunicate) (2)	Filter feeders	Grows to 5 cm in 3 months; lives at least 3 years		Sessile
Pyura haustor (2)	Filter feeders			Sessile
Boltenia *Bollenia villosa* (spiny-headed tunicate) (2)	Filter feeders		Settlement and metamorphosis occurs between 6 hours and 5 days	

TABLE 4-11. SUMMARY OF LIFE HISTORY INFORMATION OF MARINE BENTHIC INVERTEBRATES CHARACTERISTIC OF REPRESENTATIVE OF DEEP WATER HARD SUBSTRATE COMMUNITIES OF THE CALIFORNIA OCS

CLASSIFICATION/REPRESENTATIVE TAXA	COMPETITIVE INTERACTIONS	SYMBIONTS	POTENTIAL FOR RECOVERY FOLLOWING DISTURBANCE	ZOOGEOGRAPHY NOTES
Didemnum carnulentum				Oregon to Panama to 50m
Cystodytes lobatus				British Columbia to Baja to 200m
Phlebobranchia (mostly solitary forms, a few social species)	Preyed on by flatworms and gastropod		Rapid colonizers of disturbed hard substrates; do not persist in community unless a pattern of yearly disturbance. May be able to tolerate some siltation and only moderate currents	
Ciona intestinalis				Alaska to San Diego to 500m
Ascidia paratropa				Alaska to Monterey to 80m
Chelyosoma productum				Alaska to San Diego to 50m
Stolidobranchia (nearly all solitary, a few compound forms)			Recruitment usually not to hard surfaces but onto earlier colonizers. Longer lived species - may need 1 to 2 years to recruit	
Styela montereyensis	Preyed on by seastars	Copepods		British Columbia to Baja, CA to 50m
Pyura haustor				Alaska to San Diego to 200m
Boltenia villosa	Preyed on by seastars			British Columbia to San Diego to 100m

Common names are provided for those taxa that have widely accepted, "standardized" common names. Numbers in parentheses refer to references listed in Chapter b.

tends to reflect the type of food resource(s) utilized. Hard substrate communities near sources of drift algae would be expected to have more detritivores and algal feeders (e.g., urchins, amphipods, isopods) and fewer filter/suspension feeders. Conversely, communities removed from algal inputs would be expected to contain mostly filter/suspension feeders as the primary consumers. Table 4-1 indicates that filter/suspension feeding is a common feeding mode for eight of the nine phyla considered. This is particularly representative of higher relief communities of the California OCS, such as those represented in Figure 2-1. As a group, the Bivalvia (Mollusca) also are predominantly filter/suspension feeders, but in general bivalves appear to be poorly represented in these deep water hard substrate habitats and so are not included in this discussion. Filter/suspension feeders are consumed by a variety of predators representing five of the nine phyla (Table 4-l). Major invertebrate predators include large anemones, starfish, crabs, gastropod, octopus , and some polychaete worms. Predators tend to occur in lower abundance than their prey, and to be broadly dispersed within the habitat. However, some aggregations are observed, probably associated with feeding or spawning.

For many of the hard substrate areas studied (e.g., summarized in SAIC 1986 and preliminary data from the present study), photographic and video data indicate that burial by sediment, sediment resuspension, and strong currents may be common environmental occurrences. This is predicted to result in the creation of Type 2 patches (e.g., Figure 2-2) in many low relief hard substrate areas. Because the feeding efficiency of filter/suspension feeders may be affected by siltation and sediment loading, these processes can alter community composition. For example, some sponges and ectoprocta do not tolerate heavy siltation and these organisms might be expected to be rarer in low relief areas that experience such conditions. Alternately, greater height above the bottom may be an important strategy to minimize the effects of siltation and to increase feeding efficiency. Consequently, upright growth forms (e.g. , Figure 2-2) and/or the ability to colonize high relief substrata may represent important adaptive strategies in some habitats.

4.2.1.2 Growth Rate and Longevity. Many sponges, hydroids, ectoprocts, and polychaetes, and some tunicates represent early colonizers characterized by rapid growth rates and relatively short life spans (usually less than one year; Table 4-l). These early colonizers are often replaced by other, larger species, which tend to be longer-lived and slower-growing (see Chapter 2 and Section 4.1). Species of some sponges, anemones, corals, echinoderms, crabs, and molluscs may live five to ten years and some (particularly some sponges) may live hundreds of years. Growth is dependent upon numerous environmental factors, although water temperature and food supply commonly are major determinants . Warmer waters and abundant food supplies typically result in more rapid or maximum growth. Longevity, for most organisms, is dependent upon numerous factors, including growth rate, competitive ability, and the ability to withstand or recover from stochastic events such as storm damage. Many longer-lived hard substrate organisms have few predators once they achieve a certain size,- Smaller, short-lived species have the potential for longevity but are usually grazed or overgrown by more competitive early colonizers or later successional species (see Chapter 2 and Section 4.1).

4.2.1.3 Reproduction, Dispersal, and Recruitment. The data in Table 4-1 support few generalizations about patterns of reproduction. Sexual reproduction predominates, but hermaphroditism is known among barnacles, polychaetes, and ectoprocts. Brooding of eggs and larvae is common and well developed in most groups. Generally, the filter/suspension feeders tend to have short-lived larvae or direct 'development, which limits their dispersal (e.g., many Cnidaria). These results are somewhat unexpected since many taxa (e.g., some hydroids and bryozoans), assumed to be opportunistic, early colonizers with long-lived larvae (e.g., Figure 4-1), appear to have more restricted larval dispersal. However, since these organisms are widely distributed, it may be that deep water forms have somewhat different or alternate dispersal strategies. Many of the upper trophic level predators (e.g., asteroids) have long-lived planktonic larvae; this strategy promotes broader dispersal (Figure 4-1), which for these taxa presumably minimizes the probability of aggregations and the potential for overexploitation of food resources. Asexual reproduction also is common in many groups including sponges, cnidarians, ectoprocts, urochordates, and some asteroids and polychaetes. It appears to be an important strategy in the colonization of new space (e.g., Type 1 patches) or expansion through competitive interactions into space occupied by other species (Figure 4-1). Competition for space and substrate appear to dominate the dispersal and recruitment strategy of the filter/suspension feeders, and long range dispersal appears less important than the ability to colonize space established near adults. Long range dispersal for many organisms is dependent upon the ability to colonize debris, flotsam, and/or motile organisms which can disperse adults and their short-lived larvae over broader distances. The importance of this strategy for species restricted to deeper waters is largely unknown.

4.2.1.4 Competitive Interactions. A relatively simple food chain (e.g., filter feeders and invertebrate predators/scavengers such as asteroids) appears to characterize many deep water hard substrate communities, and potentially may result in numerous species interactions. The most significant factors are competition for space among the filter/suspension feeders and for food among predators. Succession and growth of larger and more competitive species provides new habitat for displaced opportunistic species and helps to maintain high community diversity. Selective predation on the larvae of competitors is thought to occur (e.g., Sebens and Koehl, 1984), but its importance as a factor structuring hard substrate communities is unknown. The more stable the environment the greater the opportunity for the biological community to develop and contribute to habitat diversity (such as sponges serving as substrate for a variety of other organisms), which in turn may lead to greater community diversity. In general, these types of interactions are poorly known for intertidal and shallow subtidal communities and have not been studied for deeper communities.

4.2.1.5 Recolonization/Recovery. As discussed in Chapter 2 and Section 4.1, community recovery following a disturbance is dependent upon successful colonization of new substrate and upon successful growth once colonization has occurred. Colonization may occur either by immigration of adults or larval recruitment. Since most of the filter/suspension feeders from these deep water areas appear to have larvae with limited dispersal ability (Table 4-1), colonization of new substrates that are isolated to some extent from resident populations (i.e., a Type 2 patch) may take many years. However, once a species has successfully colonized newly exposed substrate, recovery becomes dependent on the time required to attain adult size and/or sexual maturity. In general, small opportunistic species recover quickly (weeks to months) following removal, whereas larger species need much longer time periods (years to decades). For many species (e.g., the basket star Gorgonocephalus and many gastropod) the immigration of adults is the primary method for colonizing new areas.

4.2.2 Detailed Discussion of Phyla

This section presents a discussion by phylum of life history information on taxa which are characteristic of deep water hard substrate communities of the California OCS. The discussion summarizes and provides supplemental information to that presented in Tables 4-1A through 4-11. This information focuses on the depth range (50 m to 500 m) of interest to MMS for this report, however the depth distribution of some taxa is known to extend deeper and/or shallower than this range.

4.2.2.1 Porifera. Sponges represent an important component of deep water, hard substrate communities in California waters. Summary information is presented in Table 4-1A. Numerous encrusting and small erect species may form epifaunal communities, and large individuals (amorphous, globular, plate-like, or vase-shaped) are common in some areas. Representatives from three of the four classes of extant Porifera are found at depths ranging from 50 m to 500 m. However, members of the Class Calcarea are generally found at depths less than about 100 m, and the Hexactinellida prefer waters deeper than approximately 150 m to 200 m (Bakus and Abbott, 1980; Barnes, 1968; Berquist, 1978). The Demospongiae, which is the largest class of sponges, occur over the range of depths from 50 m to 500 m but are more common at shallower depths.

Sponges are sessile organisms that primarily occur on rocks; however, they may also be found attached to mollusc shells or on the backs of "camouflage" crabs. For example, a common association observed off California involves the sponge Suberites ficus (includes S. domuncula), which may overgrow gastropod shells often inhabited by the hermit crab Paguristes taylori (Bakus and Green, 1987; Koltun, 1966).

All sponges are nonselective particle feeders. Food particles, including bacteria, detritus, and small planktonic organisms, are apparently taken from the size range of 0.1 to 50 microns (Barnes, 1968; Reiswig, 1971). It is also considered likely that sponges are able to supplement filter feeding by absorbing dissolved or colloidal nutrients directly from the surrounding water (Berquist, 1978).

The few studies available indicate that sponge growth rates vary considerably. For example, rapid growth rates have been reported for the encrusting sponge Haliclona and Halichondria spp. (Berquist, 1978; Fells and Lewandrowski, 1981) and the encrusting or erect sponge Mycale sp. (Dayton, 1979; Reisig, 1973). Slow growth rates have been surmised for large demosponge specimens of Geodia mesotriaena (Delaubenfels, 1932) and reported for several hexactinellids (Dayton, 1979). Growth rates often vary according to the age of the individual, , with younger specimens growing faster than older specimens (Dayton, 1979; Reiswig, 1973). Growth is also affected by environmental conditions. Excessive turbidity or sedimentation can cause clogging, which inhibits sponge growth (Bakus, 1968; Storr, 1976), and growth is promoted in nutrient-rich areas (Storr, 1964, 1976).

Only limited information is available regarding the longevity of sponges. Some sponges , including the calcareous sponge Clathrina coriacea (Johnson, 1979) and encrusting demosponge taxa such as Haliclona, have been reported to be annuals (Berquist, 1978; Fell and Lewandrowski, 1981). However, many sponges reportedly live several years,. Reports of sponges living two to 50 years are noted for some species of Demospongiae, and the life spans for some specimens of Hexactinellida have been estimated at several hundred years (Berquist, 1978; Reiswig, 1973; Storr, 1964; Dayton et al., 1974; Dayton, 1979).

Sponges generally are characterized by sexual reproduction, although asexual reproduction by budding, fragmentation, and by formation of gemmules is also common (Barnes, 1968; Bakus and Abbott, 1980; Berquist, 1978). Some species are hermaphroditic, but in others the sexes are separate (Fell, 1974). Sperm are shed into the sea, but in the majority of cases the eggs are fertilized and develop within the parent sponge (Berquist, 1978; Fell, 1974). In all cases, cross-fertilization is inferred, although it has rarely been observed (Berquist, 1978).

Larvae resulting from sexual reproduction or asexual gemmule formation are released to the sea. The larvae of most sponges swim for a few hours to a few days and then creep along the bottom for anywhere from approximately 20-60 hours to 18-20 days before attaching to the substratum (Fell, 1974). Swimming and settlement are affected by currents, gravity, light, temperature, turbidity , and wave action (Bakus, 1968; Berquist, 1978). Larvae apparently prefer a pre-coated (bacterial or algal film) surface for settling, but otherwise are considered nonselective (Berquist, 1978). Dispersion of larvae into unsuitable habitats is minimized somewhat by the short duration of the free-living larval stage and by the geotactic and phototactic responses of the larvae (Berquist, 1978; Fell, 1974) . It is likely, therefore, that sponge populations in deep water hard substrate communities are maintained largely by localized recruitment via asexual budding and fragmentation.

Disturbance that produces excessive sedimentation or turbidity in deep water hard substrate communities would be expected to affect sponge growth adversely, and potentially result in the death of some individuals. Encrusting and/or erect demosponges such as Haliclona, Hymedesmia, and Mycale, and small calcareous sponges such as Clathrina and Leucandra, would be expected to be the first colonizers after a massive disturbance. However, recolonization of large Type 2 patches, generally would be expected to be slow (probably on the order of years) for specimens of Calcarea and Demospongiae that attain large sizes, such as Leucetta, Geodia, Polymastia, Sigmadocia, Suberites, and Tethya, and for Hexactinellida in general.

4.2.2.2 Cnidaria. The Cnidaria (anemones, corals, hydroids) are prominent components of many deep water hard substrate communities, and are represented by a diversity of forms. Summary information is presented in Table 4-1B. Two major classes, Hydrozoa and Anthozoa, represent the majority of the species found in deep water hard substrate communities. Many cnidarians are conspicuous and brightly colored, and all contain stinging cells used to capture food and 'to deter predation and encroachment (Haderlie et al. , 1980). All Cnidaria are carnivores, although some shallow-water species (e.g. , reef-forming corals) contain symbiotic algae (Muscatine, 1974). Most are filter/suspension feeders, but larger forms feed on large prey (e.g., fish, starfish, crabs; Hyman, 1940;

MacKie, 1978; Haderlie et al., 1980). The major predators on hydroids are nudibranchs, which utilize the cnidae for their own defenses (Day and Harris, 1978). Aglaophenia, in particular, is studded with stinging organs to protect against such predation. Many crustacea, notably caprellids, live on hydroids (Barnes, 1968).

The smallest sessile cnidarians are the hydroids (Hydrozoa), which typically form simple or branching colonies. The only comprehensive taxonomic work on Pacific coast hydroids is Fraser (1937), which is in need of review. Three genera of soft hydroids and one species of hydrocoral are listed in Table 4-1B as representative of the kinds of hydrozoans found in deep water hard substrate communities. Each hydroid colony arises from a single fertilized egg. Most deeper water hydroids appear to have a suppressed medusa stage and a short swimming larvae, which limits the dispersal of the species (Campbell, 1974). The hydroids Abietinaria spp., Plumularia spp., and Aglaophenia spp. are typical in that they do not liberate medusae or eggs, but retain them in special structures and only liberate sperm and planulae (Naumov, 1960). Hydroids are early colonizers of available substrate, and are generally short-lived with rapid growth.

The hydrocoral Allopora californica is relatively resistant to strong current conditions due to its calcareous skeleton. Eggs, then planulae, are brooded in ampullae just under the surface of the colony, and are liberated during the summer (Ostarello, 1976). The planulae have a limited range of dispersal, probably only a few meters. A notable example of this dispersal was observed from the present survey (November/December 1987) in which a colony is surrounded by several smaller colonies within approximately one quarter of a square meter. High mortality of young colonies is mainly attributable to competition (overgrowth) for space and to sedimentation (Ostarello, 1973). There are no observed predators, but at least three symbionts, a barnacle, a boring worm, and a gastropod, typically are found in colonies (Ostarello, 1973, 1976).

The sea fans, anemones, and corals (Anthozoa) constitute the most abundant and conspicuous group within the Cnidaria. The gorgonian genus Muricea, anemones Metridium senile, Urticina (= Tealia) Spp., Actinostola spp., Corynactis californica, and the corals Lophelia spp. and Balanophyllia elegans are representative of anthozoans commonly observed in deep water hard substrate areas. The Anthozoa represent solitary or colonial polyps that lack a medusa stage altogether.

The gorgonians are large colonial animals commonly found on rocky reefs and other hard substrates (e.g., pipelines). These long-lived, slow-growing filter feeders generally have larvae with a long planktonic phase, resulting in broad dispersal (Grigg, 1970). Colonies such as Muricea reach sexual maturity in five to ten years and are long lived (Grigg, 1972, 1974). The taxonomy of the seafans is poorly known because of various colors and growth forms. Some photographs from the present survey, and as noted in SAIC (1986) and Battelle (198S), show small (e.g., ≤ 10 cm), mostly reddish to pinkish, colonies ("Lophogorgia") protruding through a thin veneer of sediment overlying hard substrate, The "Lophogorgia-like" colonies are superficially similar to Lophogorgia, that is reddish with white polyps, but it may be that a few species are represented. Larval settlement presumably occurs either through a thin layer of sediments or during periods when the hard substrate is exposed.

Metridium senile, a well studied anemone, may represent three species (Bucklin and Hedgecock, 1982). It is common in rocky habitats throughout California and the North Atlantic from the shallow subtidal to over 150 m. It is a suspension feeder, apparently preferring food in size classes corresponding to the size of many barnacle cyprids, ascidian larvae, and gammarid amphipods (Purcell, 1977b; Sebens and Koehl, 1984). Morphologically it has two features, catch tentacles and acontia, that are significant for competitive interactions. Studies of Metridium and of other anemones have shown that catch tentacles may regulate inter- and intraspecific spacing of individuals (Purcell, 1977a). In Haliplanella, for example, spacing between individuals is achieved when the individual that initiates stinging moves away (Fukui, 1986); whereas, in the case of Anthopleura and Metridium, the individual that initiates the stinging drives away and often wounds or kills the intruder (Francis, 1973), Acontia appear to be the main method of interspecific defense since they are commonly ejected from the base of disturbed animals (Stephenson, 1928). Recent studies in Norwegian fjords have shown that adult M. senile are capable of quickly colonizing areas in which the resident Metridium have been killed due to oxygen depletion (Wahl, 1985). Immigration of adult Metridium may explain why few areas contain small individuals, which could be at a competitive disadvantage against adults.

Species of Urticina (= Tealia) are carnivores that can trap prey of considerable size. Urticina piscivora, which eats fish and starfish such as Dermasterias imbricata (Sebens and Laakso, 1978; Elliot, et al. , 1985), probably is one of the top-level carnivores in the food chain of the OCS hard substrate communities. Urticina columbiana commonly is observed with its column surrounded by sediment, its base attached to a subsediment rock. This species therefore appears to be somewhat resistant to sediment encroachment. Individuals produce a small number of eggs that spend approximately 10-30 days in the plankton, then transform into a barrel-shaped planula larva, and finally settle (Rieman-Zurneck, 1976). Urticina have the potential to live for many years, and probably are representative of the final successional stages in community development.

The genus Actinostola, a member of the A. callosa complex, represents anemones with giant larvae which are brooded and then released as long-term planktonic larvae (Reiman-Zurneck, 1976). This anemone has a swimming response if contacted by several species of predatory sea stars. Little else is known of the biology of these outer shelf and slope anemones.

Corynactis californica is a suspension-feeding corallimorpharian intermediate between corals and actinians, and forms attached clone sheets that may be quite stable and long lived (Carlisle et al., 1964; Hand, 1954). Corynactis californica is an aggressive colonizer that can invade and overgrow other organisms, largely through the use of mesenterial filaments that contain toxic nematocysts. Metridium senile appears to be one of the few species that is not displaced (Chao, 1975). Even starfishes are sensitive to dense clonal sheets of Corynactis because their podia are stung by the nematocysts (McLean, 1962a). Colonies of Corynactis have been observed to approximately 65 m depth, Lophelia pertusa, an ahermatypic suspension-feeding coral species, from English waters is very similar in growth form to L. californica observed off California. Lophelia pertusa, however, can establish itself on small cobbles; whereas L. californica appears most commonly on steeper rock faces. Lophelia forms heads that may be broken apart by the action of borers or by disturbances (e.g., anchoring or trawling). Broken heads often litter the substratum around the original colony; these can in turn become centers of growth. In this fashion a colony spreads apart, forming rings, or is distributed over a broader area (Wilson, 1979). There are many associated organisms, including ophiuroids and gastropod, living on or within the colonies (Wilson, 1979). Burial probably would destroy existing colonies, but some dredging or trawling might actually spread parts of colonies to serve as nuclei for further growth and dispersal.

Balanophyllia elegans, ano the r suspension feeder, is a solitary cup coral common to deep water hard substrate areas. Unlike Lophelia, B. elegans is not capable of dispersal through fragmentation and disruption. This species liberates a few short-lived larvae which usually disperse to less than 0.5 m from the adults and which consequently appear to have a very low capacity for colonizing distant new areas (Gerrodette, 1981). This lack of dispersal ability may account for apparent aggregations of this species within its range.

In general the Cnidaria represent one of the most successful groups in offshore hard substrate habitat. This success appears to be the result of efficient partitioning of food resources among the different groups (e.g., noted in Sebens and Koehl, 1984), multiple strategies of colonization, aggressive and defensive utilization of nematocysts, and adaptations of some species to strong currents and sedimentation.

4.2.2,3 Brachiopoda. The brachiopods generally constitute a minor component of the extant marine biota, and are represented in deep water hard substrate habitats by only a few species. Summary information is presented in Table 4-1C. However, at times brachiopods can occur in high numbers and may dominate the biomass of the community (e.g., observed from the present November/December 1987 survey). Species of the Class Articulate, of which Terebratalia transversal is a local representative, inhabit marine hard substrates and are found worldwide from the intertidal to 5000 m (Hyman, 1959). The Articulate actively filter feed and use external water movements to augment their ciliary feeding currents by orienting the shell gape at right angles to prevailing current flows. They feed primarily on unicellular flagellates and diatoms, detrital particles, and through absorption of dissolved organics (Chuang, 1956; Cowen, 1971; McCammon, 1969; McCammon and Reynolds, 1976). All brachiopods reproduce sexually; Terebratalia transversal appears to release a nonfeeding larva which settles within hours of release. It has a moderate growth rate, reaching 10 mm the first year and up to 25 mm by the end of the second year (Paine, 1969a). This species probably lives several years, and often the shell is heavily encrusted by other organisms. Dense aggregations may result, in part, from the limited dispersal ability of the larvae and/or a preference for settling near adults. Recovery from a disturbance by an existing population would require several years. Colonization of a newly exposed substrate (e.g. , a Type 2 patch) may occur slowly because of their limited dispersal ability.

4.2.2.4 *Echinodermata*. Representatives of all five extant classes of echinoderms including sea lilies (Crinoidea), sea cucumbers (Holothuroidea), sea stars (Asteroidea), brittlestars and basket stars (Ophiuroidea), and sea urchins (Echinoidea) are often common or dominant members of deep water hard substrate communities. Summary information is presented in Table 4-ID. The only species of Crinoidea found off California is *Florometra serratissima*. *Parastichopus*, *Cucumaria*, and *Psolus* all of which occur subtidally off California, are representative of the Holothuroidea. Details of the life histories of the many species of Asteroidea found on hard substrates are exemplified by the genera *Henricia*, *Pycnopodia*, *Stylasterias*, and *Mediaster*. The Ophiuroidea are represented by *Ophiothrix spiculata*, *Amphipholis squamata*, *Ophiopholis aculeata*, and the basket star *Gorgonocephalus eucnemis*, all of which are common on many hard substrate areas off California. Finally, the Echinoidea are exemplified by *Stronglocentrotus*.

The crinoid *Florometra serratissima* generally is restricted to deeper water along the California coast (60-1000 m). This species is a conspicuous member of the hard substrate community, and sometimes dominates the biomass. *Florometra* is a filter/suspension-feeder, trapping zooplankton and detritus on mucus trails driven by ciliary currents. All crinoids have separate sexes and produce larvae that are short-lived, thereby limiting their dispersal ability (Hyman, 1955). *Florometra* is probably long-lived and slow-growing, and larval recruitment to distant areas (e.g., Type 2 patches) may be difficult. Adults, however, swim freely when disturbed or to escape predators and can creep up to 40 m/hr (Hyman, 1955). Immigration via swimming or tumbling with current flows and creeping may help adults colonize new areas.

The other four classes of echinoderms are common throughout intertidal and subtidal habitats. The sea cucumbers (except for *Parastichopus*) are not a conspicuous component of the offshore rocky community. *Parastichopus*, the largest sea cucumber on the California coast, is abundant on both soft and hard substrates, where it feeds by ingesting sediments and detritus accumulated in cracks and crevices (Brumbaugh, 1980). *Parastichopus* release larvae that spend up to 13 weeks in the plankton. Other sea cucumbers are more intimately related to rocky habitats and include some species in the order Dendrochirotida (e.g., *Cucumaria* spp.). These sedentary cucumbers usually are hidden in holes and cracks and are observed only when the tentacular plume is extended above the substrate during feeding (Smith, 1962). Sexes are usually separate. Unlike *Parastichopus*, the larvae are either brooded, resulting in direct development, or released for a brief planktonic stage, resulting in indirect development (Hyman, 1955; Chia and Buchanan, 1969; Fish, 1967). Regardless of the mode of development, larval dispersal for this group appears to be limited, as noted for many filter/suspension feeders in other phyla. *Cucumaria* appear to grow slowly, some species requiring four years to become sexually mature, and probably are long lived (Rutherford, 1973; Smith, 1962). Since adults tend to be sedentary, colonization of new areas most likely occurs from larval settlement. Factors that determine initial colonization success for larvae are unknown, and recovery times would be dependent upon these factors.

Sea stars (Asteroidea) are large, distinct members of many deep water hard substrate areas. Sea stars appear to be most diverse in the North Pacific, where they occupy a wide variety of habitats (Feder, 1980). Most species are carnivores but some also are omnivores or scavengers. The methods of obtaining food are diverse (Feder and Christensen, 1966). Some species, such as Henricia, trap food particles in mucus and sweep them into the mouth on ciliated tracts, a form of suspension feeding (Anderson, 1960), while others, such as Pycnopodia swallow whole prey items, which they digest internally (Christensen, 1970; Paul and Feder, 1975). Pisaster has a partially eversible stomach and initiates digestion of prey items externally (Christensen, 1957; Feder, 1959). Many potential prey organisms, such as anemones (Ward, 1965), sea cucumbers (Margolin, 1976), gastropod (Bullock, 1953; Margolin, 1964), and bivalves (Ansell, 1967), exhibit avoidance responses to contact with, or the presence of, predatory starfish (Mauzey et al., 1968; Feder and Christensen, 1966).

Most starfish exhibit external fertilization and planktonic larvae, representing the potential for broad dispersal. Other species, such as Henricia, brood eggs which develop directly into juveniles, thus limiting potential dispersal (Chia, 1966). Echinoderms in general have the ability to regenerate body parts (Swan, 1966). This type of asexual reproduction may be an important mechanism in competing against other potential colonists.

Growth in starfish depends mainly on temperature and food supply (Feder, 1980); consequently, size may not be a good indicator of actual age. Sea stars living where food is sparse may be conspicuously smaller than individuals from areas where food is plentiful (Feder, 1980; Paine, 1976). Individuals that are starved slowly decrease in both weight and size (Feder, 1980). Growth is usually slow and life spans may be fairly long. Pisaster ochraceus, for example, may live at least 20 years (Feder, 1970; Feder and Christensen, 1966; MacGinitie and MacGinitie, 1968).

Starfish larvae suffer heavy mortality from filter\suspension feeders; however, once adult size has been reached starfish have few enemies (Feder, 1980). Some nudibranchs, gastropod, fishes, and other sea stars are the major predators. The seastars, Pycnopodia helianthoides and Solaster species, represent the top level invertebrate carnivores in many offshore rocky habitats. Starfish predation may determine the distribution of prey items; and thus, directly influence community composition in intertidal and subtidal areas (Dayton, 1971; Paine, 1969b, 1974).

Brittle stars (Ophiuroidea) commonly occur on soft substrates; however, many species, such as Amphipholis squamata, Ophiothrix spiculata, and Ophiopholis aculeata are restricted to rocky habitats. In general, the biology of rocky offshore ophiuroids is poorly known. This group of animals appears to utilize a broad range of feeding strategies. Some species utilize filter/suspension feeding methods by extending their arms into current flows. Other species are surface deposit feeders, feeding either by sweeping their arms across the bottom or by direct ingestion of sediments and detritus trapped in cracks and crevices. Some ophiuroids also are predators or scavengers (Austin and Hadfield, 1980). Many species appear to be opportunistic, utilizing several or all of the different feeding modes depending upon the available food resources (B. Thompson, pers. comm., 1987).

Reproduction includes both internal and external fertilization. External fertilization usually produces large numbers of small planktonic larvae which are long-lived, thereby representing the potential for broad dispersal (Austin and Hadfield, 1980). Other species, for example, Amphipholis squamata, produce a few large eggs which are brooded and develop directly into juveniles (Fell, 1946) . Still other species exhibit an intermediate condition, producing short-lived larvae with a yolk supply which provides for some dispersal, but presumably minimizing mortality in the planktonic stage.

The largest ophiuroid, the basket star *Gorgonocephalus eucnemis*, has been the subject of several studies, so that some aspects of its biology are well known. The species is common in the North Pacific and Atlantic from 10 m to 2000 m (typically between 15 and 150 m) depth. Outstretched adults may have a diameter of over 0.5 m. *Gorgonocephalus eucnemis* is primarily a suspension feeder with its arms outspread more or less perpendicular to ambient currents. Basket stars capture zooplankton on an array of microscopic hooks on the arm branches. The species also may feed on small benthic animals, including sea pens (MacGinitie, 1949; May, 1924; McDaniel, 1975; Patent, 1970).

Reproduction and early development of basket stars is relatively direct; the larvae are non-swimming and thus have limited ability for dispersal. Young basket stars are commonly observed within the pharynges of the soft coral *Gersemia* (Patent, 1969, 1970). This is believed to be the result of passive ingestion of larvae, and it may provide a nursery habitat that offers good current flows and relatively few predators. After developing for a time inside the soft coral, the juveniles emerge and cling to the outside for a period before moving onto an adult basket star. Once established on adults, juveniles feed on food captured by the adults, and they do not move until their arms have grown sufficiently long and branched to be efficient in feeding (Patent, 1969, 1970) . Recolonization"by this species apparently would require adults in the vicinity or immigration of adults. Larval settlement and growth in the absence of adults may be an extremely slow process.

The final echinoderm group is the sea urchins (Echinoidea), of which only a few species are commonly found in offshore rocky areas. *Strongylocentrotus purpuratus* and *S. franciscanus* are most common in intertidal and shallow subtidal areas but have been observed in some hard substrate areas at depths of over 160 m (Lissner, pers. ohs.). These species tend to be algae feeders (particularly on *Macrocystis*), but they also are capable of scraping hard substrate for food, and can absorb organics directly (Hyman, 1955). The presence of these species in offshore rocky habitats may be an indicator of regular algal inputs to the habitat. Typically, sexual reproduction and external fertilization produce large numbers of small larvae. Larvae are planktonic for a few days to months, thereby representing the potential for broad dispersal, Large *S. purpuratus* may live 8 to 10 years and *S. franciscanus* may reach 15 to 20 years of age (Ebert, 1968; Swan, 1961). Recovery and recruitment for these species probably would require several years.

4.2.2.5 *Arthropoda.* Crustacea are the dominant arthropods in the marine environment. Ecologically, the crustacea are extremely important as an intermediate trophic group between primary producers and larger carnivores. Summary information is presented in Table 4-1E. Although the crustacea are well represented in many offshore hard substrate areas, many species (e.g. , amphipods, isopods, tanaids), are small and very poorly known and are therefore not included in this summary. Barnacles and crabs are the most conspicuous crustaceans that are commonly found in offshore areas *Arcoscalpellum californica* and *Conopea galeata* are generally representative of deep water hard substrate barnacles. Cancer magister represents the only crab characteristic of deep water that has been studied in any detail. The biology of deeper water forms (e.g., Galathea, Paralithodes, and Paramola) in California waters is virtually unknown.

The barnacles (Cirripedia) are sessile, highly modified crustaceans, that live attached either to hard surfaces or to other organisms. Hermaphroditism is common, although cross-fertilization may be more important than self-fertilization. Fertilized eggs generally are brooded, and long-lived planktonic nauplius larvae that eventually metamorphose into cyprid larvae are released. The cyprid is a nonfeeding, swimming stage that represents the potential for broad dispersal, such as is common to Type 2 patches. Settlement cues depend upon a variety of physical and chemical stimuli (reviewed by Lewis, 1978); most cyprid larvae are strongly attracted to adults of their own kind, although Conopea galeata larvae settle on gorgonian corals (Newman and Abbott, 1980). Adults of some species live for only a few weeks or months; others persist for several years to decades (Newman and Abbott, 1980).

The other common crustacean group are the true crabs (Brachyura), which represent the highest development attained by articulated marine animals (Garth and Abbott, 1980). Most crabs are carnivores; others are omnivores or scavengers. The deep water galatheid crabs also may utilize suspension feeding to some extent. The large and commercially important Dungeness crab (Cancer magister) has been found to eat over 40 different species of crustacea, bivalves, worms, and fishes (Gotshall, 1977; Poole, 1967). Males of this species mature in 1 1/2 to 2 years and require at least six years to attain maximum size (MacKay, 1942; Waldron, 1958). In contrast, the deep water crab Paralithodes appears to be a slow-growing species, living up to 15 to 20 years (Barr and Barr, 1983). Crabs generally can recolonize areas rapidly by the immigration of adults. Some species may have limited mobility as adults, and thus may be slower recolonizers. However, the abundance of long-lived planktonic larvae could cause recruitment to occur relatively quickly, within a few years.

4.2.2.6 Mollusca. The snails, slugs, and their allies (Class Gastropoda) are the most numerous molluscs, representing about 80% of all molluscs. octopus (Class Cephalopod) are common on some hard substrate areas. Chitons (Class Polyplacophora) are occasionally collected on hard substrate. Summary information is presented in Table 4-1F. Placiporella velata and Lepidozona are presented as representative of deep water hard substrate chitons. Although gastropod are relatively common in some hard substrate habitats, many of them are small and cryptic. Two subclasses of gastropod, Prosobranchia (snails) and Opisthobranchia (including nudibranchs), include most of the gastropod found in deep water hard substrate areas. Two large snails, Ceratostoma foliatum and Fusitriton oregonensis were selected as representative of the prosobranch gastropod, and Aeolidia papillosa and Dendronotus spp. are presented as examples of the nudibranchs (Opisthobranchia). Ceratostoma foliatum and F. oregonensis are active predators, feeding on barnacles and bivalves (Abbott, 1974) and tunicates (Young, 1985), respectively. The eggs of both species are brooded and laid in egg cases attached to hard substrate. Development takes several months (four months for Ceratostoma at 11°C) and results in direct development of small juveniles. Growth is slow (8 to 15 mm per year); Ceratostoma reaches maximum size in about 4 years. Individuals of Ceratostoma may live up to 16 years (Spight et al., 1974; Griffith, 1967).

Recovery of populations of these large snails requires the immigration of adults, and large-scale disturbances (e.g., sediment encroachment) could present barriers to rapid recovery.

The other common group of gastropod, the nudibranchs, generally are short-lived primary predators on a wide variety of sessile organisms, including sponges, hydroids, and anemones. Reproduction is variable, often involving a complex hermaphroditic reproductive system. Many nudibranchs lay egg cases, which may directly develop into juveniles or planktonic larvae (Beeman and Williams, 1980). Most species are small and probably are annuals; a few may live for several years. Recovery of most species would probably occur within a year.

The nudibranch *Aeolidia* is a large predator on anemones. It prefers *Metridium*, but also eats *Urticina*, both of which are common in many deep water hard substrate areas. *Aeolidia* appears to be selective for damaged or wounded individuals. *Aeolidia* lays eggs in thin-walled capsules on hard substrate (Braanis and Geelen, 1953; McFarland, 1966, Marcus, 1961; McDonald and Nybakken, 1978; Russel, 1942; Stehouwer, 1952; Waters, 1973). Another nudibranch, *Dendronotus iris*, is one of the largest species. It prefers to feed on tube-dwelling anemones which may be common on soft substrates (Robilliard and Baba, 1972; McDonald and Nybakken, 1978; Wobber, 1970). Eggs are often laid on anemone tubes; they hatch into planktonic veliger larvae in 10-20 days.

Chitons (Polyplacophora) are primarily grazers of the algae or epibiota on rock surfaces. Some are omnivores, and *Placiphorella velata* can also function as a predatory carnivore (McLean, 1962b; Haderlie and Abbott, 1960). In general, little is known of their life history. Most chitons brood their eggs, releasing short-lived veliger larvae. Thus, they probably have limited dispersal ability.

The final molluscan group is the Cephalopod, which includes *Octopus* spp. *Octopus* are common predators in many offshore and intertidal rocky areas, feeding primarily on crabs, molluscs, and fish (Lane, 1960; Pickford, 1964). The sexes are separate. Eggs are brooded for a few months and hatch into young, which tend to be pelagic for days to weeks (Gabe, 1975). *Octopus dofleini* may live up to five years in the field (Pickford, 1964). Recruitment by adult immigration is probably important for rapid recovery. Recruitment of young would result in a delay of a few years before a breeding population became established.

4.2.2.7 Annelida (Polychaete Worms). A diverse polychaete fauna is characteristic of many offshore areas, and new species are commonly discovered. In this section, a brief summary is presented of the more common genera found in key families of subtidal hard substrate areas. Summary information is presented in Table 4-1G. Papers by Schroeder and Hermans (1975) and Fauchald and Jumars (1979) provide the best current reviews of polychaete reproduction and polychaete feeding, respectively. The life history summaries are derived primarily from Abbott and Reish (1980), Jumars and Fauchald (1977) and Hartman (1968, 1969).

Species of Halosydra and Harmothoe, of the Family Polynoidae (scale worms), are known to inhabit hard substrate and soft substrate habitats from the intertidal to a depth of at least 500+ meters, from Alaska to Baja California. They can be commensal within the tubes of other polychaete species, within the shells of hermit crabs, with sea stars, or free living. They have a jawed, muscular, eversible proboscis, and are considered to be carnivorous. They reproduce sexually, producing planktonic larvae. Some species have been reported to brood their larvae between the scales and the dorsal surface of the body and release late-phase planktonic or demersal larvae. Thus, they can recruit either to the immediate area or to distant areas. They are generally considered to be slow-growing and relatively longer-lived.

Members of the Family Phyllodocidae (e.g., Eulalia, Phyllodoce) are known to inhabit hard substrate and soft substrate habitats along the California coast from the intertidal to shelf depths. They are motile, but occasionally have been seen in the tubes of other polychaetes (e.g. , Chaetopteridae). They have a muscular, eversible pharynx; some are thought to be carnivorous, others deposit feeders. Reproduction is generally sexual and usually results in planktonic larvae. Some species have been reported to brood or to lay eggs in a gelatinous mass. Phyllodocids can thus recruit to distant areas, or they may, in specific cases, recruit to the immediate area. They are considered to be fast-growing and short-lived, although a few species can grow quite large and may be long-lived.

Species in the Family Syllidae (e.g. , Exogone, Syllis) occur On hard and soft substrates from the intertidal to shelf depths, and they range from Baja, California to Alaska and Japan. They are motile, but some have been reported in the tubes of the foraminiferan Astrorhiza. They have an eversible, jawed pharynx, and are considered to be carnivores and/or herbivores. Reproduction in this family may be asexual or sexual, the latter producing planktonic larvae. Thus, syllid polychaetes can recruit to distant areas via planktonic larvae, or they can populate nearby areas by budding. Syllids are small, fast-growing, short-lived animals.

Phyllochaetopterus prolifica (Chaetopteridae; Potts, 1914) has been reported from hard and mixed substrates from British Columbia to southern California. It occurs from approximately 3 to 450 m depth. It is a sedentary tube-dweller which actively filter feeds by pumping water through its tube, or passively suspension feeds by holding tentacles erect in the water column. It also can feed on surface deposits. P. prolifica can reproduce and disperse in two ways. Small, young individuals reproduce asexually by fission, and larger individuals reproduce sexually to produce planktonic larvae. This species is well adapted to settle in new habitats, colonize, then disperse to other areas. It is a larger, slow-growing species. Chaetopterids can host commensal animals, and clusters of their tubes can provide habitats for other invertebrates.

Sabellaria cementarium (Sabellariidae) has been reported from hard and/or mixed substrates from Alaska to southern California to depths of 80 m. It is a sessile tube-dweller and a tentaculate filter-feeder. It reproduces sexually and has a long planktonic larval phase. When the tube is opened by some sort of disturbance, spawning may be stimulated (Abbott and Reish, 1980). It is considered to be a slow-growing, long-lived species.

Species in the Family Sabellidae, notably Eudistulia polymorpha and Sabella crassicornis, inhabit hard and soft substrates on the continental shelf and slopes from Alaska to southern California and off northern Europe. They are sessile or discretely motile tube dwellers, passively filter feeding with prostomial tentacles (commonly referred to as gills). They can reproduce sexually, yielding planktonic larvae. Hermaphroditism is common in sabellids, but they can also reproduce asexually by fission. Sabellids are thus capable of dispersing to distant areas or of populating the immediate area. Because their tentacles are exposed when feeding, sabellids are preyed on heavily by fish, and collected individuals are commonly in the process of regenerating their anterior regions. Some hydroids live symbiotically on the tubes of sabellids with the feeding zooids of the hydroid ringing the distal margin of the worm tube. The Sabellidae include both small, fast-growing species, which would be expected to recover rapidly from a disturbance, and larger, slow-growing species,

The Serpulidae are known from hard substrates from the intertidal to at least 100 m depth from Alaska to southern California. They are sessile, build calcareous tubes, and are tentaculate filter feeders (Straughan, 1968). Some species form dense clusters of tubes, thus excluding some competitors for living space. Serpulids reproduce sexually and have long-lasting planktonic larvae, but can also reproduce asexually by fission. Therefore they are capable of recruiting to both distant and nearby areas. Serpulids are like the sabellids in that there are both small, fast-growing and large, slow-growing species.

Members of the Family Spirorbidae inhabit hard substrates worldwide from the intertidal to shelf depths. They are sedentary, calcareous-tube builders, and tentaculate filter feeders. They reproduce sexually and have short term planktonic larvae; some species brood larvae in their operculum or tube and release them as late-stage larvae. Many species are hermaphroditic and breed throughout the year. They are small and fast-growing and have been spread worldwide, in part via ships. Many live less than one year. Because they grow quickly, spirorbids would be expected to recover rapidly from disturbance.

4.2.2.8 Ectoprocta (Bryozoa). Ectoprocts are broadly distributed over all the world's oceans to depths in excess of 4,500 m (Hyman, 1959). Diversity is highest on the shelf, where there can be hundreds of species, and drops-off rapidly below approximately 300 m (Hyman, 1959; Schopf, 1968). There have been few deep-water collections of ectoprocts off central and northern California. Geographic and depth-range data listed in Osburn (1950, 1952, 1953) are drawn principally from studies in Puget Sound and north, or from Point Conception and south . The present study and the ongoing MMS CAMP program will provide important data to augment the ranges and species reported by Osburn. In view of the poor state of knowledge concerning any of the deep water species, ectoprocts generally are considered as a group in this section. Summary information is presented in Table 4-1H.

Ectoprocts typically are found in hard substrate habitats and in or on the surfaces of other organisms, with the exception of a few species that can utilize sand grains as a substrate (e.g., see Larwood, 1973). Deep water taxa that harbor ectoprocts (principally as epibionts) include calcareous sponges (Osburn, 1952), tunicates, hydroids, and the shells of taxa with external calcareous skeletons (Hyman, 1959). Encrusting ectoproct species are common in shallow subtidal areas. However, with increasing depth arborescent genera (for example, Cellaria and Phidolopora) become more prevalent than encrusting species, Ectoprocts are generally suspension feeders (Hyman, 1959), feeding predominantly on plankton and protozoa in shallower waters (Ryland, 1970) and on detritus in deeper waters (Schopf, 1968).

Ectoprocts produce new colonies through sexual reproduction and larval dispersal (Hyman, 1959). The numbers of larvae produced and the length of their planktonic life vary greatly among groups of species, resulting in a broad mix of reproductive strategies (e.g., Ross, 1979). In general, nonbrooding species (for instance the common shallow water species of Membranipora spp. that colonize marine algae) produce larger numbers of larvae with longer larval lives than do brooding species. Some brooded larvae may settle immediately adjacent to the adult colony (Scanland, 1971). For two common brooding species off California, Nielsen (1981) reported that settlement began within 1 to 2 hours and was complete within 12 hours from the time of larval release. He further reported that a new egg was in the brood chamber within 24 hours after the release of the prior brood.

Available information on ectoproct recruitment suggests that the common factors such as substrate type and some chemical cues (e.g. , Eggleston, 1972) are important to larval recruitment. The probability of recruitment by a particular species may be low (Winston and Jackson, 1981), but since a few hundred species , typically occur in a shelf/slope region (Schopf, 1968), some ectoprocts are likely to recruit to available surfaces. The relatively small dispersal distances for many brooding species will tend to limit recruitment in areas which have sparse local hard substrate habitat, and to enhance recruitment within areas of more continuous hard substrate habitat.

Ectoprocts are, with a single exception, sessile organisms, and are thus unable to move to avoid deteriorating environmental conditions. Arborescent species have some ability to avoid sediment accumulation by growing above the surface of their attachment point. However, most ectoproct species would be suffocated by deposition of the sediment more than a few millimeters deep, and recruitment would be expected to be hindered by high deposition rates.

Growth rates of ectoprocts are usually expressed in terms of numbers of individuals added to the colony per unit time. Estimates of the number of individuals produced in a month's time range from a few hundred to more than 10,000 (Hyman, 1959; Ryland, 1970). Many ectoprocts reproduce for the first time at an early age, usually less than one year (Winston and Jackson, 1981) and sometimes in as little as three to five weeks (Hyman, 1959). Typical life spans are greater than six months (Winston and Jackson, 1981).

Ectoprocts can be rapid primary surface colonizers (e.g. , both Type 1 and Type 2 patches), settling on new surfaces within one week, but they are poor competitors for space (Scanland, 1971). They are also continuing colonizers of epifaunal associations due to their ability to colonize the surfaces of other epifaunal species (e.g., Hyman, 1959). It is not presently known how long it would take for a disturbed ectoproct association in deeper water to recover from a disturbance, such as a deposition of sediment. However, key factors would include the proximity of other undisturbed associations as a source of recruits and the post-event exposure of suitable settling surfaces which are relatively clear sediment accumulations.

4.2.2.9 Urochordata. The taxonomy of shallow subtidal tunicates of the eastern Pacific is very well known from at least Alaska to Mexico. Huntsman (1912a,b), Ritter (1907, 1913), and Van Name (1945) described the majority of species, and only a few new species have since been described. There is some information on deeper water forms from Alaska and the Bering Sea, and from southern California. However, little is known on the deeper water species from central and northern California. Three orders of urochordates are represented in the hard substrate fauna: Aplousobranchia, Phlebobranchia, and Stolidobranchia. However, too little is known of individual species to illustrate life history data of each class on the basis of representative species. Therefore, the majority of the information in this section is an extrapolation of data from other regions, based on current knowledge of ascidian life history (e.g., Abbott and Newberry, 1980; Berrill, 1950). Summary information is presented in Table 4-11.

Van Name (1945) states that it is difficult to divide the Pacific coast into faunal regions because "cold water prevails along the entire Pacific coast from the southern boundary of California northward, and ascidians characteristic of the latitude of British Columbia can find temperature conditions favorable to them" much farther south at a variety of depths. The most valuable taxonomic reference works on ascidians are Van name (1945), Tokioka (1967), Abbott and Newberry (1980), and Kozloff (1987). Tokioka (1963) observed that a number of Japanese ascidian species are also found on the north American Pacific coast, so that some additional species may be found at the 50-500 m OCS depths, due to the larvae being carried by the Kuroshio Current.

Common genera in the Order Aplousobranchia include Aplidium, Polyclinum, Didemnum, Archidistoma, and Cystodytes. Most are colonial forms, and most of those are compound (in a common tunic); a few species are social. All tunicates are filter feeders. Most species are annuals, although basal portions may over-winter. Most species produce their young during spring and summer and recolonization of bare rock can be very rapid. It is unknown whether recolonization will occur on silty rock. There may be intense interspecific and intraspecific competitive interactions within this order, especially during the spring and summer. Species in this group do not tolerate siltation, and most require active water flow.

Common genera within the Order Phlebobranchia, include Ciona, Ascidia, Chelyosoma, and Agnesia. Nearly all are solitary forms, although a few are social. The life span of many species is less than one year, although Ascidia Spp. may live one to two years. Some species breed all year, others are seasonal (either spring/summer or winter/spring). Most species spawn their eggs and sperm, but a few are brooders. In all California species the tadpole larvae are small and numerous, and not yolky. The duration of the larval stage is several hours or days. Most species are rapid colonizers of disturbed hard substrates, but most do not persist in a community over many years unless there is a pattern of yearly disturbance. Most species can tolerate some siltation and pollution, and prefer to live in areas at reduced water flow (C. Lambert, pers. ohs.). Predators include some prosobranch and opisthobranch molluscs, flatworms, and fish (Lambert, 1968; Young, 1985).

Nearly all of the species in the Order Stolidobranchia are solitary, including *Styela*, *Pyura*, and *Boltenia*; there are a few compound species (*Botryllus*, *Botrylloides, Metandrocarpa*). The life span may be five to seven years or more for solitary species, but is probably shorter for the compound species, Reproductive maturity is reached by some botryllid (compound) zooids in a few weeks. The solitary forms probably do not reach maturity until the second year.

Both brooders and spawners occur among the Stolidabranchia, so it is difficult to provide generalizations about reproductive strategies. This order is considered to be the most highly evolved and complex of all the tunicates. Tadpole larvae may persist for one to two days, so dispersal may be more widespread than in the phlebobranchs. Recruitment is not usually to bare surfaces. The solitary stolidobranchs replace early colonizers on hard substrates, and frequently displace phlebobranch tunicate populations. The botryllids are usually epizootic on mussels and solitary ascidians (either phlebobranchs or stolidobranchs). Recovery and recolonization by solitary forms usually occurs slowly over several years if the substrate, once disturbed, remains subsequently undisturbed. Botryllids may recolonize at a faster rate. Larval selectivity for substrates is not well known.

CHAPTER 5: RECOMMENDATIONS AND FIELD SAMPLING METHODOLOGIES FOR FUTURE STUDIES

This chapter identifies the primary study areas where there are data gaps on recovery and recolonization, as noted in Chapters 2 through 4 (Section 5.1); makes recommendations for future studies, including proposed methodologies, based on these gaps (Section 5.2); and discusses the relevance of recovery and recolonization studies to the MMS decisionmaking process for oil and gas development activities (Section 5.3).

5.1 SUMMARY OF DATA GAPS

Informed decisionmaking by the MMS regarding oil and gas development activities that might impact hard substrate communities of the OCS requires knowledge of several factors:

- Types and frequencies of natural and potential oil and gas related disturbances;
- Areal extent and type (e.g. , high relief and low relief) of hard substrate features;
- Biological communities (species taxonomy and life history characteristics) associated with the hard substrate features; and
- Processes which influence community dynamics including biological and physics'1 interactions that affect recovery and recolonization.

As discussed in Chapter 2, disturbances (natural or anthropogenic) to hard substrate communities typically create a patch or space that subsequently becomes available for recolonization. The significance of the disturbance event generally can be defined in terms of the destruction or alteration of the community, but this determination requires knowledge of the type and extent of the substrate and associated organisms that occurred prior to the disturbance. Accurate prediction of the recovery of a community then requires a knowledge of species' life history characteristics including the availability and selectivity of larvae, growth rates of juveniles and adults, the processes which influence biological interactions, and the frequency and severity of subsequent disturbances .

The types and frequencies of disturbances, in terms of patch creation, from oil and gas development are generally predictable. They are associated with anchoring and disposal of drilling muds and cuttings (e.g., National Academy of Sciences, 1985 ; Neff, 1987), are of relatively short duration, and are localized near individual platforms, In addition to these studies, information on potential impacts (e.g., from drilling muds and cuttings) to hard substrate communities near Platform Hidalgo will be available from the MMS California Monitoring Program (CAMP).

In contrast to the knowledge of anthropogenic disturbances, there is little information on natural disturbances to deep water hard substrate communities, particularly as related to the effects of sedimentation. As noted in Chapter 3, accurate prediction of effects from man-induced disturbances requires detailed knowledge of the frequency and severity of natural disturbances. This knowledge is critical to distinguish natural from anthropogenic effects. It also may provide supportive data on organisms' responses to these disturbances since some effects (e.g. , natural sediment encroachment and disposal of drilling muds and cuttings) may somewhat mimic each other. Data anticipated from the MMS CAMP program potentially will provide information on sediment movement and associated bottom currents at two sites along the California coast. This information will be important to demonstrate site specific effects but also will be generally applicable to studies of benthic sediment processes. Additional site characterizations , including measurements of near bottom currents, will be necessary to determine the frequency and intensity of sediment movement in other geographic regions such as the MMS Northern and Central California planning areas. However, ongoing and planned programs such as CODE (Coastal Ocean Dynamics Experiment), STRESS (Sediment Transport Events on Shelves and Slopes),and BECOST (Biological Effects of Coastal Ocean Sediment Transport) will provide significant data related to sediment transport events, processes, and effects on biological communities (Newell et al., 1987). It is evident from numerous studies (e.g., reviewed in Sebens, 1986), that the frequency of disturbances can have a profound effect on the recovery/recolonization process.

Prediction of potential effects from disturbances within a specific geographic area also requires detailed knowledge of the type of communities and the areal extent and type of substrate. This information is generally available for many of the communities of the California OCS (e.g., SAIC, 1986; Battelle, 1988; present study) and allows some predictions of which organisms may be encountered on a given substrate type (e.g., vertical relief), Substrate information obtained remotely from side scan sonar records exists for many OCS areas; however, these records generally cannot distinguish exposed low relief outcrops from those that are covered by a thin (up to one meter or more) sediment veneer. The side scan records therefore tend to overestimate the percentage of exposed (coIonizable) hard substrate area (e.g., SAIC, 1986; present November/December 1987 survey). Verification of exposed low relief areas is best obtained using photographic methods (e.g. , ROVs).

Information on the taxonomy and life history of most deep water hard substrate organisms is severely limited, especially for some groups such as sponges and hydroids which are important components of many of these communities. Detailed information on every species is not necessary to make useful predictions of impacts and the potential for recovery and recolonization of a disturbed area. However, this knowledge needs to be expanded significantly, particularly for common or dominant taxa, by additional collections of voucher specimens, selected laboratory studies (e.g., related to larval recruitment), and field experiments (Section 5.3).

Finally, as noted by Boesch et al. (1987) there is a "remarkable ignorance about the processes and rates of recovery of living resources and ecosystems. . . after perturbations caused by either natural events or human activities. " Chapter 2 summarizes current ecological theories and models that should be important to the processes influencing the recovery/recolonization of deep water hard substrate communities. However, most of these theories and models were derived from studies of intertidal or shallow subtidal communities. There are few experimental data to demonstrate their applicability to deep water communities few (however, see Witman, 1987) . Studies to address these processes should include testing of biological effects and community interactions; study design should be in accordance with rigorous, testable hypotheses and approaches (e.g., Boesch et al., 1987).

The following section describes some recommended studies that could be performed to address species and community level effects from anchoring and sedimentation disturbances, as defined in Sections 3.1 and 3.2, respectively. These studies attempt to combine rigorous experimental study designs with proven survey methodologies to test the applicability and predictive power of key ecological theories and models to deep water hard substrate communities of the California OCS.

5.2 RECOMMENDATIONS FOR FUTURE STUDIES

Based on an assessment of the primary disturbance factors which appear to affect hard substrate communities of the California OCS coupled with apparent research needs of the MMS, as related to data gaps (Section 5.1) on potential impacts from oil and gas development, two areas of study are recommended: anchoring effects and sedimentation effects. These studies would provide a focus that is directly applicable to MMS decisionmaking regarding the possible long-term impacts of anchoring operations associated with platform and pipeline placement and installation, and the sedimentation effects from disposal of drilling muds and cuttings. Other data gaps noted in Section 5.1, such as taxonomy and life history strategies of some organisms, also are important; however, this knowledge will continue to expand automatically based on the present Study , the MMS CAMP Program, and experimental studies such as those discussed in this section.

As noted in Chapter 3, anchoring effects are more-or-less unique to anthropogenic activities, at least on a scale that commonly is observed, while sedimentation effects can result from both natural and anthropogenic sources. Increased sedimentation, which can result in burial of organisms and substrate and in increased turbidity, may reduce survival and influence community composition. Sedimentation is therefore felt to be a major factor that affects many deep water hard substrate communities. Some elements of these topics undoubtedly will be addressed during the MMS CAMP Program, particularly as related to specific effects from drilling muds and cuttings and “serendipitous” (before versus after) effects from anchoring activities associated with Platform Hidalgo. However, as discussed below it is important to conduct manipulative experiments where practical which can address (quantify) the severity and frequency of the disturbance and the pre-disturbance and post-disturbance (recovery) process of affected communities.

This section first presents a discussion on experimental design (Section 5.2.1). Recommended studies on sedimentation and anchoring effects are presented in Sections 5.2.2 and 5.2.3, respectively, followed by suggested statistical analyses (Section 5.2.4).

5.2.1 Experimental Design

There is strong evidence that physical and biological disturbances are important in structuring deep water hard substrate communities of the OCS. Therefore, many of the objectives of the proposed studies are concerned with estimating disturbance rates and the effects of disturbance on the community. Using an appropriate study design and assuming the operational definitions of disturbance presented in Chapter 3, the effects can be documented of natural or man-made disturbances on the community and the changes that take place subsequent to the disturbance. This section, therefore provides background on considerations and approaches in developing experimental study designs.

The detection of population or community level effects from a disturbance is conceptually straightforward, However, in practice it is often difficult to accomplish because of problems in the study design. Frequently, the data that are available consist of a time series of density estimates at a single site with few or no estimates of the disturbance factors that are thought to be important. It is very difficult to assign causality based on these types of data unless the disturbance is large, discrete and obvious, and the changes in the community are large and essentially contemporaneous. Many studies of the effects of disturbance are serendipitous in that community studies are unexpectedly interrupted by a massive disturbance with obvious biological consequences (e.g., Connell, 1973; Ebeling et al., 1985). A major advantage of very long-term studies is that the likelihood of observing disturbances is high, so that the significance of relatively infrequent events can be assessed (e.g. , Connell, 1978). In other cases, the disturbance may not be extensive, but the occurrence is fairly predictable and the local effects are severe (or can be identified after-the-fact) and often quantified (e.g., Dayton, 1971; Osman, 1977; Sousa, 1979; VanBlaricom, 1982). In cases where the effect of the disturbance is less severe and there are no characteristic "markers" to assess, the problem is considerably more difficult. In these cases, the suspected disturbance may be quantified or estimated and regression techniques applied. However, there is a significant danger that important factors may not be measured or that during a short period of observation the factors measured may not vary sufficiently to provide relevant data. Further, there are likely to be problems of multicolinearity of the independent variables (Freund and Minton, 1979; Freund and Littell, 1981). Studies of this type can be greatly strengthened by experimental demonstrations of the mechanism(s) predicted to underlie the observed patterns (e.g. , Schroeter et al. , 1983) .

If a disturbance can be identified there are several general approaches that can be used to study subsequent changes in community composition and species abundance:

1. Populations that were known to be disturbed can be monitored along with controls, if possible;

2. Disturbances can be mimicked experimentally; or

3. Biological and physical processes can be studied and the effect of disturbance can be evaluated using a model, The model could be a formal mathematical construct, but frequently is a narrative argument or "word model".

In studying the effects of disturbance on community composition and structure, it is important that observations are frequent relative to the disturbances and the population turn-over rates. If study sites cannot be visited frequently, or if the disturbance cannot be well-monitored, the difficulty of the task is multiplied. In these situations it becomes relatively more important to devise experiments to test whether suspected mechanisms of disturbance can cause significant biological changes. Although manipulative experiments are desirable to use where they are feasible, other approaches are possible. Out of necessity, students of geology, evolution, and other historical phenomena that cannot be directly observed rely on "thought experiments". For example, hypotheses can be formulated to describe the phenomenon of interest, followed by predictions which are tested with available field data. These studies are appropriate to the extent that the predications are unlikely to be suggested by alternative hypotheses, i.e. , to the extent that they are "risky".

Studies of disturbance and recovery/recolonization of deep water communities are inherently difficult due to the relative inaccessibility of the habitat which puts severe constraints on the types of observations and experiments that can be attempted. In addition, many of the important species (e.g. , some sponges) are slow growing and long-lived, and population turn over rates may be low. Finally, although little is known of natural disturbance rates, they may also be low. The studies proposed in this section reflect specific experimental designs that focus data collection and analysis needs on a process oriented approach.

Many traditional views of deep water habitats included high environmental homogeneity and seasonal stability (Sanders and Hessler, 1969). In a critique of Sanders' (1968, 1969) "stability-time" hypothesis, Dayton and Hessler (1972) accepted the notion that physical factors were unlikely disturbance agents, but suggested that predation might be an important source of disturbance. An underlying assumption of these and other investigators was that seasonal pulses of primary production at the surface were damped and dissipated before the particles reached the bottom. However, as more studies are conducted, these views are being modified. For example, based on early information it seemed unlikely that seston flux in the deep sea would show seasonal peaks because it was thought that most food (and inorganic materials) reached the bottom as small, slowly sinking particles. However, the presence of organic aggregates in many areas of the world's oceans is now well known (Sheldon et al, 1972; McCave 1975; Silver et al 1978; Hamner et al 1975). These aggregates serve as "enrichment sites" for organic carbon and nitrogenous and phosphorous compounds (Aldredge, 1979; Shanks and Trent, 1979). Additionally, sinking rates of the particles were determined to be much more rapid than assumed (e.g., Aldredge, 1985; Lampitt, 1985). Based on these conclusions it is reasonable to expect that seasonal phenomena at the surface are mirrored somewhat in later events on the bottom.

Just as deep habitats are less seasonally stable than once thought, they also may be less spatially uniform than commonly believed, particularly along continental shelf and slope areas. There is good photographic evidence that water motion and sediment transport vary substantially from one area to another. At one extreme are quiescent areas where the bottom is more or less smooth but broken by mounds of sediments excavated by various infaunal animals (Smith and Hamilton, 1983) . In other areas there is no persistent evidence of bioturbation but the bottom also is relatively smooth. In contrast, in many parts of the world's oceans there are obvious ripple marks on the soft bottom which are evident in photographs taken in water greater than 300 m depth (Menard, 1952;

Rowe and Menzies, 1968; Conan et al., 1981). Sand waves up to 10 or 20 m in height have been observed in some areas at depths of 160 to 770 m (Cartwright and Stride, 1958; Jordan 1962, Shepard et al 1976),

These sediment ripples and waves are evidence of submarine currents of a great range of magnitudes. It is likely that the current regime in a given area is a characteristic feature of the environment and differences between areas may be more-or-less persistent. However, within an area there may be considerable seasonality in the velocity of bottom currents (Rowe and Menzies 1968).

The importance of this temporal and spatial heterogeneity in the present context is that it may provide an opportunity to conduct "natural experiments" in a habitat where manipulations are very difficult. In addition, the seasonality in food supply may be reflected in growth rates which suggests the possibility of aging individuals of some of the sessile species.

5.2.2 Sedimentation Effects Studies

The general approach to the study of sedimentation effects involves six primary elements:

- Selection of hard substrate study sites that represent different regimes of sedimentation (high versus low) and bottom current flow (high versus low), but which have similar areas of low and high relief substrate;
- Selection of a" subset of species that appear to be sensitive to sedimentation;
- Determination of physical variables (e.g., rainfall, stream/river discharges, sediment load, significant wave heights, bottom currents, etc.) by direct measurement or extrapolation that affect sedimentation at the sites;
- Conduct frequent (e.g., quarterly) surveys of the biological communities at each site using ROV photographic methods with two quadrat sizes (e.g., close-up/0.1m^2 and "standard"/0.3m^2) to examine species interactions, and colonization, and general distribution and abundance, respectively);
- Conduct transplants of selected sensitive species to sites characterized by low versus high sedimentation; and
- Perform statistical analyses of the data using ANOVA, cluster, and principal coordinate analysis methods.

In order to maximize the chances of observing disturbance and recovery processes within a reasonable study time, it is important to select sites that vary as much as possible in sedimentation rates. One of the first tasks of the research program should be to identify such sites within several strata of interest. Strata, in this context may include homogeneous areas of depth, substrate relief (low or high), substrate type, and sedimentation and current regimes. If resources are limiting, the number of strata can be reduced to maintain adequate replication within strata.

It is important that relevant physical variables be measured during the course of the biological observations. Since sedimentation is an important variable, it is critical to know as much as possible about the factors affecting this process (i.e., determinants of the frequency and severity of sedimentation) . For example, stream/river discharges and sediment loads, significant wave heights, and primary production in local surface waters might be obtained or estimated from existing sources.

The study of sediment transport using dyed sand was pioneered by Inman and his students at the Scripps Institution of Oceanography. Many of these techniques described by White (1987) in a recent study potentially could be adapted for deep waters (e.g., by experimenting with different-sized sand particles). In order to estimate average current velocities marked sediments could be placed at each study site and their movement monitored. This could be accomplished by collecting shallow cores using the manipulator arm of an ROV. Different colored sediments could be deployed during the surveys in order to collect information on the seasonality of sediment transport. Also, sediments could be graded by size, dyed distinctive colors, and deployed in adjacent piles. The relative disappearance rates would provide information on the relative frequency of currents of different magnitudes. Other methods such as the instrumented tripods utilized for the MMS CAMP Program would provide more quantitative data but at a much greater program cost.

Knowledge of sedimentation regimes is important to understanding the processes of disturbance and recovery of hard substrate communities of the OCS. Unfortunately, there are significant logistical problems of measuring sediment flux in deep-water habitats. Even relatively simple devices such as sediment traps may be quite expensive to deploy and recover, and recovery rates may be low because of difficulties in relocating the instruments or because of accidental losses such as can occur in fishing areas (e.g., Butman et al. , 1988). Additionally, the design of different sediment traps has a significant effect on data quality and estimates of rates and processes.

An alternative to measuring sediment flux rates directly would be to repeatedly map marked plots (e.g., 100 m^2 areas) and estimate changes in the coverage of soft sediments on different parts of the plots from survey to survey. Such mapping could be done by estimating the percentage cover of hard and soft substrata from photographic quadrats used to characterize the biological communities within the same plots. Since estimates of the presence or absence of hard and soft substrates does not require the same resolution as the estimates of biological cover, video tape records from an ROV also could be used to make very precise maps of substrata over fairly large areas of the bottom. To enable repeated sampling of the same areas, large numbers of numbered pyramid or “jack-shaped” markers also could be deployed more-or-less uniformly in selected plots. This scheme would allow fairly precise matching of substrata maps from different surveys and good estimates of net changes in the distribution of soft sediments on a plot. These estimates of net sediment flux probably will underestimate the actual rates of change since the frequency of surveys may be low relative to significant sediment transport events. Additionally, sediment depths can not be estimated accurately from videotape or photographic records. The latter problem might be addressed by attaching a marked probe to the ROV; the probe could be used to measure depths of substrata repeatedly along the ROV track according to a stratified random sampling scheme. The problem of underestimating flux rates due to infrequent sampling could be addressed by making sure that one of the surveys was made soon after a severe storm. The after-storm survey would most likely occur in the late winter or spring, and would require the scheduling of a sampling "window" rather than a specific sampling date.

A related task is to identify species which are particularly sensitive to sediment accumulation. Some species, like the gorgonians, can be identified on the basis of existing knowledge of their biology. For example, Grigg (1977) found that shallow water populations of *Muricea californica* and *M. fruticosa* suffered mortality from smothering by sediments. He also reported that their larvae required solid, cleanly swept substrates. Other gorgonians also probably prefer areas where strong currents potentially reduce sedimentation (and increase food availability). Similarly, in a study of deep water ahermatypic corals, Sartori (1980) found that densities were highest in rocky areas which were swept by currents. He speculated that the distribution of corals in the Mediterranean was a function of sedimentation.

Other potential species may be suggested based on existing data from the present study, SAIC (1986), and MMS CAMP. Abundance or presence\absence data for these species could then be subjected to cluster analyses to identify groups of species that tend to be associated with the various disturbance regimes, which are known or could be estimated from these studies. A subset of species which are amenable to manipulation could then be used in the transplant experiments described below.

There is a great deal of habitat heterogeneity represented by the range of hard substrate OCS habitats. These include large differences in water depth, slope, hard substrate type and relief (e.g., outcrops and boulders), percent of bottom covered by hard substrate, composition of the surrounding soft bottom matrix, and current regimes. Related differences in the associated biological communities also are expected. Therefore it is important to confine the study program to a few carefully selected strata and to have sufficient replication within a stratum to provide sufficient statistical power to detect changes.

Within a stratum, at least two sites with very different estimated rates of sedimentation should be selected and replicated within each of these "treatment" sites. Repeated sampling of the same sites is important because in a very heterogeneous environment spatial differences in population densities may often mask temporal differences unless a large number of random samples is taken. The benefits of this approach have been demonstrated repeatedly (e.g., Connell, 1973, 1978; Sebens, 1986; Sebens and Lewis, 1985).

For the study, two sizes of quadrats are recommended (e.g., $0.1m^2$ and $0.3m^2$), corresponding to the surface area of the close-up (35mm macro) and standard survey quadrat (70mm) photographs collected during the present (November/ December 1987) reconnaissance survey of the Northern and Central California Planning Areas. The close-up quadrats are particularly useful for examining species interactions and observing colonization by small life stages. The abundance of larger or more motile species such as sea stars, ophiuroids, and anemones can be estimated from the larger photographic quadrats and from video transects.

In addition to the community level study, some manipulative experiments probably are feasible. However, they must be relatively simple and not require overly fine manipulations by the survey system (e.g. , ROV). After a group of species is identified which appear to be sensitive to sedimentation, a subset which also is found in shallow waters should be chosen. This subset may include several species of gorgonians and cup corals such as Lophogorgia, Paracyathus , and Balanophyllia. Organisms can be collected using SCUBA and affixed to artificial substrates. These substrates would then be attached to weighted racks in both vertical and horizontal orientations. The racks would be placed at the same study sites representing different sedimentation regimes and at the collection site to control for handling artifacts. For these species, higher mortality would be predicted at the high sediment site and, at both sites, higher mortality on horizontal surfaces (e.g., Grigg, 1977). These data would be particularly relevant to distinguish effects of sedimentation from limitations in larval dispersal (e.g., for Balanophyllia) and the effect of sedimentation on growth and survival (e.g., for "Lophogorgia").

5.2.3 Anchoring Effects Studies

In addition to sedimentation effects, oil and gas development may disturb some hard substrate communities through anchoring activities (see Chapter 3). This may abrade or crush stable substrates and flip moveable boulders. These activities would create large and small Type 1 patches (sensu Connell and Keough, 1985) on stable outcrops, and both Type 1 and Type 2 patches on moveable boulders.

The general approach to the study of anchoring effects involves four primary elements:

- Selection of hard substrate study sites that represent low relief and medium relief (e.g., <0.5m and <2m, respectively), ideally with some small boulder areas;
- Conduct a pre-disturbance survey using ROV photographic methods over precise, gridded transects, followed by clearing/disturbance of an experimental area by dragging heavy sleds or chains along the bottom, and finally a post-disturbance photographic survey;
- Conduct frequent surveys (e.g., biannual over a two to four year period) at control and experimental sites using ROV photographic methods and two quadrat sizes (as noted for sedimentation effects) to assess variability and recovery; and
- Perform statistical analysis of the data using ANOVA, cluster, and principal coordinate analysis methods to test for differences in natural or “background” rates of disturbance, recolonization, growth, and recovery in the different habitat types.

In order to evaluate the impacts of these disturbances, large and small clearings can be created on stable outcrops and on boulders. On boulders, abrasions would create Type 1 patches of various sizes, while dislodgement and turnover would create Type 2 patches. On the rock outcrops, both large and small clearings would be large Type 1 patches, since they probably still would be surrounded by organisms.

Creating clearings of two sizes is useful because it would mimic the range of perturbations caused by anchoring activities. It also would be useful because there is a body of theory relating to recovery and recolonization in Type 1 and Type 2 clearings (Connell and Keough, 1985; Sousa, 1985). Therefore, if the results of this experiment indicate that the processes acting in deep water rocky habitats are similar to those studied in more accessible environments, predictions (e.g., Chapters 2 and 4) based on these theories will have more credence. In the future, one could then make more accurate predictions based on a knowledge of the existing fauna and the expected perturbation.

The design of such a clearing experiment should include repeated measures of density or percent cover on experimental and control surfaces both before and after the experimental perturbation. After several surveys have been completed (e.g., four biannual surveys to estimate seasonal and year-to-year variation) the experimental clearings can be made.

The clearings probably can be accomplished by dragging or bouncing heavy sleds or chains across the bottom from a survey vessel. This will not result in a uniformly cleared areas. Rather, some boulders will be overturned, some will be missed, some will be haphazardly scraped, and some will have large areas denuded. This could be controlled partially by careful design of the drag-weight and by tracking the weight's position using a pinger, similar to the standard tracking of-an ROV. However, the results of the perturbation will only be known after-the-fact. Treatment and control areas can then be selected based on the availability of suitable "before" photographic samples in areas which were cleared in the desired manner. The fact that there will undoubtedly be considerable variation in the size of clearings within a given category (e.g., "small") underlines the importance of replicate photoquadrats within areas.

To facilitate sampling the same substrate repeatedly, we suggest that the areas of appropriate substrate be marked with graduated steel markers affixed to a weighted foot and bearing a numbered tag. These could be scattered over the area in a haphazard or more-or-less uniform pattern, depending on the logistic constraints of placement. The intent is to have reference markers to aid in mapping the area from video tapes and photographs. A possible side benefit is that the markers might also function as "sediment stakes" so that some quantitative estimates of changes in sediment depth can be made. After the areas are marked, they should be intensively surveyed photographically and the position of the photographs related to the map of the area as accurately as possible. This is important because it will not be possible to specify beforehand the precise locations of the clearings.

If possible, the manipulations should be repeated in two areas with very different current and sedimentation regimes. This is desirable since there undoubtedly will be differences in recovery and recolonization between such areas and there probably will be interactions between level of sedimentation and substrate type. We are, in essence, recommending a factorial experiment with two levels of sedimentation, three rock types, and two clearing sizes within each clearing swath. This results in 12 treatments which need to be replicated. However, because of logistical or cost constraints it is likely that some of the cells in the treatment matrix may not be filled. Nonetheless, we believe it is important to specify a design that includes the most important variables so that experimental possibilities will not be overlooked when examining the results of preliminary surveys. At a minimum it should be possible to create Type 1 patches of a variety of sizes on low-relief boulders in areas of different current regimes. With such a reduced design it would probably also be feasible to replicate the experimental treatment.

Since it probably is not possible to mimic oil and gas anchoring activities exactly, an alternative would be to site the experimental areas where these activities will take place (e.g., may be possible for MMS CAMP). The decision to use actual oil and gas related activities versus a manipulation that mimics them involves a trade-off. While simulation lacks reality, it is easier to control. The main difficulty in using actual activities is predicting where they will occur in order obtain "before" measures. Whether it is feasible to obtain such observations depends on the size of the area in which anchoring is expected to occur. However, if it is known beforehand that such accuracy cannot be achieved, then more controlled manipulations should be used. Another potential problem in studying areas having ongoing drilling activity is that platform discharges may complicate the interpretation of experimental data.

Finally, any information that can be obtained on the importance of competition and predation to the composition of the communities will be useful in predicting the effects of anthropogenic perturbations. Similarly, information on growth rates and colonizing rates would be extremely valuable for some species (e.g., the coral Lophelia, the gorgonian "Lophogorgia", and many sponges and anemones). For sessile species a great deal of information concerning growth, colonization, and competition for space could be obtained directly from temporal series of macrophotographs.

Current knowledge (e.g., from the present November/December 1987 survey) about hard substrate habitats in the OCS suggests that predation may be important, and that ophiuroids and asteroids are two groups that are likely to include important predators. Ophiuroids tend to be very abundant in most of the photographic samples from many outcrop areas (e.g., indicted from the present survey) and could have a significant effect on recruitment and recolonization of epifaunal organisms. Asteroids usually are much less abundant than ophiuroids, but in some low and medium relief areas are found in dense patches on small "islands" of hard substrata surrounded by soft sediments. These local concentrations may be formed partly when asteroids move to avoid influxes of soft sediments on hard substrates. If this is accurate, it may represent a novel, indirect effect of sedimentation. Unfortunately, since predators are mobile, predation often is much more difficult to study than competition or the effects of disturbance. Gut analyses provide some information about trophic relationships but are not very useful in assessing the population consequences of predation. Caging experiments are unlikely to work in the OCS habitats because of severe artifacts associated with reduced water flow and increased sedimentation (Newell and Jumars, 1984). However, it would be possible using an ROV to remove or add asteroids or ophiuroids on islands of hard substrata, as referenced above. Replicate control and treatment sites should be identified and sampled photographically for at least two biannual surveys. This would establish reference abundance levels before the addition or removal of asteroids or ophiuroids, after which the manipulation could be made. Changes in community composition on the experimental islands then could be compared to changes on control islands using a statistical design and analysis similar to that proposed for the anchoring effects study.

ANALYSIS

In order to judge whether the hard bottom OCS communities are impacted by natural, experimental, or drilling manipulations (disturbances), a careful statistical design must be developed. To distinguish the unique effects of location and time from a possible impact, a minimum requirement is that there be at least one sample at the impact and at one or more control sites both before and after the impact (Green, 1980; Stewart-Oaten, et al., 1986). This design defines a minimum of four cells (Before: control and impact, and After: control and impact). To avoid the problem of confounding the effect of an impact with time by location interactions (one of the problems of "pseudoreplication" pointed out by Hurlbert, 1984), it is necessary to sample multiple times at control and impact sites before and after the impact (Stewart-Oaten, et al. , 1986) . Since the data to be collected will include numerous species, a common approach is to perform some variety of multivariate clustering and to determine whether the cells in such a Before/After, Impact/Control analysis are consistent with a hypothesis of no significant impact (Williams, 1971; Boesch, 1977). While such clustering techniques are useful in preliminary analyses to summarize complex, multi-species data sets, there are some problems in using them alone to make statistical inferences about the effects of an impact. First, the procedure of comparing clustering patterns with regard to the four cells of the study design is almost always done without a procedure to test for statistical differences (Hruby, 1987). Another problem is that different clustering algorithms can provide qualitatively different clustering patterns for the same data sets (Hruby, 1987). Finally, comparisons of cluster diagrams may suffer from lack of clarity unless the groups cluster sharply. A possible solution to the problems of testing is provided by Bloom (1980), who devised a statistical test for changes in multivariate samples expressed in principal coordinate spaces of two or three dimensions. Another alternative is to conduct analyses on single species (e.g. , to focus on the sensitivity of selected taxa), using analysis of variance or covariance (Stewart-Oaten, et al. , 1986) . This has the advantage of ease of interpretation, and the availability of more standard statistical test procedures. These procedures include explicit" tests of the assumptions underlying the analysis, and provide a procedure for detecting spurious results.

5.3 RELEVANCE OF RECOVERY/RECOLONIZATION STUDIES TO MMS DECISIONMAKING

Pursuant to the Outer Continental Shelf Act and Amendments and the National Environmental Policy Act, the MMS has the responsibility for leasing and development of OCS areas for oil and gas development, subject to the integration of appropriate scientific information in decisionmaking processes that may have a significant environmental impact. In association with proposed oil and gas sales such as those planned for the Northern, Central, and Southern California Planning Areas beginning in 1989, MMS needs information on the potential impacts to biological communities that might result from development activities. Specifically, for the benthic communities off California there is a general lack of information on the types of organisms, their life history characteristics , and the potential for recovery from natural and anthropogenic disturbances. This lack of information is particularly notable for deep water hard substrate communities. The sensitivity of these communities, in terms of the length of time to recover from a disturbance, can best be determined by detailed studies of the rates and patterns of recolonization by associated species and species groups. The perceived rarity of particular species and assemblages can be defined additionally in terms of their abundance and distribution including the occurrence of species of special interest. For example, the areal extent of exposed hard substrate in many areas of the Northern and Central California Planning Areas appears to quite limited (e.g. , < 5%) as judged by preliminary assessments from the present November/December 1987 surveys of potential hard substrate sites. The communities associated with these hard substrate areas therefore might be perceived to be relatively uncommon for this geographic region, even though the potential for rapid recovery from disturbance might be high.

Informed management decisions on the significance of potential impacts to these communities must therefore be based on sufficient knowledge of biological community and substrate types and distributions and the processes that influence recovery and recolonization. Recovery and recolonization information should include data on larval recruitment, organism growth rates, competitive interactions, predation effects, and the frequency and severity of disturbances. Knowledge of natural disturbances (particularly sedimentation effects) and potential anthropogenic disturbances (particularly anchoring effects and effects from drilling muds and cuttings) is particularly significant to predict accurately any long term effects (e.g. , > two years) that might result from oil and gas activities or other potential disturbances including some fisheries activities.

CHAPTER 6. REFERENCES

References followed by a number in brackets (e.g., "[l]" for Abbott and Haderlie, 1980) correspond to the numbered references listed in Table 4-1.

References preceded by an asterisk (*) represent additional reports that were reviewed for this study, but which did not contain information pertaining to recovery and recolonization. They are included as a guide to later reviewers to limit duplication of effort.

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