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CHAPTER 18

Disturbance

DEANNA J. STOUDER AND MICHELLE L. McMULLIN

Introduction

Disturbance influences all elements of ecological organization (Pickett & White, 1985). Previous chapters on community organization (unit IV) have discussed important biological elements that may contribute to the organization of California marine fish assemblages, yet physical disturbance affects all of these (i.e., feeding and trophic interactions, dispersal, recruitment, predation, and competition). Despite limited information on the role of natural disturbance in California marine systems, we will describe examples on the effects of hypoxia, freshwater inflows, salinity changes, and storms on fish assemblages.

We use Pickett and White's (1985) definition of disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." There is some disagreement and confusion among ecologists in defining disturbance. While the above definition is commonly used and includes both the cause and effect, others advocate referring only to the causes of disturbance without referring to the effects (Lake, 2000). However, the purpose of this chapter is to present a generalized perspective on the influence of disturbance on assemblage organization. It remains important, especially for scientific study of disturbance ecology, to understand that the characteristics of disturbances differ.

A general definition of disturbance is useful because it necessitates specification of scale and process for every event in relation to the organism(s) and ecosystem(s) involved. Natural disturbance is a natural occurrence! It is an intrinsic property of ecosystems and is not a deviation from a normal state. Thus the definition must be understood relative to spatial and temporal contexts and relative to the appropriate hierarchical levels of community and assemblage organization. Not only does this definition require a description of the cause (mechanism) of disturbance, it also requires a description of the effect (response). It is useful to describe the mechanism and response of disturbances while maintaining the premise that disturbance happens at different frequencies and magnitudes. Thus, responses reflected in marine temperate fish assemblages, as in many others, will vary widely.

Disturbance may incorporate both short- and long-term changes at both local and larger spatial scales; examples of disturbances that result in long-term changes include El Niño-Southern Oscillation (ENSO) and global warming (see chapters 1 and 26). Disturbance may elicit both physiological and behavioral responses in fishes, but in this chapter we will include mostly behavioral responses (especially those behaviors included in unit IV). Anthropogenic disturbances will be covered in Unit V.

Theoretical Context

A whole host of theoretical constructs exist to describe the outcomes of disturbance. These theories operate with the premises of equilibrium or non-equilibrium conditions. For equilibrium conditions to occur, the rate of increase (e.g., immigration, population increase) must equal the rate of decrease (e.g., emigration, mortality). These constructs of equilibrium can be applied to ecological processes and species changes. Several equilibrium-based hypotheses have been suggested including Niche Diversification and Compensatory Mortality (Connell, 1978). Ebeling and Hixon (1991) noted that there is no evidence in temperate reef fish systems to support or refute another equilibrium hypothesis—Circular Networks (Jackson and Buss, 1975; Connell, 1978). The Niche Diversification Hypothesis predicts that because populations are at equilibrium, competition either past ("ghost of competition past," Connell, 1980) or present drives the evolution of specializations to minimize competition among species. In other words, species within assemblages partition resources (i.e., habitat, prey, time) to coexist. Ebeling and Hixon (1991) reviewed 26 studies of temperate rocky reef fishes and determined that 88% supported, or could support, the concept of competition and therefore niche diversification among species. They noted that the experimental evidence is even stronger (all 12 experimental studies they reviewed generally supported the Niche Diversification Hypothesis; Ebeling and Hixon (1991)). In contrast, the Compensatory Mortality Hypothesis (Connell, 1978) predicts that highest mortality will occur on the strongest competitors or the most abundant species within the community. Mortality is therefore density dependent and elimination by competition among species is absent.

Equilibrium seldom occurs. Changes and disruptions occur often, therefore species assemblages are rarely constant. Non-equilibrium theories include: the Intermediate Disturbance (Connell, 1978), Equal Chance or Lottery (Sale, 1977, Hubbell, 1979), and Gradual Change (Hutchinson, 1961, Connell, 1978) Hypotheses.

The Intermediate Disturbance Hypothesis suggests that at low levels or rates of disturbance species diversity will be low due to the predominance of dominant or climax species. When disturbances are large or frequent, diversity will also be low because colonizing or pioneer species will be prevalent. At intermediate levels of disturbance, species diversity is highest because neither biological (i.e., competition, predation) nor physical (i.e., habitat change) processes are favored keeping local assemblages at a non-equilibrium state. However, Mackey and Currie (2000) reviewed 130 published studies examining the relationship among species richness, for a range of terrestrial and aquatic systems, and disturbance and found that only 19% exhibited highest levels of species richness with intermediate disturbance levels. In the Equal Chance or Lottery Hypothesis species composition and total abundance of individuals within a guild should remain relatively constant, even though local populations may vary in size. In these situations space is limited and unpredictable disturbances create open spaces. Patches or entire reefs may become available and filled, in a random order, by individuals from the plankton. Therefore, the unpredictability of the process prohibits one species from dominating or displacing another.

Environmental variation that occurs on seasonal and even decadal to longer time scales (e.g., El Niño, global climate change) favors a Gradual Change in species composition. This occurs because the changing environment favors different species over time, therefore preventing one species becoming more dominant within the assemblage. Species will track the environment but the populations never reach equilibrium because resource availability changes at a different rate than species' responses. Temperate reef fishes (e.g., Embiotocids, Scorpeanids), in regions where seasonal variation in temperature is common, exhibit patterns consistent with this hypothesis (see Ebeling and Hixon, 1991 for review).

Defining Disturbance

It is our premise that natural disturbances are important agents of change in ecosystems. Various characteristics such as spatial scale and time of disturbance result in differential abilities of species (and ecosystems) to respond. Generally, the impacts of disturbance can be addressed by asking questions such as: How big is it?; How complete is the disturbance?; and How close are disturbances to each other? Disturbance characteristics include distribution, area (or size affected), frequency, predictability, magnitude (intensity versus severity), and the synergism or interactions among these characteristics (White & Pickett, 1985, see table 1-1 chapter 1).

Fishes are, by definition, mobile, however, the relative types and rates of mobility differ. The size and distribution of disturbances across a particular location or ecosystem can influence whether mobile organisms can avoid or respond. If the disturbed area is small, mobile species or individuals may take advantage of adjacent undisturbed areas. In contrast if the affected areas include an entire reef or bay, organisms may be unable to leave the location (due to physiological constraints), to respond without risk of predation (by the need to travel across large open areas), or successfully compete for remaining intact locations.

Both the frequency and predictability of disturbance can affect the ability (and adaptability) of fishes to respond. If disturbance events are frequent (i.e., the time interval between disturbances is short) and predictable (e.g., always occur at the same time of year), species that are successful in seeking refuges during disturbances may be able to survive. However, frequent or unpredictable disturbances may only enable the existence of those individuals or species that just happened to be "in the right place at the right time." As the interval between disturbances becomes longer and possibly more predictable (e.g., winter storms on coastal reefs or estuaries) species may have adapted responses to these local conditions. Assemblages, and therefore ecosystems, may be incapable of changing in any predictable way to even longer interval duration events such as ENSO and global climate change. In situations, such as these, physiological constraints may be the primary driver in species' responses and therefore the resulting community and assemblage structure. The disturbance magnitude, either intensity (force per event per unit time) or severity (impact) can also affect species' and ecosystem responses. It would not be unusual for some or all of the above mentioned disturbance characteristics to interact and work synergistically. This may increase the relative impact of any particular disturbance.

In general, physical disturbance decreases the benefits gained by fishes but this can vary by species, life stage, and assemblage structure. Disturbances lead to spatial and temporal variation in habitat and ultimately species composition. Biologically driven (e.g., predation, grazing, parasites, and disease) and anthropogenic (e.g., pollution, habitat destruction, and low oxygen) disturbances also affect fish assemblages, however, anthropogenic disturbances will be described in the Pollution and Habitat Alteration chapter within this volume (see chapter 24). Relevant questions for organisms responding to disturbance include. Where is the organism at the time?; What is the organism doing?; and At what life stage is the organism? Thus, the impacts of disturbance vary with habitat type (e.g., estuaries, tidal habitats, and rocky reefs), life history stages (e.g., eggs, larvae, and adults), behavior (e.g., habitat use, feeding), and timing (i.e., are the organisms in the right/wrong place at the right/wrong time?).

Natural Disturbance

Natural disturbances occur at different frequencies and magnitudes in marine coastal systems. Seasonal changes including variation in tidal heights and magnitude of wave and wind action can affect organisms and ecosystems in predictable ways. For example, California giant kelp (*Macrocystis pyrifera*) beds change seasonally, and as a result of decadal oscillations. These changes alter habitat characteristics for fish use, recruitment, prey availability, and a host of other conditions. When the magnitude or frequency of winter storms increases the impact of these disturbances can be devastating to marine communities and assemblages. Climatic change (discussed in more detail in chapter 1) can cause unusual or unseasonal temperature shifts. In addition, climate changes that alter seasonal rains and influence temperature (e.g., causing droughts, higher than average rainfall, etc.) can affect aquatic systems by changing water quality. Increased runoff from higher than average rainfall can decrease salinity in coastal areas (e.g., bays, estuaries, and sea grass beds), whereas droughts may cause increased salinity in these areas. Similarly, as temperatures increase above historical normal levels (possibly as a consequence of pollution), coastal areas may develop depleted oxygen levels (hypoxic) and become lethal to many organisms.

Direct versus Indirect Effects of Disturbance

Although disturbance may affect fish assemblages directly due to instantaneous mortality (i.e., death) and subsequent disruption of interrelationships among species, this has been documented infrequently. Indirect effects may ultimately be a more pervasive impact for mobile organisms. If habitat structure is of primary importance in characterizing the fish assemblages then disturbances that result in habitat modification or degradation are likely to assert more profound or long-term effects (Jones and Syms, 1998, Syms and Jones, 1999). Impacts of disturbances can be negative if habitat changes affect habitat heterogeneity and complexity, prey distribution and abundance, and limit refuges and spawning habitat. The potential costs to fishes are weight loss, decreased or zero fitness, increased vulnerability to predators and disease, and eventually death.

Fishes have ways to minimize costs so the consequences of disturbance do not always have to be strongly negative. Individuals can move away from the affected area by changing location or leave the disturbed site. For generalist fishes, they may be able to alter what they eat, where they eat, and possibly how much they eat to adjust to changes in prey types, abundance, and locations. Fishes can also change behaviors to minimize energy expenditures. For example, it may be beneficial for territorial fishes (e.g., garibaldi (*Hysypops rubicundus*)) to minimize energy spent defending territories. Similarly, some fishes may postpone reproduction or produce fewer offspring to minimize the energy expenditures to eggs and young. In general the costs of disturbance can be negative, but unless the direct effect of disturbance is death, fishes usually have mechanisms to minimize the costs to enable them to survive.

Examples of Disturbance

Hypoxia

Hypoxia in coastal marine environments is an example of disturbance affecting assemblage structure and function through behavioral and physiological responses of predators and prey. Due to vertical stratification on a seasonal or tidal basis, low oxygen concentrations occur in bottom waters. As a consequence, hypoxia can reduce the availability of suitable habitat. The increased frequency of hypoxia occurrence is usually due to high nutrient loading resulting from human activities. Mortality is a direct result of hypoxia, but tolerances differ among species and life stages, potentially affecting species composition and abundance. Other physiological responses may include reduced fitness and growth. Hypoxia also affects organisms through indirect effects such as distribution or habitat shifts, and behavioral changes (Wannamaker and Rice, 2000). This combination of individual physiological and behavioral responses to hypoxia may ultimately influence community structure and function.

Hypoxia occurs in many locations worldwide. Hypoxia off the California coastline may be an infrequent or rare occurrence due to predominant and persistent upwelling and this is not a well-studied subject in California. Oxygen levels can decrease as a consequence of local and climatic conditions. Climate shifts change the amount of upwelling off coastal California, thereby altering the distribution of the oxygen minimum layer. Prior to upwelling, this layer (comprised of low oxygenated and high salinity water) remains offshore and fishes are distributed throughout inshore waters (fig. 18-1). During periods of upwelling, the oxygen minimum layer becomes distributed in shallower and inshore areas causing increased concentrations of benthic and epipelagic fishes. In tidepools with algae or marine plants, oxygen concentrations and pH can increase during the day and decrease at night. Congleton (1980) observed species distributions in tidepools near La Jolla, California. Despite being one of the most common southern California tidepool fishes, spotted kelpfish (*Gibbonsia elegans*) were never observed in tidepools at night. Woolly sculpin (*Clinocottus analis*) and reef finspot (*Paraclinus integripinnis*) were present, but were observed to move to the surface or to shallow water and performed ventilation (i.e., passed water over gills). Using cage and respirometry experiments Congleton (1980) determined a higher critical oxygen concentration level for the spotted kelpfish than that of the woolly sculpin or the reef finspot. As oxygen concentrations in the tidepools decreased below the critical oxygen concentration levels for all three species, behavioral responses including ventilation proved useful and may be necessary for survival. These results explain the absence of spotted kelpfish in tidepools at night.

Although oxygen depletion may be historically uncommon, it may become more common as anthropogenic disturbances become more prevalent. Estuaries, including those in California, are highly productive habitats containing important refuge, nursery, and nutrient-rich habitats for ecologically and economically valuable fishes. Persistent hypoxia may influence distribution and abundance patterns of important commercial and recreational fisheries. For this discussion, we will primarily use two other locations to illuminate the effects of hypoxic disturbance on community structure of estuarine and marine fishes, and to demonstrate differences in size, duration, and timing that may explain differential responses of fishes exposed to these events.

Spatial and temporal patterns of hypoxia may differ among locations. In the Kattegat, Sweden, annual autumn hypoxia occurs at depths of one to ten meters above seabed over a 3,000-km^2 area for approximately four months (fig. 18-2; Pihl, 1994). Such extensive and prolonged seasonal periods of hypoxia have resulted in decreased demersal fish biomass, decreased benthic invertebrates, changing species composition, potential dominance of pelagic over demersal species, and both long-term and seasonal shifts in fish diets and available prey items (Pihl, 1994; also see review by Breitburg, 2002). In the mouth of the York River, Chesapeake Bay, hypoxia occurs on a cyclical basis throughout the summer lasting only six to 14 days at depths greater than ten meters (fig. 18-3; Pihl et al., 1992). Shorter duration, cyclical hypoxic episodes affecting a smaller area may allow exploitation of sensitive benthic invertebrates by mobile opportunistic fishes resulting in short term diet shifts (Pihl et al., 1992). Other studies in the Chesapeake Bay have focused on episodic intrusions of oxygen depleted bottom waters into nearshore shallow waters (fig. 18-4; Breitburg, 1992). Diel fluctuations characterized by rapidly changing dissolved oxygen concentrations can shift spatial distributions and bias population size structure toward older and larger or younger and smaller individuals depending on

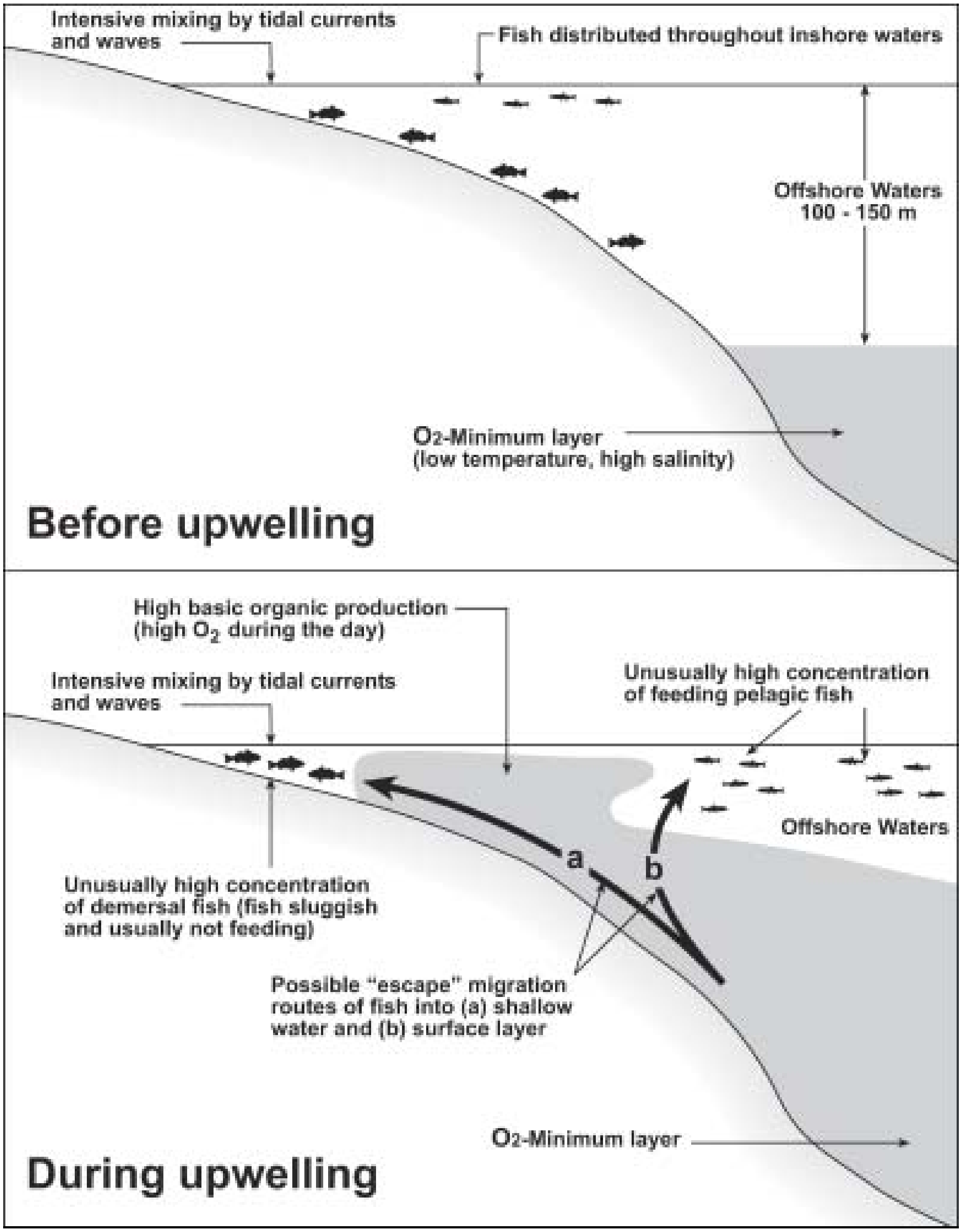

FIGURE 18-1 Impact of upwelling on the distribution of benthic and pelagic fishes along the coast of southern California (after and with permission of Southern California Coastal Water Research Project).

the timing of recruitment (Breitburg, 1992). Alterations in community structure may also affect trophic interactions, food web structure, and reproductive behavior.

HABITAT SELECTION AND USE

Direct mortality is an immediate result of disturbance. Under low oxygen concentrations, decreased survival of many fishes occurs. However, mortality can vary with age, size, or species, and this variability is the result of a range of tolerances to the event itself, mobility, and behavior. Fish larvae may be more susceptible to hypoxic exposure because they lack fully developed sensory and motor capabilities. For example, dissolved oxygen concentrations significantly decreased pre- and postflexion naked goby (*Gobiosoma bosc*) larvae survival in experimental studies, but not larger juvenile or adult survival (Breitburg, 1992, 1994). Larvae also exhibited an immediate behavioral avoidance response to low bottom water oxygen concentrations. While naked goby larvae avoided oxygen concentrations of 0.75 mgL^{-1}, adults did not respond until oxygen concentrations fell below this level. Many fishes, including naked goby, bay anchovy (*Anchoa mitchilli*), juvenile spot (*Leiostomus xanthurus*), pinfish (*Lagodon rhomboids*), croaker (*Micropogonias undulates*), menhaden (*Brevoortia tyrannus*),

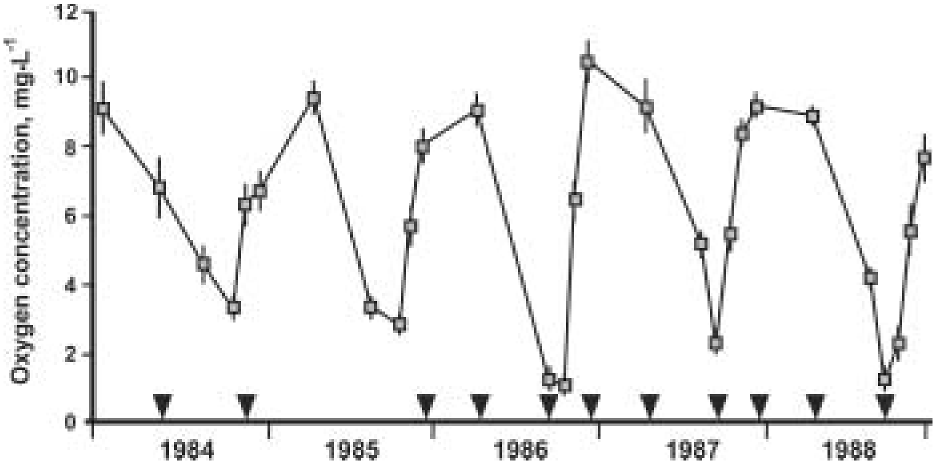

FIGURE 18-2 Mean (and SD) oxygen concentration in bottom water in the study area in the southeast Kattegat from 1984 to 1988. Measurements where conducted at five to six stations (<0.5 m above the sediment surface) on each sampling occasion. Dates for demersal fish sampling are indicated by arrows. (after Pihl, 1994).

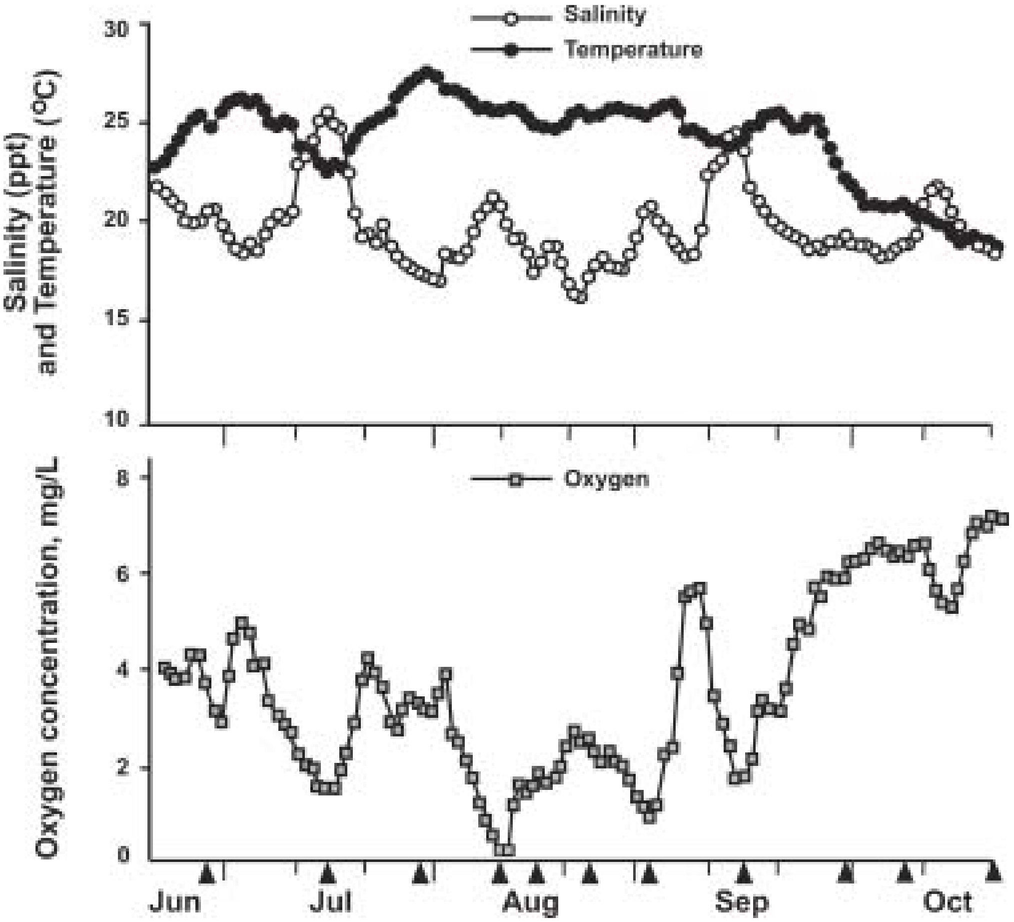

FIGURE 18-3 Daily mean salinity, temperature, and oxygen concentration in the bottom water (18 m depth) in the York River (26 June to 20 October 1989) (after Pihl et al., 1992).

white mullet (*Mugil curema*), mummichog (*Fundulus heteroclitus*), striped bass (*Morone saxatilis*), and flounder (*Paralichthys* lethostigma) are capable of detecting and responding to hypoxia (Breitburg, 1994, Wannamaker and Rice, 2000). Because hypoxia typically occurs only in bottom waters, mobile fishes may utilize surface waters as refuges (i.e., vertical water column migration in stratified waters), or fishes may also migrate to shallow waters where oxygen levels are sufficient. Although some species may detect hypoxic conditions, they may not avoid the area (e.g., mummichog) or the response may differ by species (Wannamaker and Rice, 2000). Differential mortality, avoidance ability, and subsequent recolonization following hypoxia may ultimately result in modified distributional patterns.

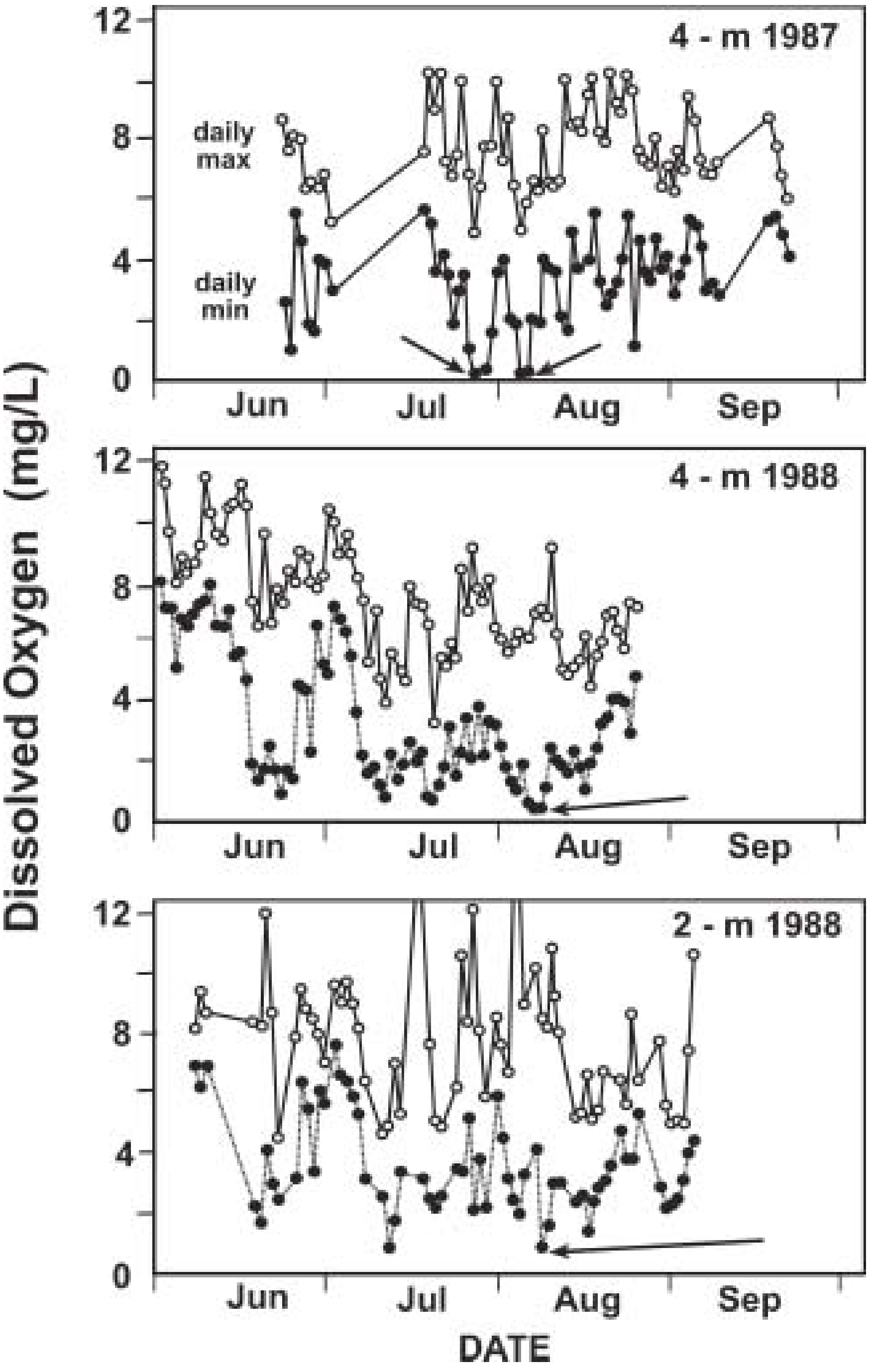

FIGURE 18-4 Daily maximum (open circle) and minimum (closed circle) dissolved oxygen concentrations at the mid (4 m) site during 1987 and at the mid and shallow (2 m) sites during 1988. Data are from DataSonde deployments. Arrows indicate severe intrusions (after Breitburg, 1992).

FEEDING AND TROPHIC INTERACTIONS

Seasonal variation in fish diet has been linked with seasonal variation in mean oxygen concentrations (Pihl, 1994). Both fish feeding behavior and food resources may be altered by hypoxic conditions (e.g., limiting or changing availability, increasing or decreasing food amounts, altering nutritional values) (Pihl et al., 1992, Pihl, 1994). Fishes may also reduce the time spent searching for food and feeding due to lowered oxygen levels (Bejda et al., 1987, Breitburg et al., 1994). Lower oxygen levels may inhibit prey escape behaviors, increase prey vulnerability or predation risk, and reduce predator attack rates (Breitburg et al., 1997). Predator and prey species may experience differential tolerances, detection rates, migration responses, and survival to hypoxia, which may ultimately influence encounter rates (Breitburg et al., 1997, Keister et al., 2000). At higher dissolved oxygen levels predation rates may increase as well as prey migration toward these locations thereby crowding predators and prey and potentially increasing prey mortality (Breitburg, 1994). These various combinations of behavioral and physiological responses of individual predator and prey species to hypoxia may ultimately lead to changes in the trophic structure.

REPRODUCTION

Reproductive behaviors may also change due to hypoxia. For naked gobies exposed for extended periods of time to near-lethal oxygen concentrations, fish abandoned nests and shelters because of a lack of embryo tolerance (Breitburg, 1992). Prior to abandonment, guarding males appeared stressed and

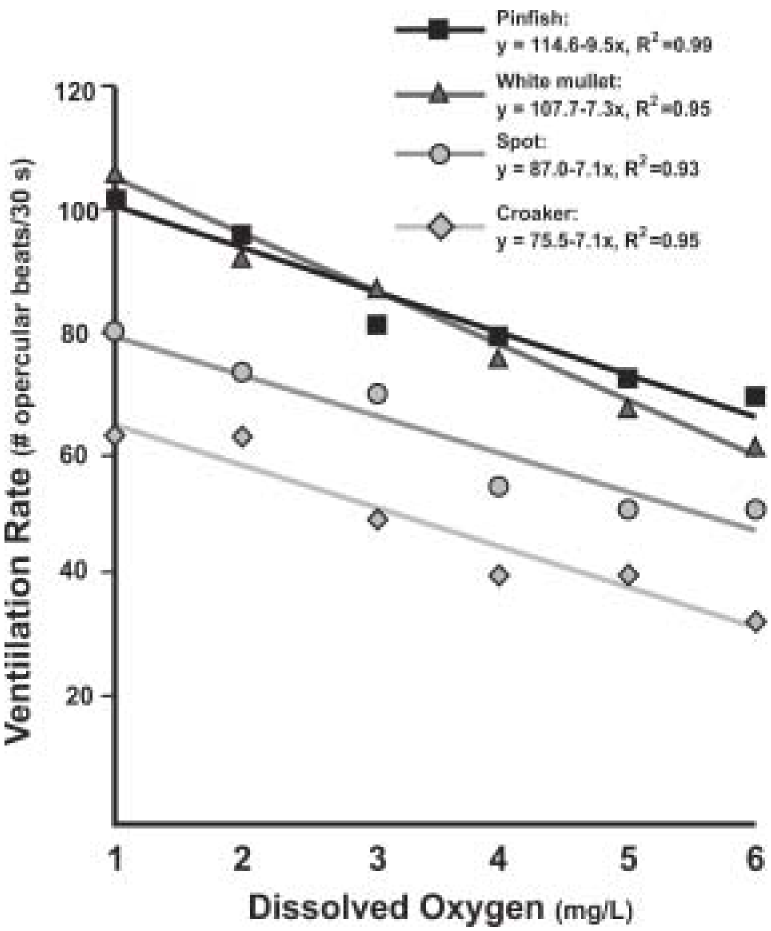

FIGURE 18-5 Ventilation rates for spot, pinfish, mullet, and croaker at all dissolved oxygen levels tested. Ventilation rate increased with declining oxygen for all species tested. Regression equations and P values for each species are given in the legend (after Wannamaker and Rice, 2000).

increased ventilation rates, and some males died without abandoning nests or shelters. Obligation to nest or shelter may reduce mobility and limit survival by negating avoidance or migration capabilities. Yet early escapement may be selected against because males typically have only one year of reproductive output and because of increased predation risk when they move away from shelter. In addition, because fecundity is generally size-dependent, a disturbance that affects the population size structure may alter reproductive output.

RECRUITMENT

Newly settled recruits may have increased sensitivity to low dissolved oxygen and lower survival rates than larger juveniles and adults (see Habitat Selection and Use above). If the highest settlement occurs in deep and mid-waters where hypoxic events are more common, recruitment can be hampered and population structure affected by hypoxia if the timing is coincident with settlement (Breitburg, 1992). Therefore, post-disturbance recolonization may not be dependent upon reproduction if large juveniles and adults that escape or migrate to avoid hypoxic conditions can later recolonize the deeper water habitats.

COMPETITION

Hypoxia may also influence intraspecific competitive interactions as demonstrated by red hake (*Urophycis chuss*; Bejda et al., 1987). Agonistic encounters significantly decreased for age 0+ red hake with decreasing dissolved oxygen. There was also a trend toward increased agonistic behavior for age 1+ red hake. In addition, multiple age 1+ fish were observed resting together in shelters, a highly unusual behavior.

FITNESS AND GROWTH

In addition to mortality and behavioral changes, hypoxia can also affect growth through increased energy allocation to ventilation. These rates increase with decreased oxygen levels for several species including spot, pinfish, croaker, and white mullet, and rates were higher for pinfish and mullet than for spot and croaker (fig. 18-5; Wannamaker & Rice, 2000). Any deviation from normal energy allocations during a disturbance may result in decreased fitness.

Some fishes may benefit from disturbance. Avoidance through migration for mobile organisms is an ideal means to mitigate for potentially harmful environmental conditions. Mobile foraging on vulnerable prey may allow for continued feeding and growth during hypoxic conditions (Pihl et al., 1992, Pihl, 1994, Rahel and Nutzman, 1994). Other fishes may use aquatic surface respiration (e.g., gulping) during hypoxic conditions, thereby allowing for survival, normal activity, and even growth. Todd and Ebeling (1968) determined that longjaw mudsucker (*Gillichthys mirabilis*), from Californian lagoons and tidal sloughs, is capable of aerial respiration when inhabiting poorly oxygenated waters.

Although hypoxia is a rare or unstudied disturbance in California estuaries, it does occur commonly worldwide. Hypoxia may become more common with increasing anthropogenic activities and with natural climate shifts that influence patterns of upwelling, stratification, or nutrient enrichment. In other locations as described above, hypoxia causes

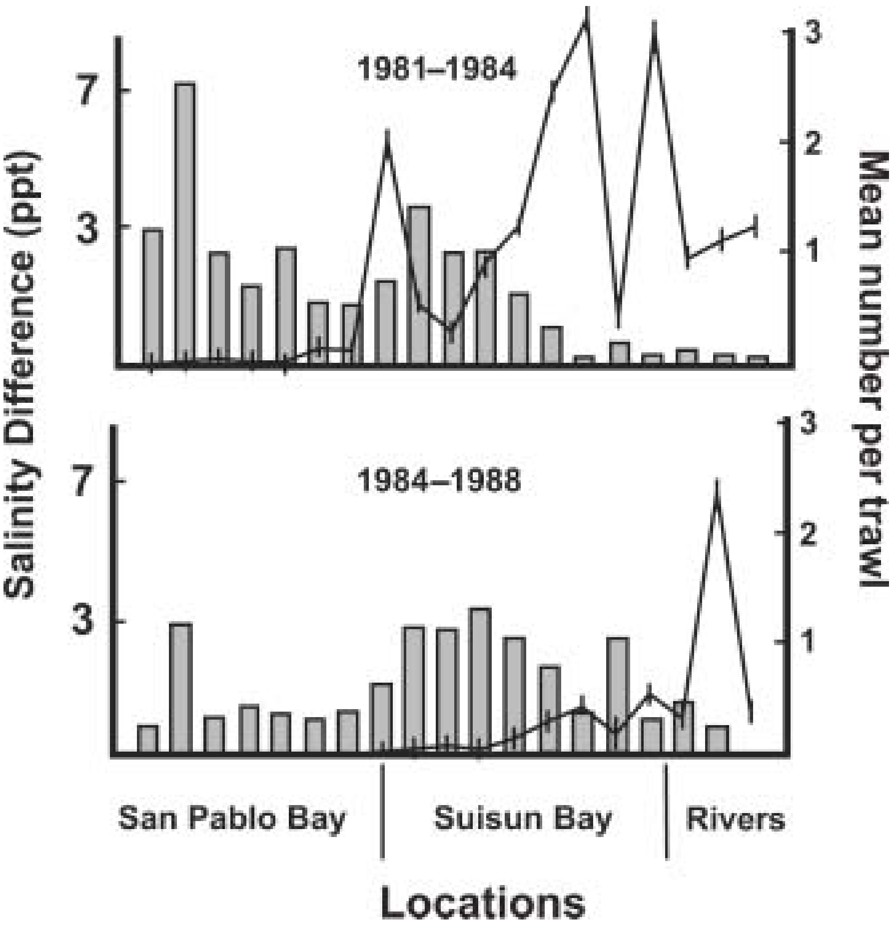

FIGURE 18-6 Mean delta smelt catches per trawl (lines) in the three regions in the Sacramento-San Joaquin estuary during the periods before (January 1981–September 1984) and after (October 1984–December 1988) the collapse of delta smelt populations. The location of the mixing zone is indicated by large differences (bars, parts per thousand) between salinities of surface and bottom waters in upstream areas. Upstream stations are to the right (after Moyle et al., 1992).

mortality, reduces suitable habitat, and affects all levels of assemblage organization.

Freshwater Inflows and Salinity

Freshwater from streams, rivers, and across impermeable surfaces can alter local circulation patterns, salinity, and sediment in coastal marine systems. This is especially true in bays, estuaries, lagoons, and tidal pools where freshwater can become concentrated. These areas can also become isolated from adjacent coastal marine water due to the formation of sand bars and extremely low tides. As water chemistry and quality change, tolerance by fishes to adjust to new conditions varies with species.

HABITAT SELECTION AND USE

Drought conditions may also influence the assemblage structure of coastal California fishes through the role of freshwater inflow. The distribution of some marine, estuarine, freshwater, and anadromous species within San Francisco Bay varied in response to wet or dry years (Armor and Herrgesell, 1985). Observed distributional changes appeared to be associated mostly to flow-related changes in salinity and circulation patterns. Some species, particularly the endemic delta smelt (*Hypomesus transpacificus*), were declining in abundance and experiencing persistent distribution shifts due to increased salinity concentrations with decreased riverine inflow (fig. 18-6; Moyle et al.1992; but see Moyle et al., 1986). Decreased riverine inflow may also reduce and shift the mixing zone to the river mouths or even confine it within the river channel. In addition to habitat reduction, decreased riverine inflow may also decrease availability of food. While decreased riverine inflows associated with drought are usually sporadic (except in the case of prolonged drought), anthropogenic disturbance in the form of water diversion for urban and agricultural uses potentially mimics drought year conditions but has far more persistent effects. As a consequence, the lower San Joaquin River essentially flows upstream at certain times of the year, and often during the delta smelt spawning season, a result of diversion (Moyle et al., 1992). During drought years human and industrial demand for water often increases.

FITNESS AND GROWTH

Intertidal areas, bays, lagoons, and estuaries can experience higher than normal salinity. High salinity concentration may be lethal to some species. Often salinity changes can be confounded by temperature, pH, dissolved oxygen, and food availability. Carpelan (1961) describes a study in a coastal California lagoon of increasing salinity levels and serial elimination of fishes when species became trapped in the lagoon by a sand bar. Of 10 species trapped when lagoon closed, only three species were still present at salinity levels of 60%. These three remaining species were euryhaline species.

Storms

Severe storms off the southern California coast in the 1970's and 1980's were excellent opportunities to study the effects of disturbance on near shore lagoons and marine temperate reef assemblages. These natural disturbances, combined with

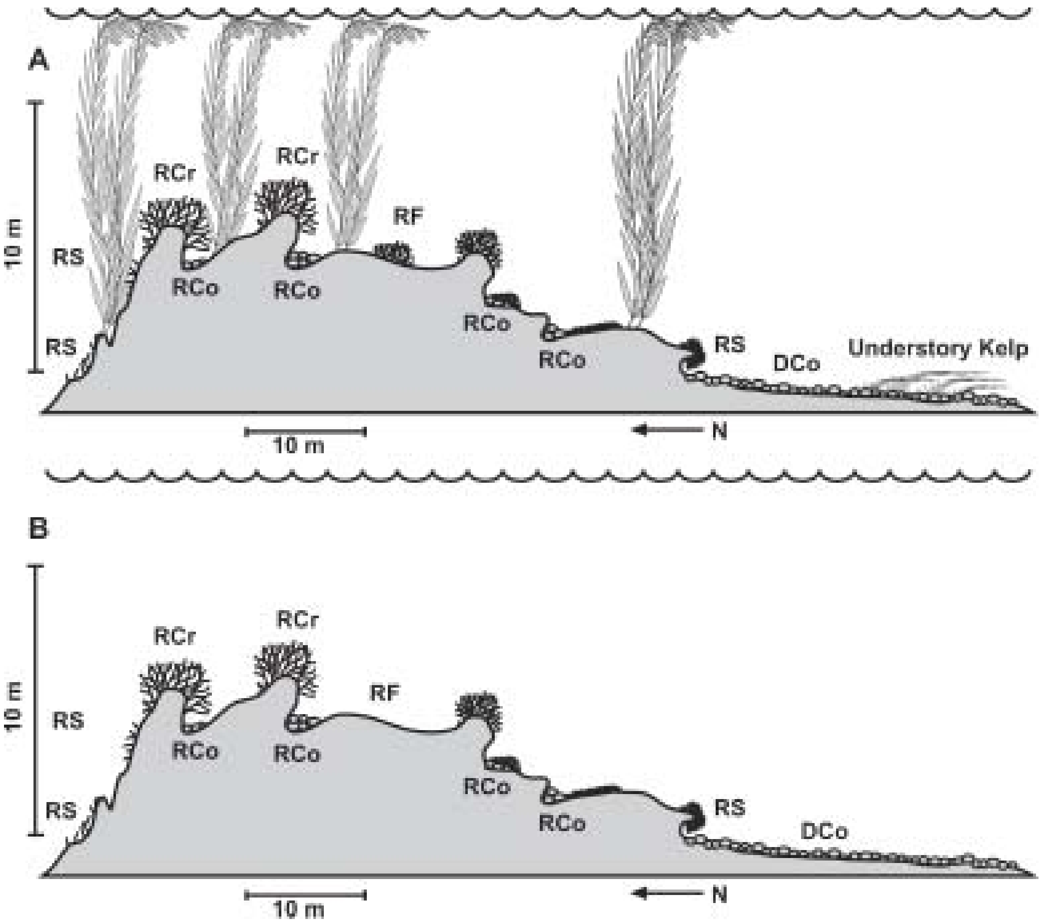

FIGURE 18-7 A) Naples Reef near Santa Barbra, California prior to the severe storm of February 1980. B) Naples Reef after the storm eliminated overstory kelp and sea urchins grazed much of the reef flat microhabitat. RS, reef slope; RCr, reef crest; RF, reef flat; RCo, reef cobble; DCo, deep cobble (after Stouder, 1987).

experimental studies in California, provided a wealth of information regarding how disturbance may affect multiple aspects of temperate reef and lagoon assemblages. Storm disturbances have also influenced the organization in other marine assemblages including coral reefs (Kaufman, 1983, Lassig, 1983, Woodley et al., 1991).

On temperate Californian reefs, macroalgal stands provide physical habitat structure. The physical substratum upon which the kelp grows provides additional habitat. Rock, sand, and cobble are predominate substrates and reef contour ranges from nearly flat to large rocky outcrops with high vertical relief and complex structure (Bodkin, 1988). Macroalgal stands are primarily composed of giant kelp, a surface canopy species, and *Laminaria* spp., *Pterygophora californica,* and *Eisenia arborea* as understory components, and associated turf algae (see chapter 7 for additional information on rocky reefs and kelp beds).

Macroalgal abundance, density, and biomass fluctuate in time through biotic disturbance (e.g., grazing) and abiotic disturbance (e.g., severe turbulence associated with storms, water temperature, nutrient availability) (Carr, 1994a). The size, shape, and structural architecture of individual plants can change in response to changes in plant density (Carr, 1994a). Seasonal variation in macroalgal stands can occur due to plant life cycles (e.g., growth and senescence). Storm effects on kelp beds vary as a function of frequency, magnitude, exposure, timing, and macrophyte and substratum characteristics (Dayton and Tegner, 1984). These effects also result from "storm of the century" type events including hurricanes and ENSO-related events, but any severe storm occurring with greater than expected magnitude can be a disturbance. Severe storms often change the physical habitat of temperate reefs and the typical result of these storms is reduction in overstory canopy, primarily by decreasing giant kelp stands (see fig. 18-7). However, this depends on the status of the temperate reef community at the time of disturbance; at times when kelp stands are not present storms may create conditions allowing for enhanced kelp growth (Ebeling et al., 1985).

As macroalgal stands compose a large portion of the physical structure on temperate reefs, many fish species are associated with the habitat they provide. Due to differential relationships between macroalgal habitat and fish species and age classes, responses to disturbances will be species and age dependent. Because disturbance alters habitat characteristics we will focus this discussion on those species and age classes affected by modification and potential simplification of physical structure (i.e., macroalgal stands). Disturbance may also result in direct mortality of kelp-forest fishes in the event of extraordinarily large waves and resultant stranding (Bodkin et al., 1987).

HABITAT SELECTION AND USE

On Naples Reef near Santa Barbara, CA, adult and young-of-year (YOY) surfperch are differentially distributed (Ebeling and Laur, 1985). Young surfperch use the kelp canopy as refuge from predation and are most abundant on the portion of the reef

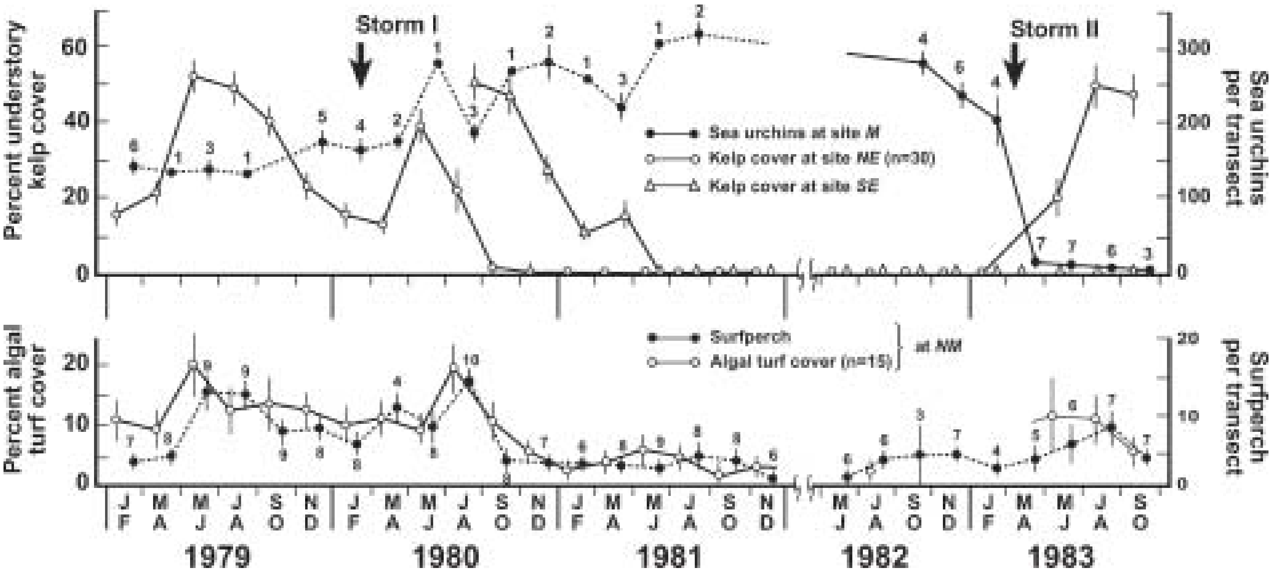

FIGURE 18-8 Bimonthly means (+ SEM) of pooled sea urchin counts (*Strongylocentrotus franciscanus* + *S. purpuratus*), percent cover of understory kelp (mosly *Pterogophora californica*), surfperch (Embiotocidae) densities, and percent cover of algal turf at monitored transect sites on Naples Reef before and after Storms I and II. Numbers next to urchins and fish means are sample sizes (after Ebeling et al, 1985).

with significantly higher percent algal cover. Their densities vary seasonally and most young surfperch regularly disappear in autumn as kelp senesces. When kelp stands were diminished in 1980 by storms, YOY surfperch were no longer observed and remained absent during 1981. However, YOY surfperch were once again sighted in 1983 concurrent with kelp stand recovery. Adult surfperch and kelp bass densities were not correlated with kelp loss (fig. 18-8). In an experimental kelp thinning study on Naples Reef to evaluate the influence of structure for YOY surfperch, counts were consistently lower in the thinned treatment plot than in the control plot, and thinning had no effect on adult surfperch (Ebeling and Laur, 1985).

At Pt. Piedras Blancas, a similar kelp removal experiment was performed to test the effect on *Sebastes* (rockfish) spp. (Bodkin, 1988). Prior to treatment, midwater rockfish species composition was very similar with juveniles more abundant in the treatment site and adults more abundant on control site; benthic species were consistent in composition and abundance. After treatment, the assemblage in the treatment site changed, but there was no assemblage change in the control site. In the experimental site, seven species declined in the abundance following removal of the giant kelp canopy. In addition, the estimated overall biomass decreased approximately 63%. Within the control site, juvenile rockfish decreased in abundance while adult *S. melanops* (black rockfish) increased. The changes in abundance at the control site may have resulted from emigration out of the experimental site. Benthic species changed little as midwater species accounted for 65% of post-treatment changes.

Storms can also effect habitat changes in near shore soft bottom ecosystems through sediment deposition. In Mugu Lagoon, a small estuary in southern California, sedimentation has been associated with very severe, normally rare, storms resulting in increased rainfall (Onuf and Quammen, 1983). The wettest season in the 36-year history of the Point Mugu meteorological station occurred between March 10, 1977 and May 16, 1978. One storm episode, occurring between February 5 and 13, 1978, released 20.7 cm of precipitation in nine days; a second major storm episode occurred in February 1980 (Onuf, 1987). As a result of these two storm episodes the average lagoon depth and volume at low tide decreased 38% (Onuf and Quammen, 1983). Sediment deposition affected sample sites differently. In two sample sites (Sites 2 and 3; See fig. 18-9) large proportions of eelgrass (*Zostera marina*) were entirely or partially covered by sediment and declined through time. Prior to the storm episodes, one site (Site 1) increased from 1% eelgrass to 20% by the end of the study (Onuf and Quammen, 1983).

From 1978 to 1981 fish catch and abundance exhibited both short-term and persistent changes. After storms short-term effects were evidenced by decreases followed by slight increases, while persistent effects were supported by approximately 50% overall reduction (fig. 18-9). If changes in substrate strongly influenced fish abundance and composition, then demersal fishes should have changed accordingly. However, only one (i.e, California tonguefish (*Symphurus atricauda*)) of the seven demersal species exhibited a storm-associated change in abundance (Onuf and Quammen, 1983). Although bottom substrates became finer following sediment deposition, substrate was not a primary determinant of fish abundance patterns.

Sediment deposition resulted in an overall decrease in lagoon water depth. Water column species, topsmelt (*Atherinops afffinis*), shiner perch (*Cymatogaster aggregata*), and bay pipefish (*Syngnathus leptorhynchus*) decreased in abundance as water became shallower. In one site, bay pipefish increased in areas where remnants of eelgrass beds remained (Site 1) although overall numbers decreased. Shiner perch, however, disappeared from the lagoon and did not recover pre-storm abundances (Onuf and Quammen, 1983, Onuf, 1987). Depth and cover were important determinants of fish abundance, and acted synergistically for a number of species.

Species are positively or negatively associated with macroalgal stands for multiple reasons. Younger fishes may rely on the refuge the plants provide from predation and all ages may forage on prey within the stands. So, in addition to habitat selection and use, disturbance may also influence feeding and trophic relationships, reproduction, and recruitment.

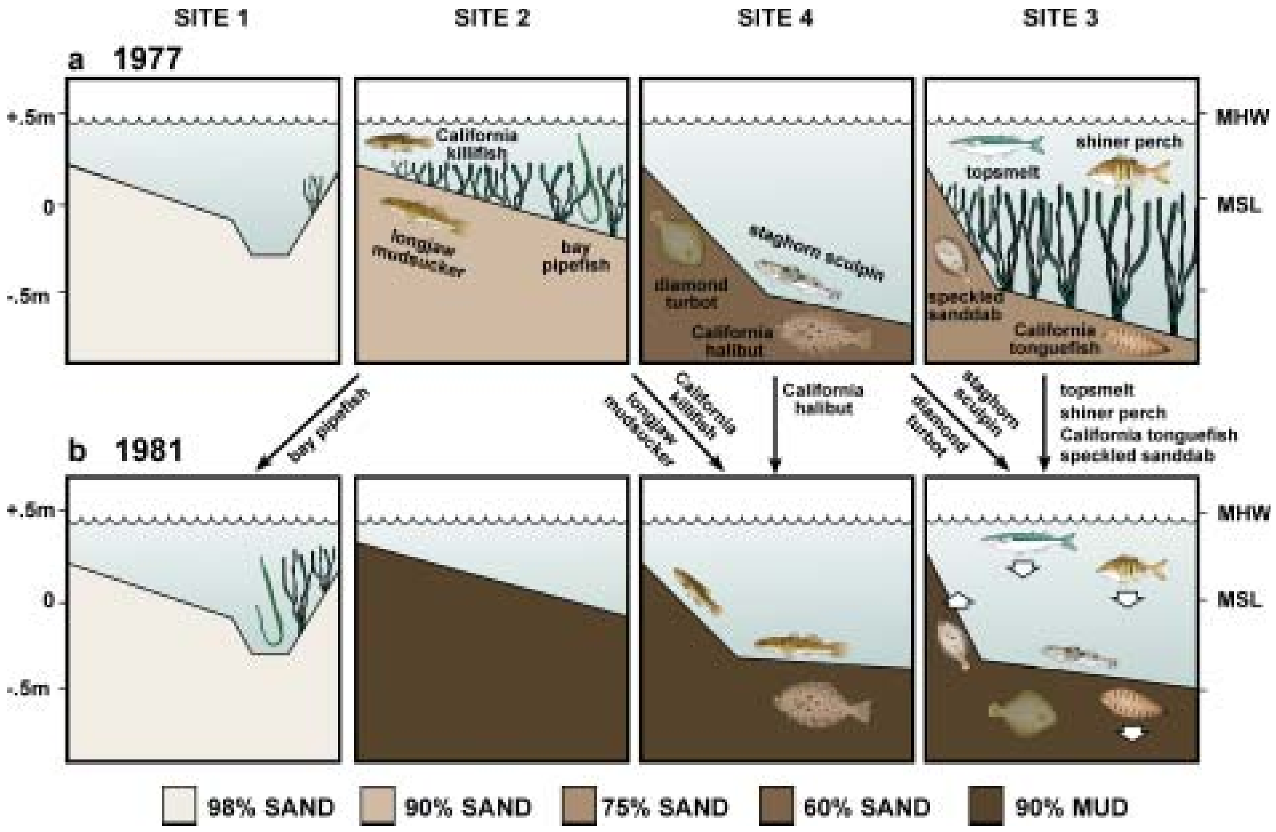

FIGURE 18-9 The characteristics of sampling sites in Mugu Lagoon, California and the locations where different species were most commonly caught in 1977 and in 1981. Significantly higher (up) abundance in 1981 than 1977 are represented by arrows; lower (down) (after Onuf, 1987).

FEEDING AND TROPHIC INTERACTIONS

In another study on Naples Reef, surfperch species altered microhabitat use following the 1980 storm (Stouder, 1987). Fishes concentrated on reef slope and reef crest microhabitats, and spent less time in reef cobble, deep cobble, and reef flat microhabitats. These changes in microhabitat use were associated with changes in food abundance. Microhabitat overlap also increased following the storm (fig. 18-10). Although foraging patterns changed, diet did not change significantly.

Ebeling et al. (1985) also examined surfperch abundance patterns following storms on Naples Reef. They monitored components of the reefs detrital-based food chain from 1979 through 1983, a period which incorporated two important storms. The 1980 storm removed the giant kelp canopy and created bare rock conditions. Understory and turf algae persisted for a short time, but removal of the giant kelp stands also reduced available detrital drift, a major food source of sea urchins. Sea urchin grazing removed any remaining macroalgae, new sporophytes, and the understory and turf algae creating a barrens-type habitat on the reef as sea urchin populations increased. Surfperch densities were correlated with turf algae and declined during the barrens period (fig. 18-11). A second severe storm occurred in 1983, which killed large portions of the sea urchin population, allowing recruitment and regrowth of giant kelp stands and an increase in detrital drift and surfperch densities.

Trophic connections may be altered as prey species shift habitat use in response to disturbance. In the Pt. Piedras Blancas kelp thinning experiment discussed above, juvenile rockfish species, principally blue rockfish (*S. mystinus*), declined following treatment (Bodkin, 1988). For blue rockfish, a reduction in giant kelp translated into a reduction in foraging substrata and refugia. Juvenile blue rockfish are important prey for piscivorous kelp forest fishes, thus the removal of blue rockfish foraging base and nursery habitat leads to loss of prey for predators, which may limit overall kelp forest fish abundance (Bodkin, 1988).

RECRUITMENT

Attributes of the benthic environment effect settlement and post-settlement survival in temperate reef fishes (Carr, 1994b). Therefore, disturbance events that change the benthic environment may change patterns in recruitment, potentially leading to changes in size and age structure, abundance, distribution, and dynamics of local populations. For example, YOY rockfish shifted their use of substrata and algal habitat types in response to diminished giant kelp and drift algae abundance following annual winter storms (Carr, 1991). Species recruitment is often positively influenced by the presence of giant kelp on temperate reefs. For other species, including island kelpfish (*Alloclinus holderi*) and other kelpfishes (*Gibbsonia* spp.), recruitment is negatively associated with macroalgal stands, usually due to indirect effects upon the understory algae (Carr, 1989).

Fishes respond to the presence or absence of macroalgal stands, as well as the architectural features of individual plants that may change based on plant density (Carr, 1994a). For example, larval recruitment of kelp bass (*Paralabrax clathratus*) increases linearly with increasing structural com-

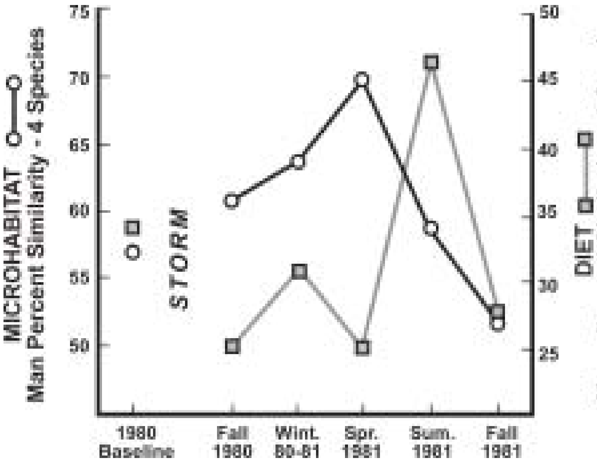

FIGURE 18-10 Mean percent similarity of microhabitat and diet for species of surfperches (*Embiotoca jacksoni, E. lateralis, Rhacochilus toxotes,* and *R. vacca)* for baseline data (1973) and seasons following the storm (September 1980—November 1981) at Naples Reef (after Stouder, 1987).

plexity of giant kelp, while structural complexity of giant kelp decreases with increasing plant density. Therefore, kelp bass recruitment decreases at high plant density. Individual species relationships vary with structural complexity and plant density, and recruitment density and plant density. Therefore, disturbance can affect larval recruitment differentially depending on species relationships (see also chapter 15 on Recruitment). Based on these interspecific differences, Carr (1994a) developed a predictive recruitment response model for three species [using data for kelp bass (Carr, 1994b) and kelp perch (*Brachyistius frenatus*; Anderson, 1993) from California, and spotty (*Notolabrus celidotus*; Choat and Ayling, 1987) from New Zealand] to changes in macroalgal density due to disturbance (fig. 18-12). Thus recruitment of fish can change as algal and plant structure varies. Macrophytes also function as a source of habitat structure and refuge in other aquatic systems (Orth et al., 1984, Heck and Crowder, 1991).

COMPETITION

Disturbance may also influence competitive interactions as a result of shifts in habitat use, foraging patterns, trophic interactions, reproduction, or recruitment. For example, when surfperch species on Naples Reef converged to one microhabitat type in response to changing food abundance, the one nonresident species, rainbow seaperch (*Hypsurus caryi*), reduced the time spent on the reef (Stouder, 1987). Typically rainbow seaperch migrated to the reef and remained for four to five months, but following the 1980 storm they stayed just one month. Food abundance is typically highest during the period of rainbow seaperch visitation. When confronted by low food abundances and aggressive resident species, these fish may have left to seek more abundant food sources in other locations.

The influence of storm disturbance on many aspects of community organization of Californian temperate reef

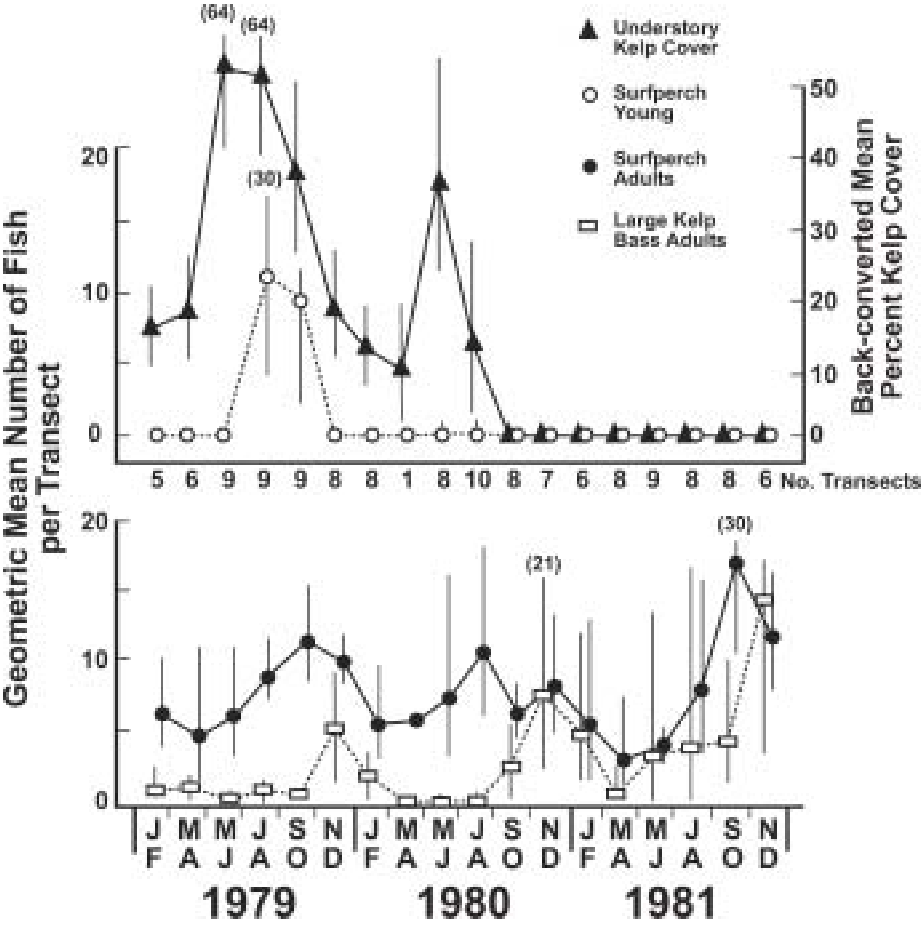

FIGURE 18-11 Mean percent cover of understory kelp compared to mean densities of young-of-year and adult surfperch and large kelp bass at the east-end study site at Naples Reef from January, 1979 (before a storm deforested the reef in February, 1980) to December, 1981. Vertical bars are the (asymmetric) 95% confidence intervals of means (after Ebeling and Laur, 1985).

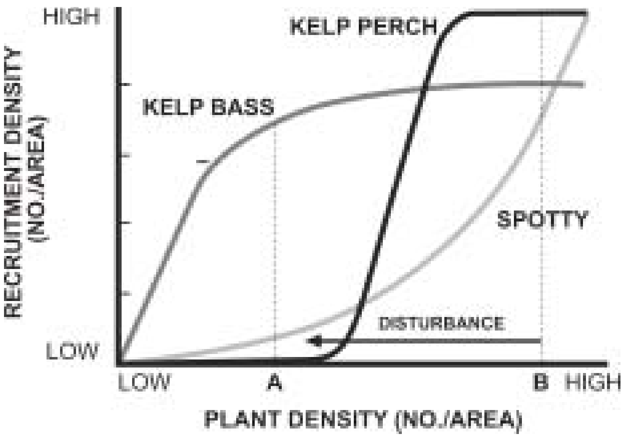

FIGURE 18-12 Predicted relative effects of disturbance on recruitment of three temperate reef-fish species, as mediated by reduced kelp density (after Carr 1994).

assemblages has been well documented. Even so, gaps in our knowledge exist, especially pertaining to the effects on fish reproduction.

Conclusions and Implications

Disturbances are common occurrences in all ecosystems. Although disturbances and their effects on fishes in all California marine systems have not been completely documented and studied, there are relevant examples from other temperate and tropical systems (e.g., intertidal areas, bays, estuaries, sea grass beds, coral and rocky reefs, kelp beds). These other studies can lend insights into potential effects of disturbance on California marine fishes. As evidenced by the few examples provided above, physiological and behavioral constraints result in different responses. Disturbances in a variety of habitats may produce similar results with regard to fish behavior (e.g., changes in feeding relationships and habitat use) while at other times disturbance may produce different results (e.g., differences in mobility affect some species or life stages ability to respond). Ultimately behavioral and physiological responses to disturbance may alter or influence community structure.

Do disturbances lead to long-term change? They can. If fish species are lost as a consequence of disturbance, and they are unable to re-colonize the area when conditions become favorable (i.e., source populations are too remote to facilitate colonization), then the fish assemblage structure in that location or habitat may be different than before the event. If conditions never return to the pre-event condition (e.g., irreversible habitat destruction), then assemblage characteristics may reflect the new set of habitat conditions. Rare and extreme disturbances, as well as those associated with global climate change or anthropogenic alterations and impacts, can especially give rise to long-term changes.

Are short-term changes bad? Not necessarily. Some disturbances can “reset the clock” by moving an assemblage away from equilibrium. The disturbance may clear some habitats and allow colonizing species to reinvade. At the same time species that were successful competitive dominants may be reduced to lower population levels thereby enabling other species to become more prevalent. It may be that non-equilibrium states created by disturbances are critical to long-term population stability and viability because assemblages never reach climax conditions.

Disturbance functions to structure marine fish assemblages by changing habitats (structurally, chemically, and thermally) and altering food resources. Fishes respond to these changes physiologically and behaviorally. Some fishes are capable of surviving in a wider range of oxygen levels, salinity and temperature ranges than others. These fishes may be much more physiologically tolerant and therefore able to remain in affected habitats until conditions become more favorable. Others will possibly die, grow more slowly, or move to habitats with more favorable conditions. Some fish life stages (i.e., eggs, larvae, some juveniles) have limited abilities to escape adverse conditions and may therefore be negatively and disproportionately affected. Adults tend to be more mobile. When mortality is not imminent, changes in juvenile and adult behaviors provide us with information on responses to disturbances. Fishes may alter their habitat selection or use, feeding behavior, reproductive activities, and movement patterns. Changes can also be represented by increases or decreases in competition among affected assemblage members, increased vulnerability to predation, decreased or postponed reproductive activities, and emigration from affected areas. Fishes have a suite of responses that make them more or less vulnerable to the effects of disturbance.

How we evaluate and view disturbance is largely the result of our perspective. Understanding disturbance lends insights to natural processes. Scientists and managers used to believe that disturbances were negative and disruptive to assemblages and ecosystems. Increasing evidence has indicated a common absence of assemblages or ecosystems at equilibrium. Improved understanding, and hence better management, of ecosystems includes knowledge and acceptance of the role of disturbance in natural systems. The larger the scale (e.g., pelagic marine) and the greater the disturbance the less we know. Although we can find some studies of natural disturbance in California marine systems, there are many other relevant examples in other marine systems (e.g., Atlantic coastal estuaries, Florida sea grass beds). Understanding community response to natural disturbances can provide us with a better template to understand the role of human impacts on natural systems. As anthropogenic influences increase, many assemblages become more sensitive to natural disturbances. Disturbance plays a critical role in the structure and stability of California marine fish assemblages and therefore it becomes crucial for us to increase our understanding of the range of conditions it creates.

Future Studies

Understanding disturbance and its effects on California marine fishes requires a strong foundation of intact marine ecosystems and assemblages. It also requires scientists and researchers to respond quickly in establishing or continuing a study examining the effects of the disturbance. Without an adequate foundation, or a slow response, it becomes increasingly difficult to understand the effects of disturbance related changes. There are, however, numerous and lengthy studies of California marine systems upon which to base comparisons of disturbance. Serendipity is in charge! With this in mind, we recommend the following initial list for future fish studies in California marine ecosystems:

1. Evaluation of hypoxia in estuaries, bays, and lagoons and the effects on fishes.
2. Examination of the consequences of increased sedimentation on vegetated (e.g., sea grasses) coastal areas including tide pools, bays, estuaries, lagoons, and near shore areas.
3. Evaluation of climatic change and its effects on current patterns, including inflow of freshwater, drought, floods, and temperature on fish assemblages.
4. Examinations of tsunamis and other severe storms provide information on catastrophic change and its influence on fishes.
5. Biological disturbances, use of combined lab and field experiments to understand observed responses.

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