Mangrove forests, for example, are currently viewed as a mosaic of gaps in different stages of regeneration following disturbance, with disturbance having a profound influence on the structure and species composition of the forest (Smith 1992; Chen & Twilley 1998; Duke 2001). Smith and Duke (1997) documented that mangrove forests in north-eastern Queensland, Australia, subjected to at least one cyclone every 5 years had more species of trees than those with lower frequencies of disturbance. Different species of mangrove trees exhibit various tolerances to shade, such that some species occur in greater abundances in gaps than under canopy (e.g. Smith 1987a, b; Sherman et al. 2000). Natural disturbance may thus provide opportunities to enhance forest diversity by facilitating recruitment and survival to the canopy (Rabinowitz 1978; Ellison & Farnsworth 1993).

For the past three decades, investigators have embraced and attempted to embellish Connell's ideas about how natural disturbance might explain patterns of species diversity in marine and other communities (e.g. Petraitis et al. 1989; Huston 1994; Mackey & Currie 2001; Platt & Connell 2003). From 1978 to 2006, Connell's (1978) now classic publication has been cited almost 2500 times (according to the ISI Web of Science). Besides Connell's own studies on coral reefs, other studies have indeed shown that disturbance, under some circumstances, may influence species diversity in a variety of marine benthic communities, including rocky intertidal boulder fields (e.g. Sousa 1979a, b; McGuinness 1987a, b; see Box 7.2), saltmarshes (e.g. Bertness & Ellison 1987; Bertness et al. 1992; Brewer et al. 1997, 1998) and mangrove forests (Smith 1992; Chen & Twilley 1998; Duke 2001).

Box 7.2 Rolling boulders across the Pacific

Wayne P. Sousa, Department of Integrative Biology, University of California, Berkeley, California, USA

Intertidal boulder fields are a common habitat along the shores of southern California, USA, and New South Wales, Australia (see also Box 15.1). The boulders are discrete patches of hard substrate, the top and bottom surfaces of which are occupied by a variety of sessile and mobile species. The assemblages occupying these surfaces are disturbed when boulders are moved or overturned by wave forces, and when scoured or buried under shifting sand. These disturbances damage or kill residents, freeing space for colonisation during the intervening disturbance-free periods. The influence of such disturbances on the diversity of sessile species living on intertidal boulders has been investigated by Sousa in southern California (1979a, b; also see Swarbrick 1984) and by McGuinness (1987a, b) in New South Wales. Do these studies tell the same story?

There are some strong similarities between the study sites and their communities. Wave forces and sand are common agents of disturbance in both places, and the ranges of boulder sizes are very similar, roughly 20 to 2000 cm^2. In both regions, the tops of boulders are occupied by foliose or encrusting algae, barnacles, and sea anemones, and the bottoms by encrusting algae, bryozoans, tube-building polychaetes, sponges, and ascidians.

The regimes of disturbance at the two sites have similarities and differences. At both locations, the probability of wave disturbance decreases with boulder size. Sand burial appeared to be a more frequent disturbance in New South Wales, but the California study intentionally

Box 7.2 ***(cont.)***

focused on the lower intertidal zone, where sand inundation was uncommon. At the Australian sites, sand burial was also less likely to kill or damage organisms on larger boulders because these substrates often rested on top of smaller ones, held above the underlying sediment. One striking difference between the sites is in the seasonality of disturbance. Along the coast of southern California, boulder movement and overturning occur mainly during winter storms, while no consistent seasonal patterns of disturbance have been observed at the Australian sites.

What is the relationship between disturbance and species diversity in these two locations? Sousa's study focused on the algal assemblages that occupied the top surfaces of low intertidal boulders. The pattern of algal diversity in his system varied with boulder size, and therefore the rate of disturbance, in a pattern consistent with the Intermediate Disturbance Hypothesis (Connell 1978; hereafter IDH). Boulders of intermediate size were disturbed at an intermediate frequency and supported the most diverse assemblages: a mix of species from all stages of succession. Small, more frequently disturbed, boulders were characterised by a low diversity assemblage comprising diatoms; the early successional green alga, *Ulva*; and the barnacle, *Chthamalus*. Large boulders were rarely disturbed, had a high percentage of cover, and supported an assemblage dominated by the late successional, red alga, *Gigartina*.

In contrast, McGuinness only found the patterns predicted by the IDH on the undersides of low intertidal boulders. Small boulders were highly disturbed and supported sparse, depauperate assemblages. With increasing boulder size, and the associated reduction in disturbance rates, the diversity of crustose algae and solitary and colonial invertebrates increased. On the undersides of large stable boulders, where the cover of these organisms became sufficiently high that space was in short supply, overgrowth interactions reduced diversity. This pattern was not observed on either the tops or bottoms of boulders in the upper intertidal, or the tops of low intertidal boulders. The higher tidal elevations of these surfaces exposed them to the air for relatively long periods during low tides. The resulting desiccation stress, combined with more intense gastropod grazing, prevented the build-up of algal and sessile invertebrate populations, so space was abundant and competitive exclusion did not occur. Species diversity rose monotonically with increasing boulder size, with no evidence of a decline on larger, more stable boulders.

So, the IDH successfully predicts patterns of species diversity both in the low intertidal of southern California and in a subset of the boulder field habitats in New South Wales. The model does not apply in areas of the Australian intertidal where desiccation limits recruitment or growth and populations never reach densities at which they compete for space. Differences in the biology of the dominant species in the two systems also affect the relationship between disturbance and diversity. *Gigartina*, the late successional species in the southern California system, forms a dense, vegetatively spreading turf that is very resistant to invasion, so it exerts strong dominance on stable surfaces. In contrast, the most common late successional algae in the Australian system are the delicate, foliose red alga, *Polysiphonia*, and relatively slow-growing crustose brown (*Ralfsia*), and red (*Hildenbrandia*) algae, none of which is likely to secure and monopolise space as rapidly or as persistently as *Gigartina*.