

Sea urchin dynamics and community-based marine protected areas¹

The role of herbivores, and sea urchins in particular, in structuring shallow temperate subtidal reef systems has been documented in different systems and regions around the world (Shepherd, 1973; Lawrence, 1975; Breen and Mann, 1976; Chapman, 1981; Andrew and Choat, 1982; Choat and Schiel, 1982; Duggins, 1983; Dean et al., 1984; Harrold and Reed, 1985; Fletcher, 1987; Vadas et al., 1986; Chapman and Johnson, 1990; Andrew, 1991, 1994). Sea urchins are important members of subtidal reef communities because some species can overgraze fleshy macroalgae to create barrens habitat and still persist in high population densities (Johnson and Mann 1982). As a result, a sharp decrease in primary production is generally associated with this transition of rocky reef habitats dominated by macroalgal beds to barrens habitat dominated by crustose coralline algae. Further, such deforestation events can wipe out entire algae (e.g. *Macrocystis pyrifera*) populations with concomitant decreases in the abundance of various associated algae. This generates well documented changes in community composition and repercussions for rocky-reef ecosystem structure and functioning (Dayton 1975a,b; Dayton et al 1984; Schmitt and Holbrook 1990; Sala et al., 1998; Gagnon et al 2004). In California, population explosions of kelp grazers, and sea urchins in particular, resulted in kelp deforestation and transition to barrens at a variety of scales (Leighton 1971, Lawrence 1975, Foster and Schiel 1988, Steneck et al 2002 and references therein).

Possible mechanisms underpinning the creation of barrens relate with either a change in sea urchin grazing behavior or an increase in their density. A behavioral shift where cryptic individuals emerge to overgraze attached algae may result from either decreased predator abundance (Bernstein et al., 1981; but see Vadas et al., 1986; Elner and Vadas, 1990) or decreased availability of drift algae (Harrold and Reed, 1985). Alternatively, increases in sea urchin population density and subsequent barrens formation can potentially arise from decreases in predator abundance (Estes and Palmisano, 1974; Duggins, 1980; Wharton and Mann, 1981; Vadas and Steneck, 1995; Steneck, 1997) or unusual massive recruitment events (Hart and Scheibling, 1988). The importance of predators structuring sea urchin populations has been long discussed, with relatively

¹ Nicolás L. Gutiérrez, School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington

little obvious evidence except in the case of the sea otter (*Enhydra lutris*) as a key predator of sea urchins at some sites in the northeastern Pacific (Estes and Duggins, 1995; Estes et al., 1998). In addition, abundant evidence support the importance of teleost fish in the northwestern Atlantic (Vadas and Steneck, 1995; Shears and Babcock, 2002) and rock lobsters in South Africa (*Jasus* spp; Mayfield and Branch, 2000; Mayfield et al., 2001) in regulating sea urchin populations, and that the regulatory effect is influenced by fishing of these predators. In California, lobsters and sheepheads are the main predators of sea urchins and potentially regulate its populations (Tegner and Levin 1983; Cowen 1983). Pycnopodia have also been shown to be predators of Sea Urchins in California (Duggins 1983). However, whether predators can be capable of naturally control sea urchins populations and hence maintain healthy kelp ecosystems depends on the system and species. Predation upon sea urchins is generally higher where predatory fish are abundant and large (e.g., within MPAs; Sala and Zabala, 1996; Guidetti, 2006). However, the patterns observed are not consistent in time, at large spatial scales, or in different systems around the world (Sala et al. 1998; Guidetti 2006; Guidetti et al. 2005; Micheli et al. 2005). For example, Andrew and Choat (1982) found no evidence of an effect of fish predation on densities of sea urchins within a marine reserve in New Zealand. Further, Shears and Babcock (2004) stated that, while increased predation may affect sea urchin population structure and density, only under certain environmental conditions are these changes likely to result in cascading effects on algal communities. Further, as stated by Sala et al. (1998), other processes (i.e. recruitment, pollution, disease, large-scale oceanographic events, sea urchin harvesting, food subsidies, and availability of shelters) may also be important in regulating the structure of algae assemblages. In summary, natural control of sea urchin population by predators may or may not occur, depending on the biological, ecological and environmental conditions of a particular system.

Sea urchins and abalones generally share similar food and habitat preferences in kelp forest communities around the world (Tegner and Levin 1982; Davis et al. 1992; Guzman del Proo, 1992) and competition between these two taxa for space and/or food has been documented worldwide (Shepherd 1973; Tegner and Levin 1982; Andrew and Underwood 1992 and references therein). Along the California coast, abalone (*Haliotis* spp.), red sea urchins (*Strongylocentrotus franciscanus*) and purple sea urchins (*S. purpuratus*) feed primarily on the same species of macroalgae and have been described as potential competitors for food and space (Tegner and Levin 1982). In addition, sea urchins capability of overgraze kelp beds with consequent formation of barrens can deprive other herbivores, such as abalone, from food sources. In this respect, and motivated by fishermen's concern that urchin-dominated barren areas were increasing in

New South Wales, Australia, Andrew et al. (1998) carried out a sea urchin (*Centrostephanus* sp.) removal experiment to assess potential benefits in abalone populations. Thirty replicates of at least 1000 m² were used to compare different patterns of sea urchin removals. Clearing the echinoids led to a habitat shift from coralline crusts to a range of foliose algae, accompanied by an order-of magnitude increase in abalones. They suggest the potential benefits of an incipient sea-urchin fishery in enhancing abalone populations and they advocate the development of an experimental approach to co-management of the two species. Moreover, Tomascik and Holmes (2003) assessed the distribution and abundance of pinto abalones (*Haliotis kamtschatkana*) in relation to habitat, competitors and predators in the Broken Group Islands, BC, Canada. They found a positive correlation between abalone size and the abundance of benthic macroalgae and an inverse relationship between abalone size and the abundance of red sea urchins (*S. franciscanus*). Further, in northern California, Karpov et al. (2001) explored spatial interactions and apparent competitive effects among red abalones (*H. rufescens*), red sea urchins (*S. franciscanus*), and purple sea urchins (*S. purpuratus*) in an area where fishing has large impacts on both taxa, and at unfished reserve sites in which invertebrate density and food availability differ. They found an inverse correlation between adult red abalone and red sea urchin abundance when density of either or both species was high. Their results suggest that differences in density, depth, and food availability play an important role in the observed spatial patterns of red abalones and red sea urchins. They suggest that an intense fishery for red sea urchins appear to have had a positive effect on kelp availability, and abalone growth and abundance. Ultimately, red sea urchin removal led to an increase in red abalone abundance even at a site that was heavily fished by recreational abalone fishers, while at a nearby reserve site where kelp populations are lower, red abalones have declined in abundance as red sea urchins increased. Finally, preliminary analyses of sea urchin and abalone data collected by the California Department of Fish and Game (CDFG 2010) in two different sea urchin closures areas, Caspar and Salt Point, show a similar inverse relationship between densities of both taxa (Fig. 1a and b).

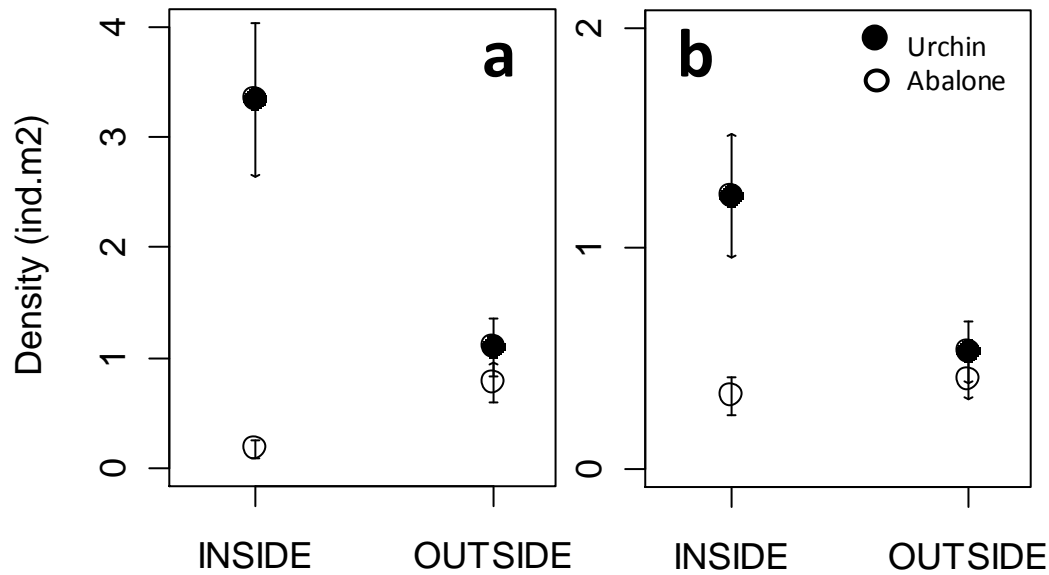


Figure 1. Mean densities for sea urchin and abalone inside and outside (a) Caspar closure for the period 1989-2008; and (b) Salt Point closure for 2008.

This analysis should be considered preliminary and exploratory, since the availability and the temporal coverage and replication of data available so far doesn't allow the use of robust statistical methods. However, difference in sea urchins densities inside and outside the reserve were significant in both cases ($p < 0.005$ and $p < 0.010$ for Caspar and Salt Point respectively). Abalone densities inside and outside Caspar were significant ($p < 0.05$) yet not significant in Salt Point ($p > 0.05$). An incomplete time series of sea urchins and abalone densities inside the Caspar reserve show, although not significant ($p > 0.05$), some visual trends of increase in sea urchins and decrease in abalones. Additional data, especially missing years, should be included in order to confirm or reject such trends (Fig. 2).

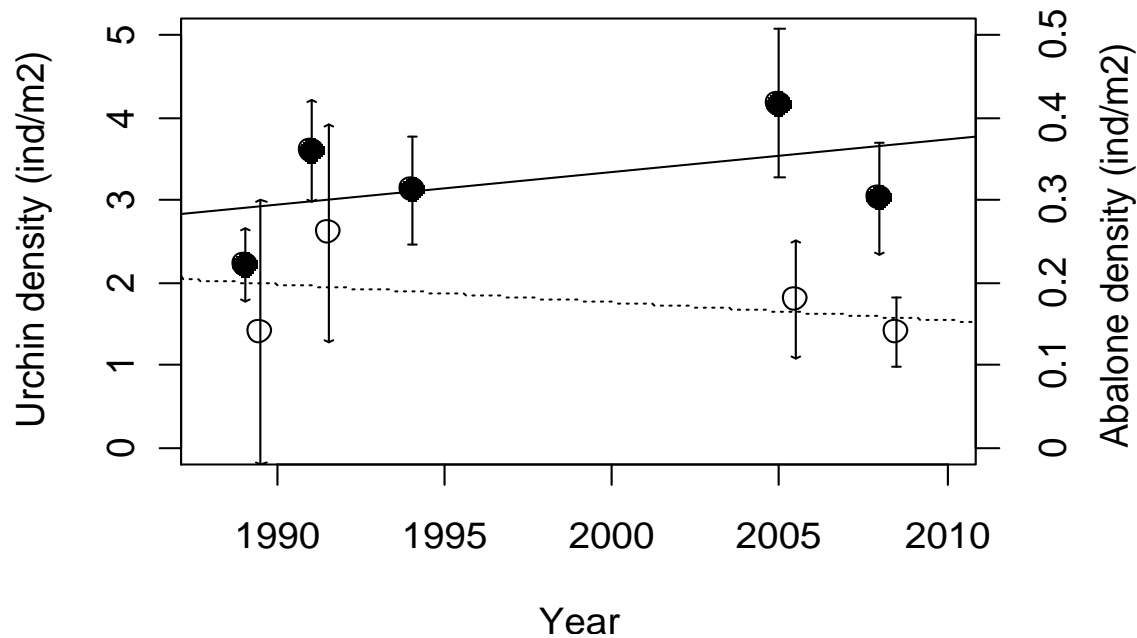


Figure 2. Time series of sea urchin and abalone densities inside the Caspar marine reserve (mean ± SE; Coefficients were positive and negative for sea urchin and abalones respectively, although linear model fits were not significant in both cases; $p > 0.05$)

In addition, percentage of algae coverage available for sea urchins (i.e. sub-canopy and canopy) showed a drastic decline after the Caspar/Salt Point reserve was established (Fig. 3), possible supporting the concept of overgrazing by an increased sea urchin population

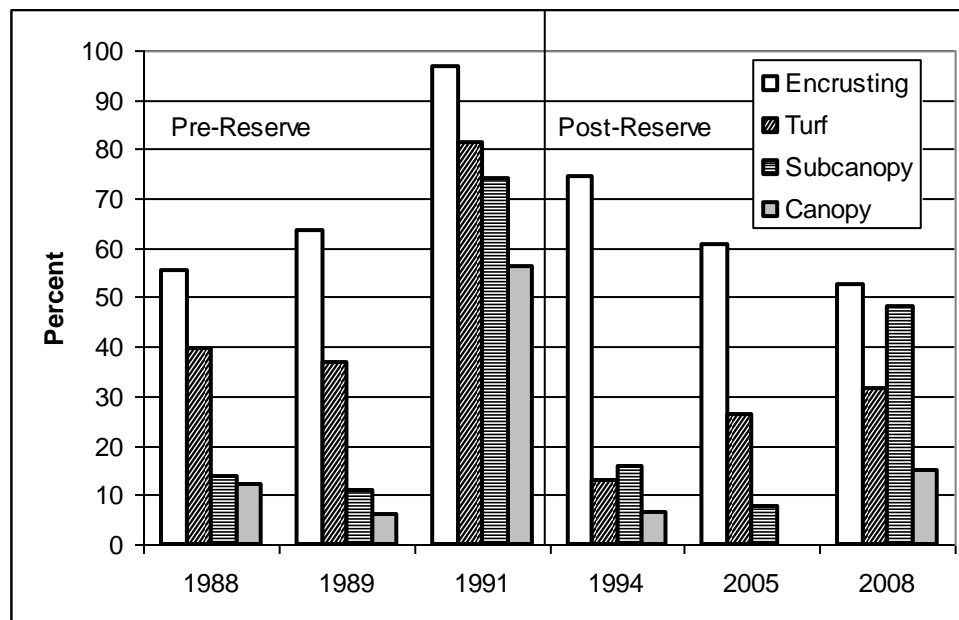


Figure 3. Percentage of algae coverage by type measured along bottom inside the Caspar closure area, period 1988 – 2008. After CDFG (2010).

In contrast with the competitive relationship observed between adult urchins and adult abalone, adult sea urchins may act as facilitators of juvenile recruitment, either providing physical protection for juvenile abalone under their large spine canopy (Tegner and Dayton, 1977; Tegner and Butler, 1989), and/or maintaining coralline algal patches by intense grazing, which have been shown to result in increased abalone settlement (McShane, 1992). Day and Branch (2000) showed a strong, positive relationship between urchins (*Parechinus anguwsus*) and abalone (*Haliotis midae*) in the southwestern Cape, South Africa. Of the juvenile abalone sampled, more than 90% were found beneath sea urchins. In addition, Rogers-Bennet and Pearse (2000) stated that red sea urchin may provide an important cryptic microhabitat for juvenile abalone sheltering beneath urchin spines in shallow waters. They investigated the abundance of juvenile red abalone (*H. rufescens*) and flat abalone (*H. walallensis*) on protected and fished rocky shores in northern California, finding that one third of the juveniles inside the MPAs were found under the urchins' spine canopy. However, the abundance of juvenile red abalone was not correlated with the abundance of conspecifics adults. Tomascik and Holmes (2003) implied a similar interaction, but only seven percent of total number of juvenile abalone (less than or equal to 45 mm) was found under the red sea urchins' spine canopy. However, given the importance of sea urchins' spine canopy for juveniles of their own species, these studies should have evaluated the competition for that microhabitat under high sea urchin densities. Another important consideration to study is the survival of juvenile abalone over time under high sea urchin densities and the likely competition for food.

Despite the variability of ecological conditions affecting sea urchin populations and consequent overgrazing of kelp communities, and the intra and inter-specific role of sea urchin in structuring rocky shore communities, the negative impacts of overgrazing and transition to barrens are quite convincing. Main effects may include losses in productivity and biodiversity (Tegner and Dayton 1981, 1987; Holbrook et al. 1990; Herrera 1998; Babcock et al 1999, Graham 2004 and references therein) and loss of habitat suitable for feeding and breeding fish and invertebrates (Brito et al. 2004). Thus, controlling sea urchin population by means of calcium oxide (quick-lime; Wilson and North 2009 and references therein), releasing fishing pressure on its predator (e.g. lobsters and sheepheads; Tegner & Levin 1983; Tegner & Dayton 2000) or by developing targeted fisheries (Sala et al 1998; Guidetti et al 2004) has been a common practice in various systems around the world and in California in particular.

A significant amount of studies show the effectiveness of marine protected areas (MPA), and marine reserves in particular, as conservation tools when they are placed and

designed properly. Marine reserves are often established with fisheries enhancement objectives or biodiversity conservation goals. Recently, studies have begun to address biodiversity conservation through community wide changes due to marine reserves. In this respect, community state transitions between barrens and kelp forests due to marine reserves have been documented in various systems worldwide. This appears to be due to indirect effects of banning fishing, which cascade down the food chain to produce a community shift (e.g. more lobsters = fewer urchins = more kelp). Several studies indicate that releasing fishing pressure on urchin's predator (e.g. lobsters) may control sea urchins populations and allow kelp beds recovery (Babcock et al 1999; Steneck et al 2002 and references therein). However, where natural predators aren't capable of controlling herbivores populations, overgrazing may cause a decrease in macroalgae abundance and productivity, with a transition to barrens as an extreme case (Sala 1997; Davenport and Anderson 2008). Some examples of drastic changes in community compositions inside no-take marine reserves include (i) two examples in Kenya, one at the Mombassa National Park where the exclusion of artisanal fishers for several years, in conjunction with manipulative programs to reduce sea urchin populations demonstrated that herbivores mediated competition between algae and coral (McClanahan 1997), and the other at the Watamu National Park where increased herbivory slowed of the recovery of macrophytes and caused a switch toward dominance of calcareous algae (McClanahan et al 2002); (ii) a study in northern and central Chile where abundance of limpets inside human-exclusion 'no-take' areas, were coupled with a drastic decline in the abundance of macroalgae with extensive food-web modifications (Oliva and Castilla 1986); (iii) in South Africa, selective fishing on mussels and limpets increased species richness and the substrate showed a significantly greater cover of sessile unexploited species (e.g. macroalgae; (Hockey 1994); (iv) in Ustica, Italy, the lack of human fishing pressure after the instauration of a protection regime caused a sharp increase of urchins density with consequent transformation of algal assemblages into barren areas, dominated by a few species of encrusting algae (Gianguzza et al 2006). These community and food web modifications may lead to losses in biodiversity and productivity, undermining the overarching objectives of MPAs. In this context, the examples mentioned have developed regulated selective fishing or experimental removals practices in order to control key dominant species and avoid drastic changes in community composition and structure.

Another important benefit of regulated fishing inside MPAs is the inclusion of fishermen and stakeholders in the regulatory and enforcement process. Cooperation in MPA implementation and enforcement and in resource management by local communities of users has been shown as a critical step in attaining the specific objectives behind these protected areas worldwide (Africa: South Africa, Kenya; Asia: Philippines, Bangladesh,

Japan; Oceania: Vanuatu, Samoa, Australia; North America: USA, Canada, Mexico; South America: Brazil, Chile, Peru; and Europe: Italy, France, Sweden, UK; Gutierrez and Hilborn in prep.) In addition, community-based MPAs that are periodically harvested are increasingly being implemented as fisheries management tools. Some examples of local community involvement in implementing and enforcing MPAs include: (1) coral reefs in Vanuatu, where a periodical fishing inside the reserve has demonstrated both ecosystem and fishing benefits (Bartlett et al 2009); (2) cooperative fishing in the Gulf of California, Mexico, where MPAs are the core component of the management system (Cudney-Bueno and Basurto 2009); (3) a cod fishery in the Baltic sea, where fishermen participation in fishery regulations inside a MPA improved rule compliance and led to a sustainable fishery (Suuronen et al 2010); Further, Pollnac et al. (2010) show in a recent review of 127 MPAs published in the Proceedings of National Academy of Sciences that high levels of compliance with reserve rules were more related to complex social interactions, such as fishermen incentives and community cohesion and leadership, than simply to enforcement of reserve rules.

Finally, besides the implementation and enforcement benefits, co-management or community-based management (CBM) of MPAs also allow time and cost efficient monitoring of resources within the protected area. Data collection on targeted resources, habitat, and its associated species by fishermen has been used and described for different fisheries worldwide (Chile, Australia, New Zealand, Spain). In the Australian abalone fishery, divers gather and process fishery-dependent information in what Prince (2003) popularized as the “Barefoot Ecologist” program. In California, the San Diego Watermen’s Association (SDWA), which includes divers that target local red sea urchins *Strongylocentrotus franciscanus*, started a CB data collection program in 2001 (Schroeter et al. 2009). In collaboration with independent scientists and biologists, the SDWA developed a program to gather, organize, and analyze both fishery-dependent and fishery-independent data on the local red sea urchin fishery. These CB data collection programs are of particular importance for sea urchins and other sedentary or low mobility invertebrates (e.g. lobsters, abalones). Fine-scale spatial heterogeneity in their life history traits demands a great amount of spatial and temporal information in order to depict patterns and processes in their population dynamics needed for proper stock assessments and management plans (Butterworth and Punt 1999; Hobday and Punt 2009). This fine-scale spatial and temporal resolution in data collection and analysis has been proved extremely difficult to achieve without fishermen involvement.

References

- Andrew NL & Underwood AJ. (1992). Associations and abundance of sea urchins and abalone on shallow subtidal reefs in southern New South Wales. *Australian Journal of Marine and Freshwater Research* 43, 1547–59.
- Andrew NL, Worthington DG, Brett PA, Bentley N, Chick RC & Blount C. (1998). Interactions between the abalone fishery and sea urchins in New South Wales. New South Wales Fisheries Research Institute, Final Report Series Number 12. 108 pp.
2.246479
- Andrew NL & Choat JH (1982) The influence of predation and conspecific adults on the survivorship of juvenile *Evechinus chloroticus* (Echinoidea: Echinome tridae). *Oecologia* 54: 80-87.
- Andrew N, Worthington D, Brett P & Bentley N. (1998). Interactions between the abalone fishery and sea urchins in New South Wales. 1998 Final report to the Fisheries Research and Development Corporation - Project Number 1993/102. New South Wales Fisheries Final Report Series No. 12. ISSN 1440-3544
- Babcock RC, Kelly S, Shears NT, Walker JW & Willis TJ. (1999) Changes in community structure in temperate marine reserves. *Mar Ecol Prog Ser* 189:125–134
- Bartlett CY, Manua C, Cinner J, Sutton S, Jimmy R, South R, Nilsson J & Raina J. (2009) Comparison of Outcomes of Permanently Closed and Periodically Harvested Coral Reef Reserves. *Conservation Biology* 23 (6): 1475-1484.
- Butterworth DS & Punt AE. (1999). Experiences in the evaluation and implementation of management procedures. *ICES Journal of Marine Science* 56:985–998.
- CDFG (2010). Caspar/Salt Point Urchin Closure Data Summaries, DRAFT Prepared by DFG, Marine Invert Project. Data are preliminary.
- Cole RG, Keuskamp D. (1998). Indirect effects of protection from exploitation: patterns from populations of *Evechinus chloroticus* (Echinoidea) in northeastern New Zealand *Mar Ecol Progr Ser* 173:215-226.
- Cowen RK (1983) The effect of sheephead (*Semicossyphus pulcher*) predation on red sea urchins (*Strongylocentrotus franciscanus*) populations: an experimental analysis. *Oecologia* 58:249–255
- Cudney-Bueno R, Basurto X. (2009) Lack of Cross-Scale Linkages Reduces Robustness of Community-Based Fisheries Management. *PLoS ONE* 4(7): e6253.
- Davis GE, Haaker PL & Richards DV. (1996) Status and trends of white abalone at the California Channel Islands. *Trans. Am. Fish. Soc.* 125, 42–48.

- Davis GE, Richards DV, Haaker PL & Parker DO. (1992) Abalone population declines and fishery management in southern California. In: Shepherd, S.A., Tegner, M.J. and Guzman del Proo, S.A. (eds.), *Abalone of the World; Biology, Fisheries and Culture*. Fishing News Books, pp. 237–249.
- Day E & Branch GM (2000) Evidence for a positive relationship between juvenile abalone and sea urchin in the South Western Cape, South Africa. *S. Afr. J. mar. Sci.* 22: 145-156
- Duggins, D.O. 1983. Starfish predation and the creation of mosaic patterns in a kelp-dominated community. *Ecology* 64:1610-1619.
- Salomon, A., E. Buhle, N. Shears, S. Katz, and S.D. Gaines 2009. Cascading effects of predator depletion can alter key ecological processes and the resilience of a kelp forest ecosystem. Western Society of Naturalists meeting, Monterey, CA. Foster MS, Schiel DR. (1988). Kelp communities and sea otters: keystone species or just another brick in the wall? In: VanBlaricom GR, Estes JA, Eds. *The community ecology of sea otters* Berlin: Springer-Verlag. p 92–115.
- Gianguzza P, Chiantore M, Bonaviri C, Cattaneo-Vietti R, Vielmini I & Riggio S. (2006) The effects of recreational *Paracentrotus lividus* fishing on distribution patterns of sea urchins at Ustica Island MPA (Western Mediterranean, Italy). *Fisheries Research* 81:37–44
- Graham MH. (2004). Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7:341–357
- Guidetti P, Terlizzi A & Boero F. (2004). Effects of the edible sea urchin, *Paracentrotus lividus*, fishery along the Apulian rocky coasts (SE Italy, Mediterranean Sea). *Fish Res.* 66, 287–297.
- Guzman del Proo SA. (1992) A review of the biology of abalone and its fishery in Mexico. In: Shepherd, S.A., Tegner, M.J. and Guzman del Proo, S.A. (eds.), *Abalone of the World; Biology, Fisheries and Culture*. Fishing News Books, pp. 341–360.
- Hamilton SL, Caselle JE, Malone DP & Carr MH. (2010). Incorporating biogeography into evaluations of the Channel Islands marine reserve network. *Proc. Natl. Acad. Sci.* www.pnas.org/cgi/doi/10.1073/pnas.0908091107
- Hobday D & Punt AE. (2009). How much spatial structure can data for rock lobster off Victoria, Australia support? *New Zealand Journal of Marine and Freshwater Research* 43:373–385.
- Hockey PAR. (1994) Man as a component of the littoral predator spectrum: a conceptual overview, in *Rocky Shores: Exploitation in Chile and South Africa* (Siegfried, W.R., ed.), pp. 17–31, Springer-Verlag
- Holbrook SJ, Carr MH, Schmitt RJ & Coyer JA (1990) Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bull Mar Sci* 47:104–114
- Karpov KA, Tegner MJ, Rogers-Bennett L, Kavass P & Taniguchi IK. (2001). Interactions among red abalones and sea urchins in fished and reserve sties of northern California: Implications of competition to management. *Journal of Shellfish Research* 20 (2): 743-753.

- Kinsford MJ, Underwood AJ & Kennelly SJ. (1991) Humans as predators on rocky reefs in New South Wales, Australia, *Mar. Ecol. Prog. Ser.* 72, 1–14
- Lawrence JM. (1975). On the relationships between marine plants and sea urchins. *Oceanogr Mar Biol Annu Rev* 13:213–86.
- Leighton DL. (1971). Grazing activities of benthic invertebrates in Southern California kelp beds. *Nova Hedwigia* 32:421–53.
- Obura D. (1996). Effect of sea urchin reductions on algae, coral, and fish populations. *Cons. Biol.* 10, 136–154.
- McClanahan TR. (1997) Recovery of fish populations from heavy fishing: does time heal all? in *Proceedings 8th Coral Reef Symposium (Vol. 2)* (Lessios, H.A. and MacIntyre, I.G., eds), pp. 2033–2038.
- McClanahan TR, Uku JN & Machano H. (2002). Effect of macroalgal reduction on coral-reef fish in the Watamu Marine National Park, Kenya. *Mar. Freshwater Res.*, 2002, 53, 223–231
- Oliva D. & Castilla JC. (1986) The effect of human exclusion on the population structure of keyhole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile, *P.S.Z.N.I. Mar. Ecol.* 7, 210–207
- Pollnac R, Christie P, Cinnerc JE et al. (2010). Marine reserves as linked social–ecological systems. *Proc. Natl. Acad. Sci* 107 (7)
- Prince JD. (2003). The barefoot ecologist goes fishing. *Fish Fish.* 4: 359–371.
- Sala E. (1997). Fish predators and scavengers of the sea urchin *Paracentrotus lividus* in protected areas of the north-west Mediterranean Sea. *Mar. Biol.* 129, 531–539.
- Rogers-Bennett L & Pearse JS. (2001). Indirect benefits of marine protected areas for juvenile abalone. *Conservation Biology* 15: 642-647.
- Sala E, Boudouresque CF & Harmelin-Vivien ML. (1998). Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* 82, 425–439.
- Sala E & Zabala M. (1996). Fish predation and the structure of the sea urchin *Paracentrotus lividus* population in the NW Mediterranean. *Mar. Ecol. Prog. Ser.* 140, 71–81
- Schroeter SD, Gutierrez NL, Robinson M, Hilborn R & Halmay P. (2009). Moving from Data Poor to Data Rich- A Case Study of community based data collection San Diego sea urchin fishery. *Mar Coast Fish Dyn Manag Ecosys Sci* 1:230–243
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA & Tegner MJ. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436-59.

Suuronen P, PekkaJounela J & Tschernij (2010) Fishermen response on marine protected areas in the Baltic cod fishery. *Marine Policy* 34: 237–243

Tomascik T & Holmes H. (2003). Distribution and abundance of *Haliotis kamtschatkana* in relation to habitat, competitor and predators in the Broken Group Islands, Pacific Rim National Park reserve of Canada. *Journal of Shellfish Research* 22 (5) 831-838.

Tegner MJ. & Levin LA. (1982) Do sea urchins and abalones compete in California kelp forest communities? In: Lawrence, J.M. (ed.), *International Echinoderm Conference*. A. A. Balkema, Rotterdam.

Tegner MJ & Levin LA. (1983). Spiny lobsters and sea urchins: analysis of a predator–prey interaction. *Journal of Experimental Marine Biology and Ecology* 73:125–150.

Tegner MJ & Dayton, PK. (2000). Ecosystem effects of fishing in kelp forest communities. *ICES J. Mar. Sci.* 57, 579–589.