

A boom–bust phylum? Ecological and evolutionary consequences of density variations in echinoderms

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Abstract. Echinoderms play a key role in structuring many marine ecosystems and are notorious for large population density variations in so-called “outbreak” or “dieoff” events. In a review of this phenomenon, we assess the causal factors and ecological and evolutionary consequences. We identified 28 species (6 Asteroidea, 8 Echinoidea, 10 Holothuroidea, 4 Ophiuroidea) that exhibit large (more than two population doublings or halvings) population density changes. Three generalized patterns were identified and named for exemplary species: (1) rapid decreases followed by no or slow recovery (*Diadema–Paracentrotus* Model), (2), rapid increase and apparent stability at a new population density (*Amperima–Amphiura* Model), and (3) population density fluctuations (*Acanthaster–Asterias* Model). Echinoderms identified were distributed from the shallow intertidal to the deep sea, and from tropical to temperate regions. In most cases, significant impacts on the respective ecosystems were observed. The most striking similarity among all species identified was possession of the ancestral-type planktotrophic larva. This larval type was significantly overrepresented in species identified within the Asteroidea, Echinoidea, Holothuroidea, and for the combined data set. We suggest three main factors that render a life history with planktotrophic larvae a high-risk–high-gain strategy: (1) a strong nonlinear dependency of larval production on adult densities (Allee effects), (2) a low potential for compensatory feedback mechanisms, and (3) an uncoupling of larval and adult ecology. The alternative (derived) lecithotrophic larva occurs in 68% of recent echinoderm species, suggesting an evolutionary trend toward this larval type. Lecithotrophic development represents a more buffered life history because compensatory feedback between adult densities and larval output is likely to be more efficient. For lecithotrophic developers, direct nutritive coupling from adult to larva to the early benthic juvenile provides a buffer against starvation. Lecithotrophic larvae are independent of the vagaries of planktonic food supply, and their short planktonic duration may promote local recruitment. Anthropogenic influences contributed to the population density variations in most cases, including increased primary productivity through eutrophication or global change, disease, overfishing, and species introductions. We suggest that anthropogenic disturbance, through its influence on the frequency and/or amplitude of echinoderm population density changes, may go beyond present ecosystem impacts and alter future evolutionary trends.

Key words: *anthropogenic impact; benthic ecology; echinoderms; invertebrate evolution; keystone species; marine population fluctuations; population dynamics.*

INTRODUCTION

Echinodermata is one of the few animal phyla that are exclusively marine. There are a total of ~7000 living species, occurring in all marine habitats ranging from

the deep sea to shallow intertidal areas, and in all climate zones. The phylum consists of five recent classes: Asteroidea (sea stars, ~1745 recent species), Crinoidea (feather stars, ~580 species), Echinoidea (sea urchins, ~900 species), Holothuroidea (sea cucumbers, ~1430 species), and Ophiuroidea (brittle stars, ~2300 species) (Fell 1982, Pawson 1982, 2007). Echinoderms have been a focus for experimental ecology because of their important functions in marine ecosystems, with several

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species identified as “keystone species” (Paine 1969, Lawrence 1975, Elnor and Vadas 1990, Power et al. 1996, Lessios et al. 2001).

Variations in the population density of ecologically important echinoderm species can have marked consequences for the ecosystem, with notable examples resulting in major ecosystem changes described as “phase-shifts” between alternate-stable states, or catastrophic shifts (Scheffer et al. 2001). For marine ecologists, the most familiar examples include the changes from coral- to algal-dominated systems associated with the die-off of the tropical sea urchin *Diadema* in the Caribbean (Lessios 1988, Hughes 1994) and the transitions between temperate kelp forests and “urchin barrens” associated with extreme abundance fluctuations of herbivorous sea urchins (Elnor and Vadas 1990, Steneck et al. 2004). Variations in predatory sea star populations are also associated with marked change in ecosystem structure, such as changes in carbon flow through the system and local extinction of prey species (Paine 1966, Johnson et al. 1995, Witman et al. 2003, Ross et al. 2004).

In addition to ecological consequences, marked population density variations also have wide implications for a species’ evolution (Nei et al. 1975). Population decline can lead to bottleneck effects with dramatically reduced genetic diversity. Although this can make species more vulnerable to variation in environmental parameters and diseases, a smaller genetic base after population bottlenecks, or in founder populations, can also lead to rapid speciation via “genetic revolution” (Mayr 1954) or “genetic transience” (Templeton 1980).

Here, we examine large variations in densities of echinoderm populations including spectacular increases (“outbreaks,” “population explosions,” “plagues”) and decreases (“die-offs,” “mortality events”). These changes are considered to be anomalous compared to the perceived natural state of the population in a given ecosystem. It is often difficult to assess the significance of mortality or outbreak events with respect to long-term averages because ecological time series needed to define the boundaries of a “natural” state are rarely available.

In marine phyla other than echinoderms, most population declines are caused by two factors (1) overfishing (e.g., fish, whales, turtles, mollusks [Jackson et al. 2001, Myers and Worm 2003]) and (2) disease (e.g., seals, dolphins, coral, abalone [Osterhaus et al. 1988, Roubal et al. 1989, Domingo et al. 1990, Goggin and Lester 1995, Harvell et al. 1999]). The intensity and potential of population recovery depends on fishing intensity and species’ life history traits such as fecundity and longevity. The most striking population “outbreaks” of marine invertebrate phyla other than echinoderms are reported from introductions of nonindigenous species, which may attain high population densities with often severe consequences for ecosystem

function and diversity (e.g., comb jelly, oysters, clams, screw shell, green crab [Nichols et al. 1990, Ruiz et al. 1999, Grosholz et al. 2000, Naylor et al. 2001, Hewitt 2003]).

In this review we synthesize available published information on population density variations of echinoderm species. We did not include short-term population aggregations that are simply clusters of individuals, and also excluded population declines caused by catastrophic events. Previous reviews synthesize data on the clustered/aggregated distribution of echinoderms (Warner 1979, Sloan 1980), and mass mortalities due to abiotic factors such as freshwater flooding and volcanic eruptions (Lawrence 1996).

After summarizing literature on species fitting our working definition of large population density variations (population density changes by two doublings or two halvings, see *Methods*), we tested the hypothesis that echinoderms showing these types of population variations share certain biological traits. The data are analyzed to determine if a suite of life history parameters and other biological traits might be associated with species that exhibit these variations. In addition, we grouped the species into one of three patterns, propose a model for the underlying causes of population variations, and discuss the ecological and evolutionary consequences of this phenomenon.

METHODS

For the purpose of this review, we define a large population density variation as a minimum fourfold increase (i.e., two doublings) or decrease to <0.25 (i.e., two halvings) of the initial population densities of a species. Thus, an increase in population density is given when

$$N_{t+x} \geq N_t \times 4$$

where N_t = initial population size or density at time t and N_{t+x} = population size or density after time period x . This can be expressed logarithmically as

$$\log_2(N_{t+x}) \geq \log_2(N_t) + 2.$$

A decrease is given when $N_{t+x} \leq N_t \times 0.25$ or, logarithmically,

$$\log_2(N_{t+x}) \leq \log_2(N_t) - 2.$$

This approach to evaluate population density variations cannot be used in cases where densities increased from an initial zero value, e.g., after species introductions, or where densities decreased to zero, e.g., after extirpations or extinctions. For these species, we made a subjective judgment whether changes are significant and warrant inclusion in this review.

For graphic presentation of density changes we transformed density data available in the literature using the logarithm to the base 2. This is a convenient way to represent doubling or halving of population sizes, since an increase of one unit corresponds to a doubling of the untransformed value. To accommodate

zero densities, such as before marine introductions or after catastrophic mortality events, we added 0.01 to original densities before transformation. Thus, the lowest value that can be obtained (corresponding to zero) is -6.64 .

RESULTS

Based on a review of available information, we identified 28 echinoderm species that fitted our definition of large population density variations and had sufficient data available on densities before and after these events. Table 1 summarizes the characteristics of these species, including geographical distribution and life history traits, as well as potential causes for and ecological consequences of the population density variations. Detailed justification for inclusion of individual species are given below.

With respect to total number, population density variations are most prevalent in the Echinoidea (8 out of 902 species = 0.89% of all species), followed by the Holothuroidea (10 out of 1430 = 0.70%) and the Asteroidea (6 out of 1745 = 0.34%; Table 1). The reported incidence of population density variations in the Ophiuroidea (4 out of 2278 = 0.18%) is low, and no examples were found for the Crinoidea. However, it is possible that reporting of population density variations is influenced to some extent by observer bias (taxonomic studies may not include ecological observations over time) or problematic accessibility of habitats.

The echinoderm species exhibiting large population density variations follow one of three generalized patterns, which we named after two most distinct and best-researched species (Fig. 1):

1. *Diadema-Paracentrotus* Model.—This pattern is a rapid to catastrophic *decrease* in population densities followed by apparently no or very slow (several decades) recovery (Fig. 1). Causes for this pattern are usually assumed to be disease, over-fishing, or changes in oceanographic conditions (e.g., by climate change).

2. *Amperima-Amphiura* Model.—The second pattern is a rapid population density *increase* followed by relative stability at a new high population level (Fig. 1). Causes attributed to this pattern include introductions, increased primary productivity (e.g., eutrophication, changes in climate), or otherwise increased food supply for adults, and/or a release from top-down population control by predator overfishing.

3. *Acanthaster-Asterias* Model.—The third pattern involves *fluctuations* in population density from very high to very low densities (Fig. 1). These fluctuations are sometimes cyclic, often on a decadal scale, e.g., for *Acanthaster*, where the high-density states persist for shorter periods than the low-density intervals (Fig. 1). In this model we also include *Strongylocentrotus* species that fluctuate with a more irregular pattern, with some populations remaining at very high or very low densities for extended periods. Population density fluctuations in

this model appear to be caused by complex interactions between over-fishing of predators or competitors, or over-harvesting of the species. Other implicated causes are eutrophication and disease.

Population density decreases: the Diadema-Paracentrotus Model

Diadema antillarum (Echinoidea).—The sea urchin *Diadema antillarum* is distributed throughout the tropical and subtropical Atlantic and can reach local abundances of between 1 and 10 individuals/m² (Lessios et al. 1984a, Hughes 1994), with extremes of up to 64 individuals/m² (Sammarco 1982). In 1983–1984, *D. antillarum* suffered a mortality event in the entire tropical West Atlantic, which was described as “the most severe mass mortality ever recorded for marine animals” (Lessios 1995). This mortality event, first observed in Panama (Lessios et al. 1984a), rapidly spread as far north as Bermuda and east to Barbados (Lessios et al. 1984b, Phinney et al. 2001). Population densities throughout the Caribbean were reduced by >93% (Lessios 1988). The cause of the mortality was assumed to be an unidentified pathogen (Lessios et al. 1984a), the exact nature of which remains unresolved. The spread of the presumed pathogen tracked the prevailing currents (Lessios 1984b). It has been suggested that an eastward spread of a disease may have been facilitated by transport in ship ballast water (Phinney et al. 2001). Although there are no pre-mortality long-term density data sets, studies in the 1960s and 1970s in Jamaica and the U.S. Virgin Islands indicate that *D. antillarum* was abundant in the region (Ogden 1973, Carpenter 1981).

D. antillarum is a major grazer of turf algae (Carpenter 1986), and its removal through mass mortality resulted in a phase shift from coral-dominated to macroalgal-dominated systems in the Caribbean (Hughes 1994). This was exacerbated by previous removal of herbivorous fish through overfishing (Hughes 1994). The ecological consequences of the urchin mortality were less pronounced in Panama, where fishing pressure on other herbivores prior to the mortality event was less severe (Lessios 1995). On the eastern side of the Atlantic Ocean in the Canary Islands, where *D. antillarum* occurs on temperate rocky reefs, hyper-abundance of this urchin led to overgrazing of macroalgae and urchin barrens (Tuya et al. 2005).

Recovery of *D. antillarum* populations in the Caribbean is extremely slow. Extensive resurveys in Jamaica and Panama about 10 years after the mortality event detected virtually no increase of population densities at most study locations (Hughes 1994, Lessios 1995). In 1998, some Jamaican populations had recovered to a maximum of 1–10% of their original density (Knowlton 2001, Moses and Bonem 2001). By 2001 and 2002, 18–19 years after the event, populations of *D. antillarum* showed clear signs of recovery in St. Croix and Curacao, although densities remained an order of magnitude

TABLE 1. Case studies of echinoderm species exhibiting large population density variations, as defined in this study.

Taxa	Event	Cause	Ecological implications	Habitat	Location	Adult feeding	Larval type
Asteroidea, Forcipulatida							
<i>Asterias amurensis</i>	I	?	ecosystem shift (reduced infauna)	TS	NW Pacific, Japan	C	P
	I	introduction			SW Pacific, Australia		
<i>Asterias amurensis</i> var. <i>versicolor</i>	F	?	ecosystem shift (reduced infauna)	TS	NW Pacific, Japan	C	P
<i>Asterias forbesi</i>	D	?	?	TS	NW Atlantic, USA	C	P
	F	?	?	TS	NW Atlantic, USA (Maine)		
<i>Asterias rubens</i>	F	?		TS	NE Atlantic, Iceland	C	P
<i>Heliaster kubiniji</i>	D	unidentified disease, triggered by unusually warm temperatures	shift in prey densities, reduced diversity	TS	NE Pacific, Mexico	C	P
Asteroidea, Valvatida							
<i>Acanthaster planci</i>	F	eutrophication or overfishing?	coral decline, loss of diversity	CR	Indo-Pacific	C	P
Echinoidea, Arbacoida							
<i>Arbacia lixula</i>	I	increased temperature		TS	Mediterranean	H	P
Echinoidea, Diadematoidea							
<i>Diadema antillarum</i>	D	disease	ecosystem shift (algal dominance)	CR	Caribbean	H	P
Echinoidea, Echinoida							
<i>Paracentrotus lividus</i>	D	changes in sea surface temperatures?	potential algal increase, increased epiphytes on seagrasses	TS	NE Atlantic, Ireland	H	P
<i>Strongylocentrotus droebachiensis</i>	I	predator removal	urchin barrens		Mediterranean		
	F	increase: predator removal, decrease: disease, harvesting	ecosystem shifts (urchin barrens/kelp forest)	TS	NW Atlantic, USA/Canada	H‡	P
	F	increase: predator removal?, decrease: parasite	urchin barrens		NE Atlantic, Norway		
<i>Strongylocentrotus</i> spp. (three species)	F	change in predator abundance	ecosystem shifts (urchin barrens/kelp forest)		NE Pacific, USA	H	P
<i>Strongylocentrotus purpuratus</i>	F	increase: predator/competitor removal, decrease: ?	ecosystem shifts (urchin barrens/kelp forest)	TS	NE Pacific, USA	H	P
<i>Strongylocentrotus franciscanus</i>	F	increase: predator removal, decrease: harvesting, disease	ecosystem shifts (urchin barrens/kelp forest)	TS	NE Pacific, USA	H	P
<i>Echinometra mathaei</i>	I	predator/competitor removal	reef degradation through erosion	CR	Indian Ocean	H	P
Echinoidea, Spatangoida							
<i>Echinocardium cordatum</i>	D	reduced oxygen due to eutrophication?	reduced bioturbation and algal fertilization?	TSS	North Sea	DT	P
<i>Echinocrepis rostrata</i>	I	climate change: fluctuations in food supply	?	DS	NE Pacific	DT	?
Holothuroidea, Aspidochirotida							
<i>Holothuria whitmaei</i> §	D	overharvesting	decreased benthic microalgal productivity?	CR	SW Pacific	DT	P
<i>H. scabra</i> §	D	overharvesting	decreased benthic microalgal/seagrass productivity?	CR/SB	Indo-Pacific	DT	P
<i>Isostichopus fuscus</i> §	D	overharvesting	?	TS	Galapagos	DT	P
<i>Synallactes profundus</i>	I (F)	climate change: fluctuations in food supply	?	DS	NE Pacific	DT	?

TABLE 1. Continued.

Taxa	Event	Cause	Ecological implications	Habitat	Location	Adult feeding	Larval type
Holothuroidea, Elasipodida							
<i>Amperima rosea</i>	I	climate change: increased food supply?	?	DS	NE Atlantic	DT	P
<i>Ellipinion molle</i>	I	climate change: increased food supply?	?	DS	NE Atlantic	DT	?
<i>Elpida minutissima</i>	D	climate change: fluctuations in food supply	?	DS	NE Pacific	DT	?
<i>Peniagone vitrea</i>	D	climate change: fluctuations in food supply	?	DS	NE Pacific	DT	?
<i>Scotoplanes globosa</i>	F	climate change: fluctuations in food supply	?	DS	NE Pacific	DT	?
Holothuroidea, Dendrochirotida							
<i>Abyssocucumis abyssorum</i>	I	climate change: fluctuations in food supply	?	DS	NE Pacific	DT	?
Ophiuroidea, Ophiurida							
<i>Amphiura filiformis</i>	I	eutrophication: increased food supply, predator removal	?	TSS	North Sea	S	P
	D	competition with crustaceans?	Decreased sediment stability		North Sea		
<i>Amphiura chiajei</i>	I	eutrophication: increased food supply	?	TSS	NE Atlantic	S	L
<i>Ophiocten hastatum</i> ¶	I	climate change: increased food supply?	?	DS	NE Atlantic	DT	P
<i>Ophiura bathybia</i> ‡	I (F)	climate change: fluctuations in food supply	?	DS	NE Pacific	DT	?

Notes: Population event categories are: increase in population density (I), decrease (D), and fluctuations between high and low population densities (F). Habitat categories are: temperate subtidal (TS), temperate subtidal soft sediment (TSS), deep sea (DS), seagrass bed (SB), and coral reef (CR). Adult feeding modes are: carnivorous (C), detritivorous (DT), herbivorous (H), and suspension feeder (S). Larval types are: planktotrophic (P) and lecithotrophic (L). Question marks (“?”) indicate that no information or uncertain information was found. In the Event column, note that more than one event took place for some species.

‡ Several sea urchins listed as herbivorous may, in a strict sense, be omnivorous; see, e.g., Briscoe and Sebens (1988).

§ Over 40 species of holothurians are commercially fished; for most of these, anecdotal evidence of population declines or local distinctions exist; however, scientific data are rare. Only *H. whitmaei*, *H. scabra*, and *I. fuscus* are included in statistical analysis.

¶ Planktotrophy inferred from small egg size, not direct observation.

|| Several other Ophiuroidea increased in these studies areas, but data given do not allow judgment whether they fit our criteria for inclusion.

lower than historical pre-mortality density estimates (Miller et al. 2003). Increased densities of *D. antillarum* were recorded from Jamaica, with some sites at densities close to pre-mortality levels (Aronson and Precht 2000, Edmunds and Carpenter 2001). Interestingly, zones of high densities showed signs of a “reverse phase shift,” with higher coral densities and enhanced coral recruitment (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006). However, the Panamanian reefs, where the die-off was originally discovered, showed hardly any recovery of urchin numbers after 20 years (Lessios 2005).

Paracentrotus lividus (Echinoidea).—*Paracentrotus lividus* is distributed from Ireland to the Mediterranean (Boudouresque and Verlaque 2001). Like other herbivorous echinoids, this species has important ecological functions in controlling benthic algal communities

through grazing (Kitching 1987). Surveys of the populations of *P. lividus* in Lough Hyne (Ireland) since the 1920s indicate that this species exhibits large, long-term (decadal) variations in densities in a no-take marine reserve (Kitching 1987, Barnes et al. 2001). With the exception of a recovery period in the late 1980s, this species has now consistently declined in the Lough. In some areas this decline is equivalent to a population decrease of over 12 population-halvings (Fig. 2), and in 2001 and 2002 *P. lividus* was considered to be locally extinct (Barnes et al. 2002). The populations elsewhere in the Lough also declined, but a remnant population still existed in 2001 (Verling et al. 2005).

Some authors (Barnes et al. 2001, Verling et al. 2005) link the cause for the decline to El Niño Southern Oscillation (ENSO) events, which reduce the maximum sea surface temperatures below those suggested to

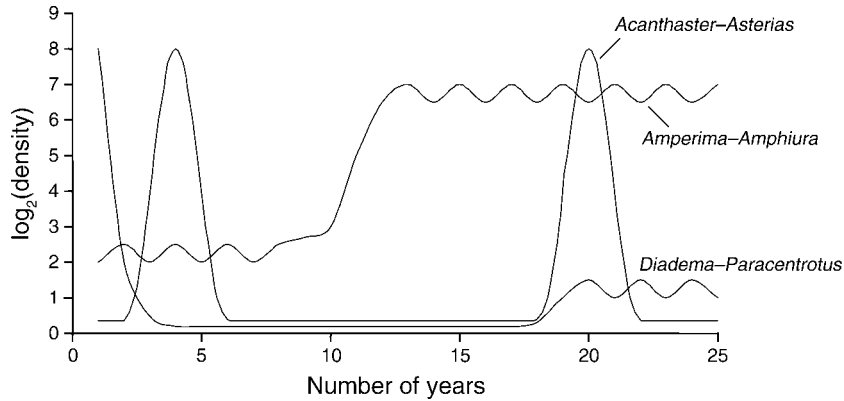


FIG. 1. Conceptual model for the three types of large population density variations discussed: (1) population decreases, *Diadema-Paracentrotus* Model; (2) population increases, *Amperima-Amphiura* Model; and (3) population fluctuations: *Acanthaster-Asterias* Model. The ordinate scale has arbitrary units. Note that population fluctuations may show irregular patterns, sometimes remaining for extended periods at very high or very low densities.

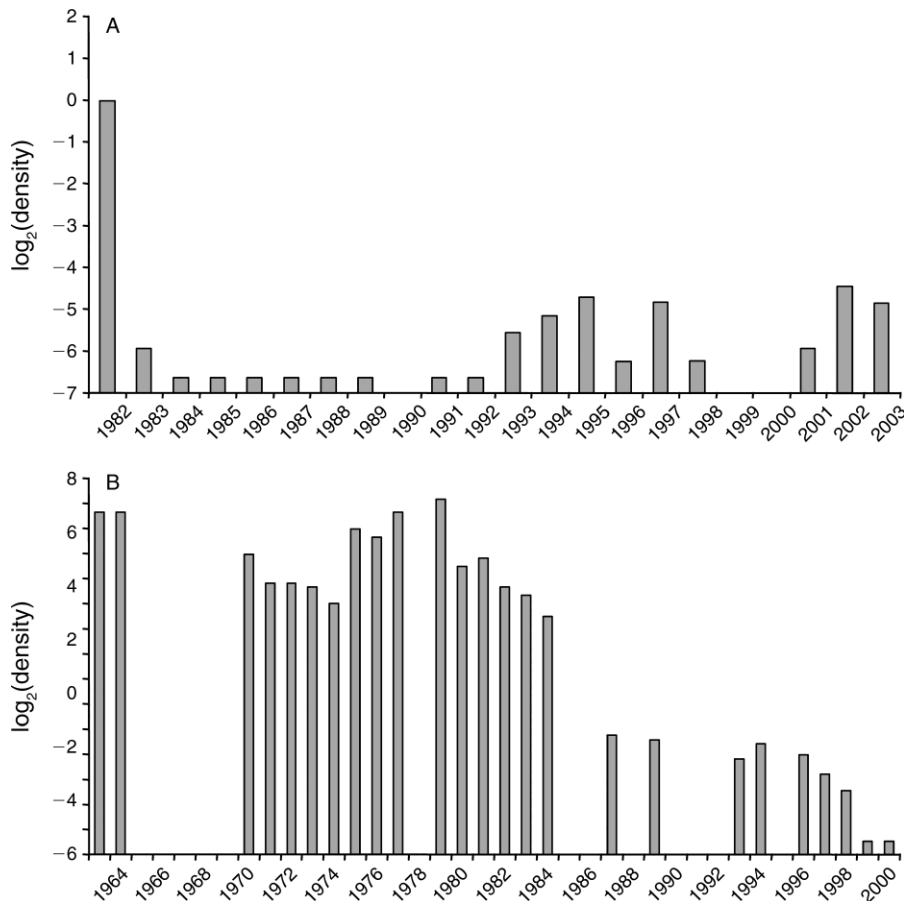


FIG. 2. *Diadema-Paracentrotus* Model, examples of large population density declines. (A) *Diadema antillarum* in Panama. Data were averaged over nine stations surveyed by Lessios (2005); stations that had initial densities more than an order of magnitude different from other stations were omitted. (B) *Paracentrotus lividus* in the south basin of Loch Hyne. Data were recalculated from an original graph in Barnes et al. (2002), including data from Muntz et al. (1965), Kitching (1987), and Barnes et al. (2001).

Note: Data are \log_2 -transformed, based on individuals/m² + 0.01; thus an increase of one unit is equivalent to a doubling of the population density.

trigger spawning, as determined for Mediterranean populations ($\sim 17^{\circ}\text{C}$, Fenaux 1968). However, Irish populations of *P. lividus* along the Atlantic spawn at lower temperatures ($11.5^{\circ}\text{--}16^{\circ}\text{C}$ [Byrne 1990]) and no data were presented to indicate that long-term temperature patterns in Lough Hyne had changed. Population decline has resulted from prolonged recruitment failure, but it remains unclear whether the decline in *P. lividus* in Lough Hyne is solely due to reduced sea surface temperatures affecting spawning (Barnes et al. 2002). Consequences of the local extinction of *P. lividus* for the ecology of the Lough are also unknown; a phase shift toward higher macroalgal biomass has not been reported. Population declines of *P. lividus* elsewhere in Ireland and the Mediterranean were linked to overharvesting, dinoflagellate blooms, and disease (Southward and Crisp 1975, Boudouresque et al. 1980, Cross and Southgate 1980).

Other echinoderm species exhibiting population decreases.—*Heliaster kubiniji*, a large predatory asteroid from the subtropical Northeast Pacific, was a common invertebrate in rocky intertidal habitats in the Gulf of California, occurring in densities of 0.1 to 1.0 individuals/m² (Dungan et al. 1982). In 1978, virtually the entire population of this asteroid in the Gulf died in a large-scale mortality event (Dungan et al. 1982). The cause was not determined, but a disease triggered by unusually high temperatures in 1978 was suggested (Dungan et al. 1982). The latter authors did not detect any recovery up to four years after the event, and the current population status is unknown. There are indications that recovery has occurred to some extent (P. K. Dayton, *personal communication*). Ecological consequences of the removal of this important predator from the ecosystem are not described. However, experimental removal of its congener *H. helianthus* results in shifts in community composition toward an increase in bivalves and barnacles and reduced benthic diversity (summarized in Paine et al. 1985), and removal of *H. kubiniji* might have a similar effect. It is interesting to note that populations of another *Heliaster* species (*H. cuninguii*) drastically declined in the Galapagos Islands after an El Niño event (Hickman 1998). The reason for this was possibly a decline of its major barnacle prey (Vinueza et al. 2006). However, sparse data on population densities did not warrant inclusion of this species as a separate case study.

The biomass of *Echinocardium cordatum*, a deposit-feeding irregular sea urchin in sandy to muddy benthic habitats in the Kattagatt area (North Sea), decreased by more than fivefold from 145 g/m² in 1911–1912 to 26 g/m² in 1984 (Pearson et al. 1985). The suggested cause for this decrease was the eutrophication of the North Sea, with the organic enrichment leading to low oxygen conditions near the sea floor (Pearson et al. 1985). However, higher intensity of trawling is also mentioned as possible cause for this decline. Interestingly, an increase in phytoplankton food availability due to

eutrophication and higher temperatures (due to climate change) has been implicated in the increased density of *E. cordatum* larvae in the plankton of large areas of the North Sea (Kirby et al. 2007). Whether this increase in larval abundance has resulted in increased recruitment is not reported. Direct ecological functions of the reduction in *E. cordatum* numbers have not been investigated. However, this urchin is known to have important ecological functions in bioturbation and enhancement of microphytobenthos production through nutrient excretion (Lohrer et al. 2004).

A total of about 20 sea cucumber species (Holothurioidea) are commercially fished in shallow water (to 40 m depth) for bêche-de-mer production. Stocks of most species have declined dramatically in the tropical Indo-Pacific region (Conand 2001), but overfishing also occurs in subtropical and temperate regions (Bradbury et al. 1998, Shepherd et al. 2004). However, baseline data are not available for most sea cucumber fisheries. Shepherd et al. (2004) estimated a fishery-induced decline in average population densities of *Isostichopus fuscus* on the Galapagos Islands from 1.2 individuals/m² in 1993 to 0.03 individuals/m² in 2002. On the Great Barrier Reef of Australia, densities of *Holothuria whitmaei* on fished reefs are <25% of those in no-take-zones (Uthicke and Benzie 2000). Stocks on the fished reefs did not recover when surveyed again 2 and 6 years after a fishery closure (Uthicke et al. 2004; S. Uthicke, *personal observation*). *Holothuria scabra* occurred in high numbers (>1500 individuals/ha) in the Torres Strait off northern Australia, and within two years of fishing the population declined to <10% of the original stock size, prompting closure of the fishery in 1998 (Skewes et al. 2006). Fishery surveys in 2004 showed no population recovery six years after closure (Skewes et al. 2006).

A decrease in the population of the ophiuroid *Amphiura filiformis* by about an order of magnitude was recently reported in the Frisian Front area of the North Sea (van Nes et al. 2007). The reasons for this are currently unknown. However, population densities of a burrowing shrimp (*Callinassa subterranea*) increased in parallel with the decrease in *A. filiformis*, and van Nes et al. (2007) suggested that two alternate stable states exist in the benthic community. In contrast to this decrease, several populations of *A. filiformis* in other regions have increased; see *Population density increases: the Amperima–Amphiura Model: Amphiura* spp. (Ophiuroidea).

Abundance of the asteroid *Asterias forbesi* in the Hudson-Raritan estuary declined by an order of magnitude from 1992 to 1997, with anecdotal evidence of a long-term decline since the 1970s in Connecticut (Mackenzie and Pikanowski 1999). The decreased density of *A. forbesi* in New Jersey and Connecticut was accompanied by the increase of one of its prey species, the commercially harvested bivalve *Mercenaria mercenaria* (Mackenzie and Pikanowski 1999). This species seems to be an exception in the genus, as most

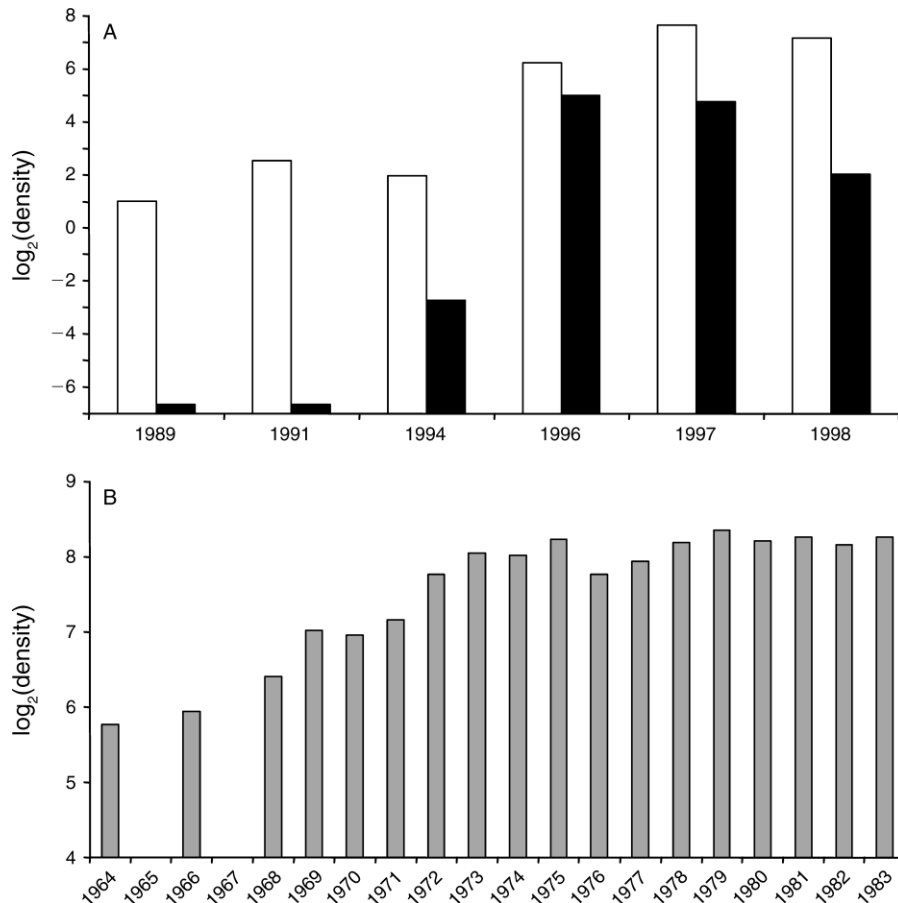


FIG. 3. *Amperima*–*Amphiura* Model: examples of large population density increases. (A) *Amperima rosea* (open bars) and *Ellipinion molle* (solid bars) in the Atlantic deep sea; data from Billett et al. 2001. (B) *Amphiura chiajei* in Loch Linnhe, data from Pearson and Barnett (1987).

Note: Data are log₂-transformed, based on (individuals/m² + 0.01); thus an increase of one unit is equivalent to a doubling of the population density.

reports for *Asterias* populations are examples for increases or fluctuations (see *Amphiura* spp. (Ophiuroidea)).

Two deep-sea holothuroids in the Pacific, *Elpida minutissima* and *Peniagone vitrea*, exhibited population density declines of 1–2 orders of magnitude over an observation period of 16 years (Ruhl 2006; for more information on these studies see the following section).

*Population density increases:
the Amperima–Amphiura Model*

Amperima rosea and *Ellipinion molle* (Holothuroidea).—One of the most spectacular population outbreaks for echinoderms, both in density increase and in the area covered, was discovered in the eastern North Atlantic deep sea. Surveys of the deep-sea benthos in the Porcupine Abyssal Plain between 1996 and 1998 revealed remarkable increases in benthic invertebrates at ~4800 m depth compared to previous surveys between 1989 and 1994 (Bett et al. 2001, Billett et al. 2001). The most conspicuous increase was noted for the

dominant elasipodid holothurian *Amperima rosea*, and the general change in the benthos was called the “*Amperima* event.”

A. rosea is a small holothurian (~20–35 mm) that occurs in the deep sea of all major areas of the Pacific, Indian, and Atlantic Oceans (Table 1; e.g., Billett et al. 2001, Rodrigues et al. 2001). Densities of this species increased at the Porcupine Abyssal Plain, northeastern Atlantic, from 2–6 individuals/ha prior to 1995 to 75–230 individuals/ha from 1996 onwards (Fig. 3A; Billett et al. 2001).

Densities of another holothurian, *Ellipinion molle*, also increased on the Porcupine Abyssal Plain by more than two orders of magnitude from pre-event values of up to 0.14 individuals/ha to values of up to 45 individuals/ha (Fig. 3A). Interestingly, during the last sampling occasion of the BENGAL project in 1998, values in that species had declined again to 0.12 individuals/ha (Billett et al. 2001).

For *A. rosea*, the event appeared long lasting (at least three years), and also unprecedented, as far as can be

inferred from generally sparse data prior to the 1980s (Billett et al. 2001). The geographical extent of the event stretched over at least 100 km along the entire Porcupine Abyssal Plain (Billett et al. 2001). The causes for this event are not known, but the most likely explanation seems to be increased food supply. These echinoderms are deposit feeders consuming phytodetritus imported from shallow pelagic areas (Bett et al. 2001, Billett et al. 2001). Wigham et al. (2003) suggested that reproductive output of *A. rosea* was enhanced by the increased quantity or quality of the phytodetritus, possibly caused by higher water temperatures due to climate change (Billett et al. 2001).

The ecological consequences of the *Amperima* event are difficult to assess because of limited understanding of the ecology of deep-sea benthos. However, Bett et al. (2001) suggest that estimated higher phytodetritus consumption rates by these holothurians may have prevented the annual summer “detritus bloom” on the seafloor after the event.

Amphiura spp. (Ophiuroidea).—The ophiuroid *Amphiura filiformis* is an abundant member of the soft-benthos community in the North Sea, with local densities of >1000 individuals/m² (Table 1; Duineveld et al. 1987). This species burrows in the mud, exposing its arms for suspension feeding. Comparison of population data from the 1930s and 1950s to those from 1986 indicated a steep increase in the abundance of *A. filiformis* in the entire southern North Sea, from 69 individuals/m² in 1932–1938 and 29 individuals/m² in 1950–1955 to an average of 416 individuals/m² in 1986 (Duineveld et al. 1987). A similar trend, albeit less distinct, was observed in the Skagerrak and Kattegatt area of the North Sea. Here, biomass increased about twofold from 29 g/m² in 1911–1912 to 63 g/m² in the 1970s (Pearson et al. 1985), a trend that continued into the 1980s (Josefson et al. 1993). Correspondingly, a steep increase of ophiopluteus larvae in the plankton, most of these likely to be *A. filiformis*, was observed from 1958 to the early 1990s (Lindley et al. 1995). The main cause for the increase of *A. filiformis* is suggested to be eutrophication of the North Sea and resulting higher food supply for these suspension-feeding ophiuroids, as well as overfishing of their main flatfish predators (Duineveld et al. 1987, Josefson et al. 1993). The link with eutrophication finds support in the fact that the less impacted northern section of the North Sea showed no *A. filiformis* population increase (Duineveld et al. 1987). The populations of *A. filiformis* in the Oeresund, Baltic Sea, and off Ireland were also stable over ~17 years (Muus 1981, O'Connor et al. 1986).

Populations of *Amphiura chiajei* increased more than sixfold, from ~50 individuals/m² in the 1960s to ~300 individuals/m² from the 1970s onward in the soft-bottom habitats of Loch Eil and Loch Linnhe, Scotland (Pearson et al. 1986, Pearson and Barnett 1987). In this instance, the increase was attributed to higher organic loads from pulp mill effluent. Interestingly, the abun-

dance of other suspension feeders (which had also increased) decreased shortly after the effluent discharge was reduced in the early 1980s, but *A. chiajei* densities remained elevated for several years, until the end of the study (Pearson et al. 1986).

We found no information about ecological consequences of the increased densities of these *Amphiura* species. However, *A. filiformis* is an ecologically important species on soft-bottom habitats for its role in bioturbation (Solan et al. 2004). The population increases in this species occurred in disturbed environments subjected to high organic inputs. Thus removal of organic matter by these suspension feeders may have ameliorated the negative impacts of eutrophication and associated anoxic conditions.

Other echinoderm species exhibiting population increases.—In association with the “*Amperima* event” (see the subsection *Amperima rosea* and *Ellipinion molle*) in the Porcupine Abyssal Plain, populations of the ophiuroid *Ophiocten hastatum* and other ophiuroids increased markedly (Bett et al. 2001). Population density estimates indicate a change from 4979 individuals/ha (1991–1994) to 53 359 individuals/ha (1997–2000), an increase of >10-fold. Population density increases in *O. hastatum* also occurred at the Rockall Trough in the North Atlantic, but specific data on densities are not reported (Gage et al. 2004).

Similar to the “*Amperima* event,” holothuroids (*Scotoplanes globosa*, *Abyssocucumis abyssorum*, *Synalactes profundus*) in the Northeast Pacific deep sea (4100 m depth) exhibit increases in a time series spanning 16 years (1989 to 2004), some of these possibly as part of longer term density fluctuations (Table 1; Ruhl and Smith 2004, Ruhl 2006). The latter is also true for the ophiuroid *Ophiura bathybia*, which showed a sharp increase in population density in 1998, but prior to that densities had slowly declined over eight years (Ruhl 2006). The population changes of these deposit feeders were correlated with alterations in food (particulate organic carbon) supply in the benthos (Ruhl and Smith 2004). Similar to the Atlantic studies, changes in organic carbon production in the photic layer were linked to climate variations, in this instance changes driven by the El Niño/La Niña cycle. Ecological consequences of the population density variations in the Northeast Pacific study were not commented on. However, it appears that deep-sea benthic megafauna can respond rapidly to increased food supply, thereby reducing the buildup of organic material in the sediments.

After its introduction to southern Australia, probably as larvae in ships' ballast water, the asteroid *Asterias amurensis* reached densities up to 24 individuals/m² over a relatively short time (~10 yrs) (Byrne et al. 1987, Grannum et al. 1996). Due to its sheer abundance, with millions of stars in some bays, *A. amurensis* has had a major impact on local ecosystems, changing benthic communities and causing drastic reductions and disappearance of prey species (Ross et al. 2002).

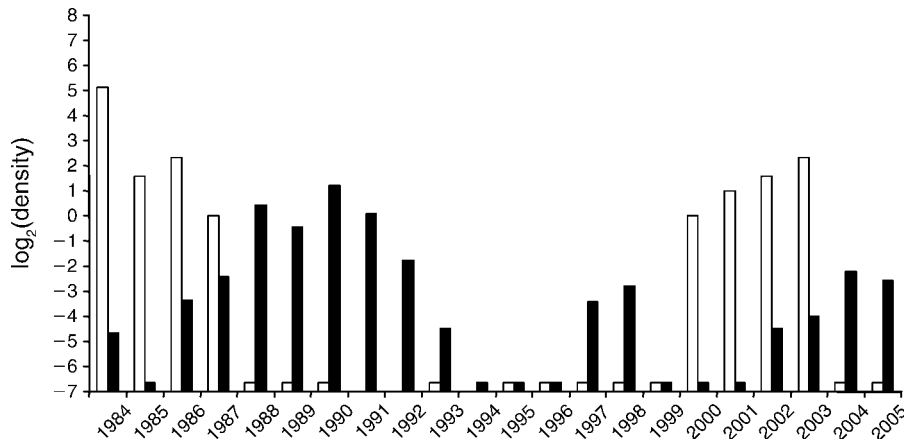


FIG. 4. *Acanthaster–Asterias* Model: examples of large population density fluctuations. Crown-of-thorns seastars (*Acanthaster planci*) on two reefs of the Great Barrier Reef as examples of populations on >100 reefs surveyed annually. Numbers are averages sited per two-minute manta tow (English et al. 1997) on Davies Reef (solid bars, 45 tows per survey) and John Brewer Reef (open bars, 75 tows per survey). The data are publicly available at the Australian Institute of Marine Science AIMS Long Term Monitoring Program (<http://www.aims.gov.au/pages/research/reef-monitoring/reef-monitoring-index.html>).

Note: Data are \log_2 -transformed, based on individual tows + 0.01; thus, an increase of one unit is equivalent to a doubling of the population density.

Densities of *Echinometra mathaei*, a widespread coral-reef-dwelling echinoid in the Indo-Pacific region, increased, assumedly following overfishing of predators, especially Balistidae (triggerfish) (McClanahan and Muthiga 1988). Averaged over several Kenyan reefs, *E. mathaei* was >100 times more abundant on fished reefs compared to unfished marine protected areas (McClanahan and Shafir 1990, McClanahan and Kurtis 1991). The increase in *E. mathaei* density has far-reaching cascading effects on the reef ecosystem, resulting in competitive exclusion of other echinoids, reduced coral cover and resulting reduction in some fish species, increased bioerosion, and decreased topographic complexity (McClanahan and Muthiga 1988, McClanahan et al. 1996).

The Mediterranean sea urchin *Arbacia lixula* mainly feeds on crustose red algae and small filamentous algae (Bulleri et al. 1999). The abundance of *A. lixula* in a marine reserve increased >10 times, from densities of 8 individuals/m² in 1983 to 100 individuals/m² in 1992 (Francour et al. 1994). It is suggested that the increase in water temperature favored population growth of this thermophilic urchin (Francour et al. 1994). Experimental exclusion of this sea urchin led to higher densities of filamentous algae (Bulleri et al. 1999); thus it may be inferred that population outbreaks reduce algal density.

Although we used *Paracentrotus lividus* as an example for population decreases (see Population density decreases: the *Diadema–Paracentrotus* Model), some Mediterranean populations of this species increased after removal of predators (mainly fishes) that control urchin population densities (Micheli et al. 2005), and after recruitment pulses (23 000 juveniles/m²) related to episodes of high planktonic primary production (Lopez et al. 1998). Other factors such as oceanographic events

are also suggested to contribute (Sala et al. 1998, Boudouresque and Verlaque 2001).

Population density fluctuations: the *Acanthaster–Asterias* Model

Acanthaster planci (Asteroidea).—The crown-of-thorns seastar (COTS), *Acanthaster planci*, occurs in the tropical Indo-Pacific from Panama to the Red Sea. This species exhibits marked repeated pulses of increased population density called “outbreaks” or “population explosions.” *A. planci* is an unusual asteroid in being a specialist corallivore. This sea star generally occurs in low densities of ~0.06 individuals/ha (Endean 1974), but apparently sustainable populations of ~26 individuals/ha have been observed in Panama (Glynn 1973). The earliest reports of massive population increases were from the Great Barrier Reef in 1957; subsequently, outbreaks were reported across the Indo-Pacific including Japan (Yamaguchi 1986), Hawaii (Branham et al. 1971), Micronesia (Colgan 1987), French Polynesia (Adjeroud et al. 2005), the Andaman Sea (Chansang et al. 1987), and the Red Sea (Ormond and Campbell 1974).

The first described outbreak in the Great Barrier Reef (with peak densities recorded 1962–1976) was followed by a second outbreak between 1979 and 1991 (Reichelt et al. 1990). A third wave of several outbreaks, which started around 1993, is currently underway (e.g., Fig. 4; Brodie et al. 2005). All outbreaks were noted to start on reefs around latitude 16°–17° S, followed by a southward spread until coming to a halt at reefs around 20° S. At reefs farther to the south (~22° S) outbreaks appear to occur temporally independent from the “wave-patterns” seen farther north (Sweetman et al. 2005).

Acanthaster planci outbreaks result in marked decreases in live coral cover, with severe ecological consequences for individual reefs. Once the tissue is removed by the sea star, coral skeletons are rapidly (in less than 24 hours [Belk and Belk 1975]) colonized by filamentous cyanobacteria and algae resulting in shifts in trophodynamic fluxes (Johnson et al. 1995). Densities of several fish species feeding on corals decline after *A. planci* outbreaks (Williams 1986).

Depending on the regions affected, *A. planci* generally prefers the abundant acroporid or pocilloporid corals (Glynn 1976, Colgan 1987, De'ath and Moran 1998), and rarer genera can be consumed once the preferred food source becomes unavailable (Pratchett 2001). Selective feeding on rare coral species can further enhance dominant species, thus distinctly decreasing diversity (Glynn 1976), while feeding on abundant coral species can favor an increase in rare species (Colgan 1987). In the short term this can increase coral diversity, but ongoing outbreaks ultimately result in a decrease in total coral cover to values below 1–5% and decreased species richness (Colgan 1987). Although there are indications that coral densities can recover to pre-outbreak values within 10–15 years, in the absence of other disturbances, there are also indications that impacted reefs are less diverse and dominated by fast-growing species (Moran et al. 1985). The recovery of reefs varies with location and depth. In Guam, coral cover, species richness, and diversity recovered to pre-outbreak values 12 years after an outbreak in 1969 (Colgan 1987). The limiting factor for adult *A. planci* is clearly the availability of food. Outbreaks on individual reefs usually end when most palatable corals are consumed.

The causes for *A. planci* outbreaks are still debated. Two of the initial hypotheses, i.e., overfishing of triton shells as main predators (Endean 1977) and the “natural phenomenon” hypothesis (Vine 1973) are considered unconfirmed. Birkeland (1982) proposed that increased nutrient runoff leads to increased food (phytoplankton) availability for *A. planci* larvae. Thus, it was proposed that enhanced larval survival leads to the establishment of “seed” populations for subsequent outbreak waves. The latter hypothesis found support through larval-rearing experiments (Lucas 1982, Okaji 1996). Outbreak populations may also result from multiple successive recruitment events (Pratchett 2005). Population models indicated that location, size, and frequency of primary outbreaks on the GBR can be explained by enhanced biomass of “larger” phytoplankton, possibly caused by nutrient enhancement (Brodie et al. 2005). The other current hypothesis of the cause of COTS outbreaks is the overfishing of fish species that are predators on juvenile *A. planci* (Ormond et al. 1990, Bradbury and Seymour 1997). The number of COTS in small islands off Fiji was positively correlated to fishing pressure on several fish species that may prey on juvenile sea stars (Dulvy et al. 2004). It seems likely that both fishing and

enhanced larval survival influence population densities of *A. planci*.

Asterias spp. (Asteroidea).—Several sea star species in the genus *Asterias* exhibit large population density fluctuations. They occur in rocky and soft subtidal habitats in the North Atlantic and Pacific and exhibit a preference for bivalve prey (Table 1). When populations of *Asterias* species increase, marked decreases in commercially harvested bivalves and newly settled cohorts of young bivalves are reported (Ino et al. 1955, Sloan and Aldridge 1981, Witman et al. 2003).

In the North Atlantic, a number of studies link sudden population increases in *Asterias rubens* and *A. forbesi* to increased food supply or enhanced recruitment (Sloan and Aldridge 1981, Witman et al. 2003). Over an 18-year study at several sites in the Gulf of Maine, densities of *A. forbesi* were 0–2 individuals/m² for 12 years, followed by a sudden increase to 15–38 individuals/m² in one year, followed by a decline to 4–15 individuals/m² (Witman et al. 2003). The increase in *Asterias* followed a massive recruitment of its prey, *Mytilus edulis*, and was due to immigration of sea stars to feed on these mussels, with subsequent density-enhanced sea star recruitment. The elimination of *Mytilus* prey triggered cannibalism by *Asterias*, which contributed to density-dependent population decline in the asteroids (Witman et al. 2003).

In the eastern Atlantic, aggregations of *Asterias rubens* (up to 89 individuals/m²) along English rocky shores are usually short-lived (one year) and appear to constitute “outbreak-like” population increases (Sloan and Aldridge 1981). A 20–50 fold population increase in *A. rubens* occurred after intense scallop dredging in the Barents Sea, and high densities (>100 individuals/m²) were reported from other scallop beds (Brun 1968, Zolotarev 2002). This sea star increased in density in response to light trawling, potentially due to enhanced scavenging opportunities, but declined in response to intense trawling where mortality outweighs advantages due to higher food supply (Ramsay et al. 2000).

In the North Pacific, *A. amurensis* and *A. amurensis* var. *versicolor* undergo sporadic increases in population density (Nojima et al. 1986). In the Ariake Sea, Japan, an embayment heavily used for fisheries and aquaculture, *A. amurensis* var. *versicolor* is a nuisance to trawl fisheries (Nojima et al. 1986). In the first reported outbreak in 1964, *A. amurensis* var. *versicolor* reached population densities of >6 individuals/m². Subsequent outbreaks occurred in 1974 and 1984, and it was suggested that outbreaks have a 10-year cycle (Nojima et al. 1986). “Natural” sea star numbers are not clearly stated, but Nojima et al. (1986) implied that these are usually <1 individual/m². These outbreaks are suggested to be due to large recruitment events (Nojima et al. 1986).

Other examples of echinoderms that exhibit population density fluctuations.—*Strongylocentrotus* species (Echinoidea) have some of the largest geographical distribu-

tions of the echinoderms reviewed here, and are widespread in the temperate North Atlantic and North Pacific (Table 1). Large population density fluctuations of *Strongylocentrotus* species have been reported from most of their distributional range. The main food source of these urchins is large brown algae, with occasional omnivory (Tegner 2001, Scheibling and Hatcher 2007) and high abundances have been the main agent in the formation and persistence of "urchin barrens," where rocky reefs sustain high urchin densities and are dominated by coralline algae, due to the urchins' preference for kelps and rockweeds. Barrens and kelp forest habitat ecosystem states alternate temporally in association with fluctuations in urchin densities (e.g., Chapman and Johnson 1990, Elner and Vadas 1990, Sala et al. 1998), but not with an obvious regular periodicity (Steneck et al. 2002). Barrens can persist for extended periods while urchins reduce growth and persist on drift algae.

Along the coasts of Maine (USA) and Nova Scotia (Canada), population outbreaks of *S. droebachiensis* have created widespread urchin barrens (reviewed in Tegner and Dayton 2000, Steneck et al. 2002, Scheibling and Hatcher 2007). Population densities of *S. droebachiensis* vary substantially in time and space. In Nova Scotia, densities are, on average, 14 individuals/m² in kelp beds, 136 in aggregated grazing fronts, and 41–71 individuals/m² in urchin barrens (summarized in Meidel and Scheibling 2001). Active grazing fronts can have densities of ~400 individuals/m². The overgrazing events in the 1970s and 1990s were terminated by an amoebic disease (*Paramoeba invadens*) leading to widespread urchin mortality, with densities decreasing to ~16 individuals/m² (Scheibling and Stephenson 1984, Scheibling and Hennigar 1997) and subsequent recovery of kelp beds (Steneck et al. 2002 and references therein).

Since the last urchin decline in the mid to late 1990s, a new ecosystem state has developed, composed of several introduced species and low urchin and kelp densities (Chapman et al. 2002). However, urchin densities have increased in some areas (Brady and Scheibling 2005). In Maine, high densities of *S. droebachiensis* declined after the development of an urchin fishery in the late 1980s, and either the kelp forests recovered (Steneck et al. 2002), or, in some areas, the introduced alga *Codium fragile* ssp. *tomentosoides* became established (Harris and Tyrell 2001). The processes that control population densities of *S. droebachiensis* in these regions are still debated. Disease outbreaks may be linked to oceanographic events (Scheibling and Hennigar 1997), and there is evidence for increased recruitment during intermittently favorable environmental conditions (e.g., Chapman and Johnson 1990, Scheibling and Hatcher 2007) and for outbreaks being sustained by density-enhanced fertilization success (Wahle and Peckham 1999, Meidel and Scheibling 2001). Removal of predators of adult urchins by fisheries is considered to be the most important factor leading to recurrent outbreaks in

some areas (Tegner and Dayton 2000, Steneck et al. 2002, 2004). Current low densities of *S. droebachiensis* in the West Atlantic appear to be maintained by the urchin fishery, abundance of crabs that prey on juveniles, and alteration of the ecosystem by introduced species (Harris and Tyrell 2001, Chapman et al. 2002, Levin et al. 2002, Steneck et al. 2004).

Population outbreaks of *S. droebachiensis* in the eastern Atlantic were reported from the Norwegian coast in the early 1980s (Hagen 1983, Sivertsen 1997). *S. droebachiensis*, rare to absent in undisturbed kelp beds, had average densities of 34 individuals/m² in actively grazed kelp beds and 48 individuals/m² in urchin barrens (Hagen 1983). Sea urchin densities decreased 3–7 years after the initial observation of outbreaks and kelp forests intermittently recovered, but shifted back to urchin barrens by the mid 1990s (Hagen 1995), which have persisted since that time (Sivertsen 2006). Urchin densities in this second period of destructive kelp grazing were 45–75 individuals/m² (Hagen 1995). Urchin mortality was believed to be caused by parasitism by the nematode *Echinomermella matsi* (Hagen 1987). However, destructive grazing has recurred despite parasite prevalence (Hagen 1995), and the spatial distribution of mortality could not be explained by parasite infection alone; other disease agents have been postulated (Skadsheim et al. 1995). Causes of the Norwegian *S. droebachiensis* outbreaks have not been identified. Current hypotheses include reduced predation on adult urchins, increased survival of urchin larvae due to reduction of larval predators (e.g., herring, crabs) and/or unidentified environmental factors such as climatic events (Sivertsen 2006).

Interpretation of paleoecological midden data from the Aleutian Islands indicate that alternate barrens–kelp forest ecosystem states occurred over thousands of years in association with local overexploitation of sea otters, a major predator of *Strongylocentrotus* species, by aboriginal Aleuts (Simenstad et al. 1978). Modern studies in Alaska and in some Aleutian Islands show that densities of *Strongylocentrotus* species and associated kelp forests have fluctuated for several decades in association with the presence or absence of sea otters (Estes and Duggins 1995, Steneck et al. 2002). Sea otter abundance was reduced by hunting (Tegner and Dayton 2000, Tegner 2001, Steneck et al. 2002), intermittently recovered, and recently decreased again due to predation by killer whales (Estes et al. 1998). In Alaska, predation by otters reduces abundance of three *Strongylocentrotus* species to near zero, while sites without sea otters support densities of up to 8 individuals/m², leading to destructive grazing; sea urchin recruitment appears episodic (Estes and Duggins 1995). In the Aleutian Islands, presence or absence of sea otters significantly changed the biomass of *Strongylocentrotus* species (~100 g/m² vs. ~1900 g/m²) but not the abundance (Estes and Duggins 1995).

Episodes of high abundances and localized destructive grazing by *S. purpuratus* and the less abundant *S.*

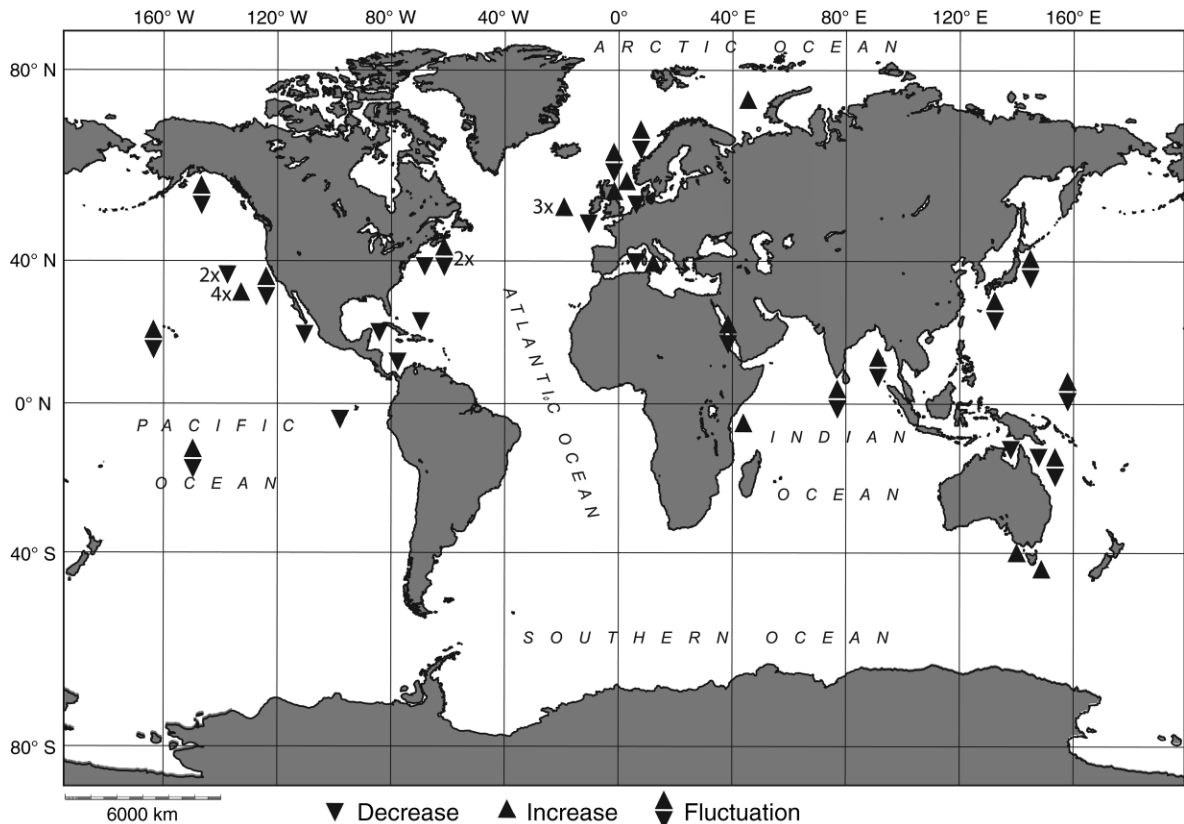


FIG. 5. World map illustrating the distribution of large population density variations in the echinoderms discussed.

franciscanus have been reported from California (e.g., North and Pearse 1970, Watanabe and Harrold 1991, Tegner and Dayton 2000). Predation is considered the most important factor for controlling *Strongylocentrotus* spp. population densities (Tegner and Dayton 2000, Steneck et al. 2002, 2004); however, present-day urchin predators (e.g., sheephead wrasse, spiny lobsters) and competitors (e.g., abalone) are affected by overfishing (Cowen 1983, Tegner and Dayton 2000, Behrens and Lafferty 2004, Lafferty 2004). Densities of *S. purpuratus* were four times higher outside a marine reserve than inside (28 vs. 7 individuals/m²), while abundance of spiny lobsters was six times higher inside the reserve and sheephead abundance was not different (Lafferty 2004). Sea urchin disease in the high-density populations outside the reserve did not replace the functional role of predators in reducing urchin populations (Behrens and Lafferty 2004, Lafferty 2004). In contrast, mass mortality of *S. franciscanus* caused by a disease decreased abundance from >5 individuals/m² to almost zero over three years (Pearse and Hines 1979). Episodes of disease associated with warm water and food limitation appear to influence the population fluctuations in *S. franciscanus* (Tegner 2001, Behrens and Lafferty 2004). Selective removal of this echinoid through fishing is suggested to facilitate outbreaks of the congener *S. purpuratus* (Tegner 2001). The role of

episodic sea urchin recruitment events is less understood in Northeast Pacific populations. A single large recruitment event during a 10-year study increased the abundance of *S. purpuratus* in a marine reserve from 0.2 individuals/m² to 5 individuals/m² (Pearse and Hines 1987). This cohort, however, only survived for one year, with subsequent decrease in abundance to 0.6 individuals/m² over four years due to undetermined causes.

DISCUSSION

We identified 28 species in four echinoderm classes that fit our definition of large population density variations of at least two doublings in population densities or a reduction to one-quarter of the initial population density. In general, these population variations were triggered by a single main factor, such as disease outbreaks, harvesting, overfishing or removal of predators and competitors, or introductions. The main purpose of this review was to identify biological or environmental characters shared by the echinoderm species showing large variations in population density. To achieve this, we examined data on the life history traits, geographic distribution, and main habitat of the 28 species identified (Table 1, Fig. 5).

One common feature of the 28 species is the indication that population density variations are associated with anthropogenic disturbance (Table 1). This connection is

clear where overfishing is implicated (12 out of 28 species), either by direct population reduction through harvesting (e.g., echinoids, holothuroids), or by indirect effects leading to population increases through overfishing of predators and/or competitors (e.g., echinoids, asteroids). This supports the view that overfishing is one of the most severe disturbances for marine ecosystems (Jackson et al. 2001, Worm et al. 2005). Other anthropogenic impacts suggested to trigger or influence large population density variations in echinoderms include eutrophication (four species) and species introductions (one species). Indirect anthropogenic impacts such as consequences of climate change are also implied (12 species). Disease outbreaks were also relatively common (six species). It should be noted that in several cases multiple causes are implicated.

Distribution and life history traits of echinoderms that exhibit variations in population density

With the exception of the Arctic and Antarctic, and low numbers in Africa and South America, examples of echinoderms that exhibit population density variations occur over a wide geographical range (Fig. 5). The dearth of examples from the polar regions and developing countries may reflect limited research effort in these areas rather than a regional trend. Examples of large variations in echinoderm population densities are known from most marine habitats and ecosystems, ranging from shallow coastal areas to the deep sea. Coral reefs provide one of the most striking examples of how changes in echinoderm densities influence ecological functions and can have cascading follow-on effects to other trophic levels. While Caribbean reefs are heavily impacted by the near total *decline* of one echinoderm (*Diadema antillarum*), one of the most distinct disturbances on Indo-Pacific reefs is caused by the cyclical *increase* of another echinoderm (*Acanthaster planci*). In either example changes in echinoderm population densities can lead to phase shifts from coral-dominated to algal-dominated systems (Hughes 1994, Johnson et al. 1995). However, reefs not impacted by other stressors, such as eutrophication or increased sea surface temperatures, have high natural resilience and usually recover to coral-dominated states once the echinoderms again attain “normal” densities (e.g., Colgan 1987, Edmunds and Carpenter 2001). These examples, together with the alternation of temperate kelp bed communities and “urchin barrens” created by echinoid population fluctuations (*Strongylocentrotus* spp.), are the best documented cases of ecological effects of echinoderms in the marine environment. There is no indication, however, that echinoderms from coral reef or kelp bed communities are particularly prone to population density variations. The fact that two studies (Billett et al. 2001, Ruhl and Smith 2004) in the deep sea, a comparatively poorly studied habitat, include several echinoderms that fit our definition of a fluctuating

species indicate that deep-sea communities may be more dynamic than previously thought. Population density variations of detritivores triggered by changes in food supply may be a common phenomenon in the deep sea.

We identified 6 carnivores, 6 herbivores, 14 detritivores, and 2 suspension feeders in the suite of species that exhibit population variations (Table 1). All asteroids identified in this review are carnivores. However, this is not unexpected because carnivory is a common feeding mode in the Asteroidea. Similarly, echinoid and holothuroid species identified in this review have feeding modes most prevalent in the taxon, i.e., herbivory and detritivory, respectively. Thus there is no clear indication that any particular trophic mode is over- or underrepresented among the echinoderms that exhibit large population density variations. The exception may be the low representation of suspension feeders.

The potential influence of several other life history parameters such as growth and longevity on population density variations cannot be fully evaluated, because little information is available. Many of the echinoderms listed here (e.g., *Strongylocentrotus* spp., *Acanthaster planci*, commercial holothurians) can have initial fast growth rates and reach sexual maturity within several years, but then have indeterminate growth and live for 10 or even 100 years (e.g., Stump 1996, Herrero Pérezrul et al. 1999, Ebert and Southon 2003). However, due to different methods, estimates of longevity can vary widely (e.g., *A. filiformis*, 2–25 years [summarized in O'Connor et al. 1983]). In addition, growth rates can be difficult to estimate because echinoderms may cease growing in times of low food supply, or even shrink soft tissues (Sebens 1987, Uthicke et al. 2004, Ebert 2007). In addition, shrinkage reported for *S. purpuratus* may be due to variability in measurements (Ebert 2007). Nevertheless, low mortality rates and high potential age may certainly contribute to population density variations, especially when high longevity is coupled with low recruitment. However, since data are sparse we cannot estimate whether these life history traits are overrepresented in the echinoderms showing large population density variations.

All of the species identified as exhibiting large population density variations in this review are broadcast spawners with pelagic larvae. However, this is also expected, because most echinoderms have this life history. Most of the species identified in this review have small eggs, and so are likely to have high fecundity (Babcock et al. 1994, Byrne et al. 1999). However, most echinoderms have high fecundity, and so this would not be a unique feature of the species that undergo fluctuating population densities. The only feature shared by most of the 28 species that exhibit large population density variations is possession of a planktotrophic larva, with the exception of the ophiuroid *A. chiajei*, which has a lecithotrophic larva (Table 1). The larval ecology of eight of the deep-sea echinoderms is unknown.

TABLE 2. Results of binomial calculations testing if planktotrophy is statistically overrepresented in each class and the total of all echinoderms.

Class	<i>n</i>	<i>k</i>	<i>p</i>	<i>q</i>	<i>R</i> †
Asteroidea	6	6	0.279	0.721	0.00048
Echinoidea	7 (1)	7	0.542	0.458	0.01373
Holothuroidea	4 (6)	4	0.324	0.676	0.0110
Ophiuroidea	3 (1)	2	0.335	0.665	0.22402
Crinoidea	0	0	0	1.0	
Echinodermata (without Crinoidea)	20 (8)	19	0.345	0.655	2.13 × 10⁻⁸

Notes: Parameters are the probability of a species from the respective class as being planktotrophic (*p*) or lecithotrophic (*q*), *n* = total number of species with known larval feeding mode exhibiting large population density variations (number omitted due to insufficient information in parentheses), and *k* = number of planktotrophic species in this group (values from Appendix: Table A1). The probability (*R*) of finding the number of planktotrophic species (or higher values) observed in a random sample of size *n* was calculated using the binomial equation: $R = (n!/k!(n-k)!) p^k p^{n-k}$ (Lockwood 1999).

† Values of *R* in boldface type are significant at $\alpha < 0.05$ after sequential Bonferroni corrections for $N = 5$ comparisons (Hochberg 1988).

Using the 20 species with known larval ecology, we tested whether species with planktotrophic larvae were statistically overrepresented in the species exhibiting large population density variations. We compiled information about larval developmental modes, which is available for 709 of the ~6800 extant echinoderm species in the families listed (see Appendix). The number of planktotrophic and lecithotrophic species per class was extrapolated from the ratio of species known to have the two developmental modes. This comparison indicated that echinoderm classes have a prevalence of lecithotrophic larvae, with the exception of the echinoids. This is most extreme for the crinoids, where planktotrophy is absent in recent taxa. In total, 68% (66% if crinoids are excluded) of all echinoderms have lecithotrophic development (see Appendix).

Based on these data, we used binomial probabilities to test whether the number of echinoderm species with planktotrophic larvae that exhibit large population density variations in each class is higher than would be expected by chance (Lockwood 1999). Knowing the frequencies of one character in a taxonomic unit (*p*, in our case planktotrophy) and its alternative (*q*, lecithotrophy), the probability that the number (or a higher number) of planktotrophic species observed is the result of chance can be calculated. This calculation was conducted for each class with the exception of the crinoids, and also for all classes combined (again excluding the crinoids) (Table 2).

In a random sample, the probability of finding the number of planktotrophic species (or a higher value) observed among the species with large population density variations is below 5% for the Asteroidea, Echinoidea, and Holothuroidea (Table 2). The highest level of significance was calculated for the combined echinoderm data (without Crinoidea). Given the frequency of planktotrophy for the phylum ($p = 0.345$), only 7.24 ± 2.18 planktotrophic species (mean \pm SD; calculated after Lockwood 1999) would be expected in a random sample. In other words, the observed number (19 out of 20) is more than five standard deviations higher than the expected number. Even under the

unlikely assumption that all deep-sea species omitted from the analysis above had lecithotrophic larvae (which constitutes the most conservative scenario), the statistical overrepresentation of the planktotrophic larval life history was highly significant ($R = 0.00025$) among the echinoderms exhibiting large population density variations.

Three generalized patterns and hypothesized causes for large population density variations in echinoderms

We propose that the propensity for large population density variations in most species that exhibit this phenomenon is mainly based on two traits: broadcast spawning and the planktotrophic larval life history. We suggest that the combination of these traits can result in positive feedback loops that lead to either rapid population increase once an “outbreak” cycle has been initiated, or very slow recovery once populations have decreased by disease or overfishing.

Fertilization rates in broadcast-spawning marine invertebrates decline with decreasing density, due to reduced sperm densities and low probabilities of egg-sperm encounters (Levitan 1991, Babcock et al. 1994, Wahle and Peckham 1999). Therefore, the changes in fertilization success and resulting reduced propagule production in broadcast spawners are disproportional to changes in adult densities, a form of Allee effect (Uthicke 2004). Fertilization kinetics in planktotrophs have only been documented for a few species, and these are based on empirical data (e.g., *Diadema antillarum* [Levitan 1991], *Acanthaster planci* [Babcock et al. 1994], *Strongylocentrotus droebachiensis* [Wahle and Peckham 1999]). All of these studies showed that there is an exponential decline in fertilization rates with decreasing densities. Larger distance between individuals is a major impediment to gamete encounter in lower density populations. Modeling studies show the influence of population density on fertilization rates in *S. droebachiensis*, indicating the importance of Allee effects (Lauzon-Guay and Scheibling 2007), whereas for *S. franciscanus*, Ebert (1998) argued that Allee effects had little influence on the population growth in this species

where sheltering of juveniles under the “test canopy” is also an important feature.

Higher adult densities can lead to limited food resources, causing reduced gonad development and fecundity (Levitan 1991, George 1994, Byrne et al. 1998), which could provide a potential compensatory mechanism. However, for planktotrophic developers, Levitan (1991) showed that reduced individual gamete output is outweighed by an enhanced population outcome and improved fertilization rates due to close proximity of individuals. Similarly, when population size decreases, a potentially higher oocyte production per individual in response to enhanced food conditions would not compensate for the lower overall fertilization rates. Therefore, for both population extremes (low and high density) there is a positive feedback loop reinforcing the trend in population state, but potential for compensation through change in adult food conditions is low.

Food supply and other ecological variables influencing planktotrophic larvae are largely independent from those influencing the benthic adults. Studies on asteroids and echinoids with planktotrophic larvae indicate a strong relationship between larval food supply, survival, and pulses of recruitment (Hart and Scheibling 1988, Fenaux et al. 1994, Okaji et al. 1997, Lopez et al. 1998). Studies of *A. planci* show that larval survival increased ninefold with every doubling of phytoplankton food biomass (Okaji et al. 1997, Brodie et al. 2005). Development time of sea urchin larvae is also shortened in response to enhanced larval nutrition, thereby reducing the most vulnerable life history stage (Hart and Scheibling 1988, Strathmann et al. 1992). In addition, the success of the early juvenile is dependent on the nutritive reserves sequestered by the planktotrophic larva (Gosselin and Jangoux 1998). Clearly, for echinoderms with planktotrophic development, the supply side of their population dynamics is highly sensitive to the vagaries of planktonic food supply, a factor typically independent of the adult environment.

Some of these factors are also likely to affect echinoderm species that have lecithotrophic larvae. As for planktotrophs, fertilization success and population output will depend on population density and adult food supply (Sewell and Levitan 1992, George 1994). The most distinct difference between the two life histories is the direct nutritive coupling of adult, larval, and early juvenile food supply in echinoderms with lecithotrophic development. The nutrients present in the large eggs of these echinoderms provide a buffer against larval and early juvenile starvation (Byrne et al. 1999, 2003, Villinski et al. 2002). Much of the energetic lipid reserves present in the eggs of asteroids, ophiuroids, and echinoids with lecithotrophic development are not used for larval development, but are stored by the larva for the early juvenile (Byrne et al. 1999, 2003, Villinski et al. 2002, Prowse et al. 2008). Lecithotrophic larvae also have much shorter development time, days to weeks

compared with the weeks to months-long pelagic periods of the planktotrophs. Thus, mortality in the plankton is reduced and the chance of settling closer to the parental habitat is higher. In summary, we hypothesize that the population regulation in echinoderms with lecithotrophic larvae functions more efficiently than in planktotrophs. Independence of larvae from the requirement to feed in the plankton, lower mortality in the plankton, enhanced local recruitment, and maternal provisioning for the early juvenile would promote more buffered population dynamics.

Population declines (*Diadema-Paracentrotus* Model) can be initiated by a disturbance of either adults (e.g., by disease, harvesting) or larvae (e.g., changes in climate or food supply). Once declines are initiated, lower adult densities lead to decreased fertilization rates and further decline (positive feedback loop). Since most marine populations are regarded as open populations (Caley et al. 1996) and thus depend to some extent on larval supply from other areas, the severity of the population decline and ultimate time for recovery of populations depends on the geographic extent of the decline, and the connectivity of subpopulations.

Population increases (*Amperima-Amphiura* Model) follow an opposite pattern. Initially, higher survival either of settled recruits, adults, or planktotrophic larvae promotes an increase in adult population size. Examples for impacts on adult densities are the removal of predators and/or competitors. Subsequently, increased adult populations lead to positive feedback loops and further larval production caused by enhanced fertilization rates, and sustain a higher population density.

Population fluctuations as described in the *Acanthaster-Asterias* Model are likely to encompass both mechanisms. Indeed, we can ultimately not judge if the other two models form part of a fluctuation cycle, only with a lower frequency, which is not detected by analyses of available data sets that are often short term. Fluctuations need a trigger or threshold density, which initiates a phase shift to either the high- or low-density state. In the case of *Strongylocentrotus* spp., high population densities may decrease because of disease outbreaks or local food depletion. In commercially valuable species such as sea urchins, high population densities may also attract human impacts through harvesting. Similarly, *A. planci* and *A. forbesi* outbreaks usually subside as food is depleted. Also, sea star population densities during the “low-density” phase may recover through a slow buildup from low local recruitment (Witman et al. 2003, Pratchett 2005), or nearby populations can provide sufficient larvae to allow recovery of a depleted population once the cause of depletion has been removed.

In conclusion, we suggest that the possession of planktotrophic larvae and the autonomy of larval and adult life stages represent a “high-risk-high-gain” strategy. Disturbance and alteration of resources affect-

ing either life stage through feedback effects can lead to large changes in population densities.

The planktotrophic larva is regarded as the ancestral larval type for extant Echinodermata, and after 500 million years of larval evolution (Raff and Byrne 2006), we find that 68% of species with known development have the derived, lecithotrophic larval type (see the Appendix). We hypothesize that the evolutionary trend in the Echinodermata is toward a buffered “lower-risk–lower-gain” strategy of direct-developing lecithotrophic larvae. This finds some support in the fact that all recent species of the Crinoidea, the only class where we did not find any examples of large population density variations, have lecithotrophic larvae. Crinoid species with planktotrophic larvae possibly did not survive the Permian–Triassic and others extinction events (Sprinkle and Kier 1987, Ausich et al. 1994, Smith 1997, Kammer and Ausich 2006). Valentine and Jablonski (1986) hypothesized that disturbance of planktonic food chains may have selected against the planktotrophic life history. Over evolutionary time we suggest that the switch to lecithotrophic development in echinoderms may be the favored trend under selection and differential extinction scenarios.

Anthropogenic influence was suggested as a causal or at least contributing factor to most of the identified large population density variations (see Table 1). One might argue that these anthropogenic influences might simply fast-track evolution, by accelerating the inevitable extinction of species with planktotrophic larval life history. However, the examples given here show that population density variations can have severe ecological consequences for the marine environment these animals inhabit. In “evolutionary” time scales, ecosystems may develop resilience to stochastic changes in their community composition. In contrast, human interference can lead to accelerated change and reduced ecosystem redundancy, e.g., by overfishing of species with ecological roles similar to the fluctuating echinoderms, not allowing ecosystems to adapt or compensate. Similar to terrestrial environments, diversity and redundancy in marine ecosystems is crucial for ecosystem functioning, productivity, and resilience (Worm et al. 2006). For these reasons we suggest that focused scientific study and conservation effort is required for protection of the natural dynamics of these fluctuating species and their ecosystems.

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APPENDIX

A table showing developmental modes of echinoderms and associated literature (*Ecological Archives* M079-001-A1).