Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas

Heike K. Lotze,[1]* Hunter S. Lenihan,[2] Bruce J. Bourque,[3] Roger H. Bradbury,[4] Richard G. Cooke,[5] Matthew C. Kay,[2] Susan M. Kidwell,[6] Michael X. Kirby,[7] Charles H. Peterson,[8] Jeremy B. C. Jackson[5,9]

Estuarine and coastal transformation is as old as civilization yet has dramatically accelerated over the past 150 to 300 years. Reconstructed time lines, causes, and consequences of change in 12 once diverse and productive estuaries and coastal seas worldwide show similar patterns: Human impacts have depleted >90% of formerly important species, destroyed >65% of seagrass and wetland habitat, degraded water quality, and accelerated species invasions. Twentieth-century conservation efforts achieved partial recovery of upper trophic levels but have so far failed to restore former ecosystem structure and function. Our results provide detailed historical baselines and quantitative targets for ecosystem-based management and marine conservation.

Estuaries and coastal seas have been focal points of human settlement and marine resource use throughout history. Centuries of overexploitation, habitat transformation, and pollution have obscured the total magnitude of estuarine degradation and biodiversity loss and have undermined their ecological resilience (*1*–*5*). This poses potential for disaster, as demonstrated in numerous fisheries collapses (*1*–*3*) and the recent impacts of the 2004 Asian tsunami and 2005 Hurricane Katrina that were exacerbated by historical losses of mangroves and wetlands (*5*–*7*). With recognition of their essential role for human and marine life, estuaries and coastal zones have become the focus of efforts to develop ecosystem-based management and large-scale restoration strategies. To be successful, these approaches require historical reference points and assessments of the degree and drivers of degradation in an ecosystem context (*8*, *9*).

We reconstructed historical baselines and quantified the magnitude and causes of change in 12 temperate estuarine and coastal ecosystems in Europe, North America, and Australia from the onset of human settlement until today (Table 1). We used paleontologic, archaeological, historical, and ecological records (table S1) to quantify changes in 30 to 80 species per system standardized into 22 guilds and six taxonomic and seven functional groups, as well as seven water-quality parameters and species invasions (*10*). Species were selected for their economic, structural, or functional significance throughout history. We estimated relative abundance of each species over real time and across seven cultural periods reflecting the stage of cultural and market development rather than calendar dates (tables S2 and S3). Relative abundance was quantified as pristine (100%), abundant (90%), depleted (50%), rare (10%), or extinct (0%) (table S4). Recovery was quantified as partial or substantial when increasing from <10% to >10% and >50%, respectively (*10*). Our estimates are conservative compared with available absolute abundance records.

Overall historical change in each study system was tracked by using arithmetic and multivariate means of relative abundance of taxonomic and functional groups (*10*), all of which yielded similar results (Fig. 1 and fig. S1). Despite wide geographic distribution and unique regional histories, all systems showed similar trajectories of long periods of slow decline followed by rapid acceleration over the last 150 to 300 years (Fig. 1A). Severe resource depletion first began during Roman times (2500 years B.P.) in the Adriatic Sea, Medieval times (1000 years B.P.) in the Wadden and Baltic Seas, and in the wake of European colonization in North America and Australia (Fig. 1A). Substituting cultural periods for calendar dates revealed low human impacts during the hunter-gatherer, agricultural, and market-colonial establishment periods (Fig. 1B), when exploitation was mainly for subsistence purposes. However, signs of local resource depletion were evident in some systems such as San Francisco Bay (Fig. 1B), where prehistoric populations depleted highly valued resources such as sea otters (*Enhydra lutris*), large

Table 1. Location and characteristics of study systems. Species richness (SpR, fish richness as proxy for overall richness) and primary productivity (PP) represent regional data for large marine ecosystems [table S1 (*10*)]. Origin indicates the time when the system developed today's size and shape. Impact length and human population growth rate were calculated since beginning of the development period. Human population total and density refer to today's population in provinces and countries bordering the studied systems (*10*).

System	Lat.	Long.	Size (km²)	SpR (fish)	PP (mg C· m^{-2}·d^{-1})	Origin (years ×10^3 B.P.)	Impact (years)	Human population Growth (x-fold)	Human population Total (×10^6)	Human population Density (km^{-2})
W. Baltic Sea	55 N	16 E	390,077	156	1,804	7.0–9.0	1,000	4	84.94	230
Wadden Sea	54 N	8 E	13,500	189	1,067	7.5	1,000	26	6.50	699
N. Adriatic Sea	44 N	14 E	160,000	606	385	8.0	2,500	21	103.00	746
S. Gulf St. Lawrence	47 N	63 W	65,000	197	1,044	6.4–14.5	240	135	7.41	114
Outer Bay of Fundy	45 N	67 W	148	197	1,044	7.0–15.0	240	18	0.03	260
Massachusetts Bay	42 N	71 W	768	645	1,124	6.3–12.0	320	156	2.50	5,230
Delaware Bay	38 N	75 W	2,070	645	1,124	7.0–8.0	240	95	3.33	2,693
Chesapeake Bay	37 N	76 W	6,974	645	1,124	7.4–8.2	240	19	6.93	1,004
Pamlico Sound	35 N	76 W	4,680	1,170	564	7.2–8.2	300	144	0.22	43
Galveston Bay	29 N	95 W	1,456	972	417	7.7–8.2	180	2,659	3.99	4,482
San Francisco Bay	38 N	123 W	838	803	501	8.5–9.3	180	4,533	6.80	8,200
Moreton Bay	27 S	153 E	1,600	1,239	441	6.5	150	710	2.20	1,375

---

[1] Biology Department, Dalhousie University, 1355 Oxford Street, Halifax, NS, Canada B3H 4J1. [2] Bren School of Environmental Science and Management, Bren Hall 3428, University of California, Santa Barbara, CA 93106–5131, USA. [3] Department of Anthropology, 155 Pettengill Hall, Bates College, Lewiston, ME 04240, USA. [4] Resource Management in Asia-Pacific Program, Research School of Pacific and Asian Studies, Australian National University, Canberra, ACT 0200, Australia. [5] Center for Tropical Paleoecology and Archeology, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002–0948, Republic of Panama. [6] Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, IL 60637, USA. [7] Florida Museum of Natural History, University of Florida, Museum Road, P.O. Box 117800, Gainesville, FL 32611–7800, USA. [8] Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, USA. [9] Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093–0244, USA.

*To whom correspondence should be addressed. E-mail: hlotze@dal.ca

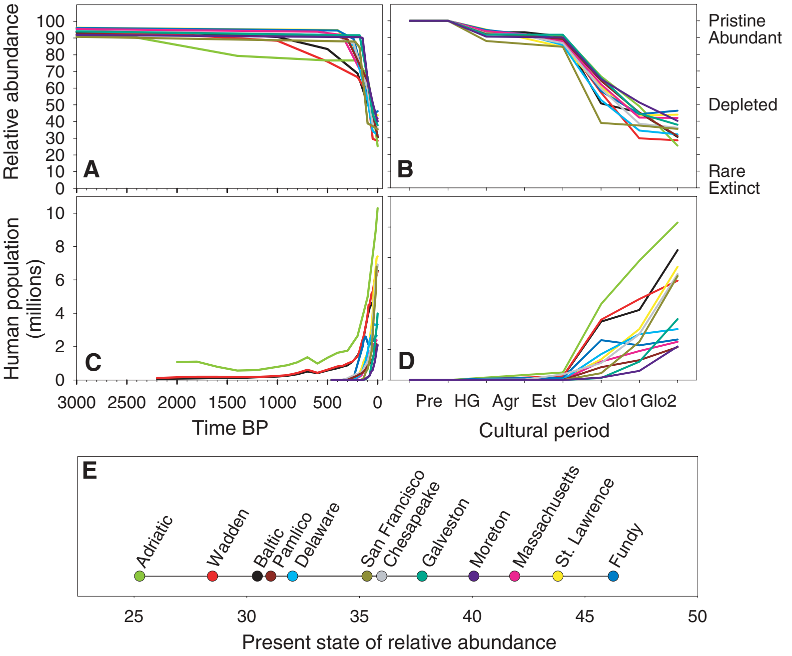

Fig. 1. History and present state of 12 estuarine and coastal ecosystems in North America, Europe, and Australia. (**A**) Relative abundance of six taxonomic groups (as arithmetic means) over real time and (**B**) cultural periods (Pre, prehuman; HG, hunter-gatherer; Agr, agricultural; Est, market–colonial establishment; Dev, market–colonial development; Glo1, global market 1900–1950; and Glo2, global market 1950–2000). (**C**) Human population growth over real time and (**D**) cultural period (Baltic and Adriatic, ×10^{-1}; Fundy, ×10; Pamlico, ×10^{2} to fit scale). (**E**) Present state of relative abundance. Color codes depict study systems as shown in (E).

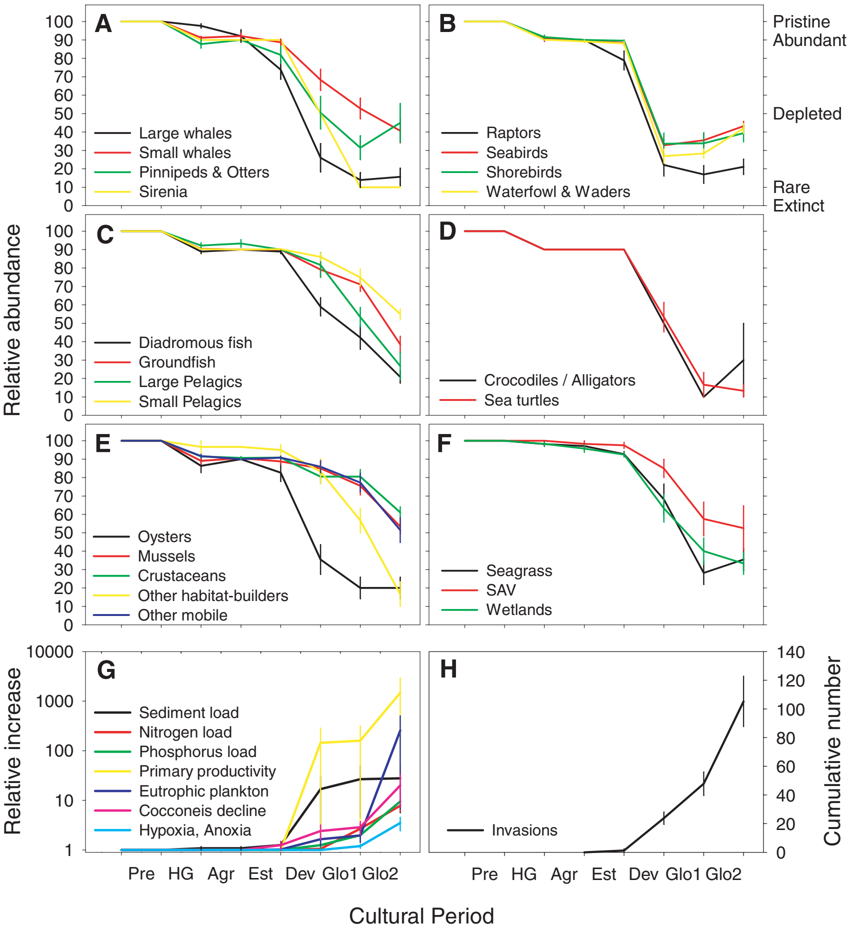

Fig. 2. Common patterns of decline in 22 species guilds averaged over 12 study systems for (**A**) marine mammals, (**B**) coastal birds, (**C**) fish, (**D**) reptiles, (**E**) invertebrates, and (**F**) vegetation. (**G**) Degradation of water quality as indicated by the relative increase in eutrophication parameters [eight systems (*10*)]. (**H**) Cumulative increase in recorded species invasions [five systems (*10*)]. Data are means ± SEM.

geese (*Anser*, *Branta*, *Chen* spp.), white sturgeon (*Acipenser transmontanus*), and native oyster (*Ostreola conchaphila*) (*11*).

Human impacts escalated into rapid resource depletion during the market–colonial development period and continued in the two global market periods, 1900–1950 and 1950–2000, in all systems (Fig. 1B). These were the periods of (i) rapid human population growth (Fig. 1, C and D) and increasing demand, (ii) commercialization of resource use and development of luxury markets, and (iii) industrialization and technological progress toward more efficient but also unselective and destructive gears (table S2). In the two global periods, degradation trends slowed in most and reversed in some systems because of conservation efforts (Fig. 1B). These general trends suggest that rapid degradation was driven by human history rather than natural change and that we may have passed the low point and are on a slow path to recovery—at least in developed countries. In developing countries, however, expected future population growth associated with growing pressures on coastal ecosystems may increase degradation.

The degree of degradation, as indicated by the endpoints of historical trajectories (Fig. 1E), was independent of system size, species richness, primary productivity, and human population density and growth rate (Table 1, linear regressions, $P > 0.05$). Nevertheless, systems with the longest history of intense human impacts and highest total human population were among the most degraded, including the Adriatic, Wadden, and Baltic Seas {Fig. 1E, linear regressions, log[length impact], $F(1,10) = 10.3$, $P = 0.009$, $r^2 = 0.51$; log[total population], $F(1,10) = 5.06$, $P = 0.048$, $r^2 = 0.34$, see fig. S1 for alternative measures}. The outer Bay of Fundy, Southern Gulf of St. Lawrence, and Massachusetts Bay were consistently ranked as the least degraded systems (Fig. 1E and fig. S1).

Detailed time lines for species guilds, taxonomic and functional groups, water-quality parameters, and species invasions followed similar patterns of degradation across study systems (Fig. 2 and fig. S2). Most mammals, birds, and reptiles (Fig. 2, A, B, and D) were depleted by 1900 and declined further by 1950 because of intense exploitation for food, oil, or luxury items including furs, feathers, and ivory (*2*, *12*). Among fish (Fig. 2C), diadromous species such as salmon and sturgeon were highly desired, easily accessible, and depleted first, successively followed by large pelagics such as tuna and sharks, groundfish such as cod and halibut, and small pelagics such as herring and sardines. Oysters were the first invertebrate suffering depletion (Fig. 2E) because of high value, accessibility, and destructive exploitation methods (*13*). Because of their reef-forming and filtration capacity, depletion of oysters reduced the ecosystem's ability to provide high water quality and complex habitats. Other habitat-building filter-feeders including corals, sponges, and hydrozoans were little affected until the development period, but rapidly declined with expanding seafloor trawling (*12*). Mussels, crustaceans, and other mobile invertebrates have been harvested throughout history, but only recently became targets of expanding low–trophic level fisheries (*2*, *14*). Thus, among mammals, fish, and invertebrates, we see sequential depletion of the most valued and largest species and subsequent replacement with smaller, less valuable ones (*14*).

Over time, 67% of wetlands, 65% of seagrasses, and 48% of other submerged aquatic vegetation (SAV) were lost because of reclamation, eutrophication, disease, destruction, and direct exploitation (Fig. 2F). Declines in coastal vegetation caused substantial losses of nursery habitats, nutrient and sediment sinks, and coastline protection. By the late 20th century, 91% of the recorded species were depleted; 31% were rare; and 7% were extinct. Conservation efforts in the 20th century led to partial recovery of 12% and substantial recovery of 2% of the species, especially among pinnipeds, otters, birds, crocodiles, and alligators (Fig. 2, A, B, and D). Large whales, sirenia, and sea turtles, however, remain at low population levels.

Degradation of water quality occurred in two phases (*10*). During the development period (Fig. 2G), primary productivity and sediment loading strongly increased, mainly driven by deforestation that mobilized sediments and nutrients. These trends stabilized during the first global period (1900–1950) except for increasing nitrogen loading. In the second global period (1950–2000), sediment loads stabilized but strong increases occurred in nitrogen and phosphorus loading, primary productivity, eutrophic plankton, oxygen depletion, and losses of epiphytic diatoms (*Cocconeis* spp.), commonly associated with seagrass. These trends reflect coastal eutrophication driven by nutrient loading from point and nonpoint sources and losses of filtering and buffering capacity of vegetation and suspension feeders (*1*, *15*).

The first identified invasion was by the soft-shelled clam *Mya arenaria*, introduced from North America into the Baltic and North Seas probably by Norse voyagers before 1245 A.D. (*10*, *16*). In the following centuries, invasions were only gradually recorded but increased during the development and accelerated during the global periods (Fig. 2H), driven by increased global navigation and commerce (*17*).

The recorded causes of past changes (*10*) highlight priority targets for ecosystem-based management and marine conservation. Exploitation stands out as the causative agent for 95% of species depletions and 96% of extinctions in our study systems, followed by habitat destruction (Fig. 3A). This is consistent with reported causes of marine (*18*) and terrestrial (*19*) extinctions worldwide. Pollution, disturbance, disease, eutrophication, and introduced land predators were associated with fewer species losses (Fig. 3A) but contributed to declines of habitat-building species and may hinder recovery. In our records, which focused on commercially, structurally, and functionally important species, no depletion or extinction was caused by invasive species or climate change, although such cases have been documented (*3*, *18*, *20*). We caution, however, that the relative importance of these factors may shift in the future with exploitation becoming more restricted, but invasions and climate change accelerating (*21*).

Our results indicate that human impacts do not act in isolation. In 45% of species depletions and 42% of extinctions, multiple human impacts were involved, commonly, exploitation and habitat loss. Such synergistic effects have been significant for terrestrial extinctions (*19*) and estuarine depletions (*22*). Cumulative impacts were even more important for recovery. Although 22% of recoveries resulted from mitigation of a single human impact, mostly exploitation, 78% resulted from reduction of at least two impacts, mostly habitat protection and restricted exploitation but also pollution (Fig. 3A). Reduced

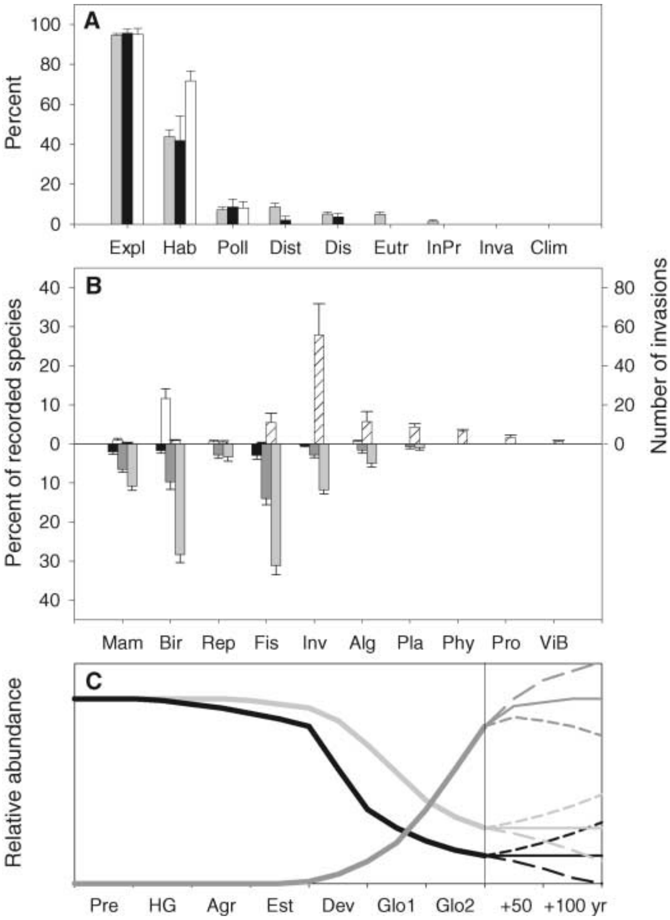

Fig. 3. Causes and consequences of change in 12 study systems (means ± SEM). (**A**) Percent of species depletions (light gray) and extinctions (black) caused by different human impacts (Expl, exploitation; Hab, habitat loss; Poll, pollution; Dist, human disturbance; Dis, disease; Eutr, eutrophication; InPr, introduced land predators; Inva, invasive species; and Cli, climate change), and percent of recoveries (white) resulting from impact reduction. (**B**) Diversity shift due to biased losses and gains across different taxonomic groups (Mam, mammals; Bir, birds; Rep, reptiles; Fis, fish; Inv, invertebrates; Alg, macroalgae; Pla, higher plants; Phy, phytoplankton; Pro, protozoa; and ViB, viruses and bacteria): percent of recorded species currently depleted (light gray), rare (dark gray), extinct (black), or recovering (white), and number of species invasions (cross-hatched; data for seven systems). (**C**) Past, present, and potential future changes in important structural and functional ecosystem components: large consumers (black), habitat and filter organisms (light gray), eutrophication and invasive species (dark gray) [cultural periods as in Fig. 1, adapted from (*28*)]. Future scenarios depict stabilizing (solid lines), improving (short dashed), or worsening (long dashed) trends.

exploitation, habitat protection, and improved water quality need to be considered together, and the cumulative effects of multiple human interventions must be included in both management and conservation strategies (*22*).

Marked shifts in diversity were caused by the taxonomic bias of almost all extinctions (93%) and most depletions (81%) affecting large vertebrates (Fig. 3B) (*10*). This bias was amplified by the high incidence of invasions among invertebrates, plants, and smaller organisms (Fig. 3B) (*10*). Given past trends in depletions, extinctions, and invasions (Fig. 2), this shift in species composition is likely to accelerate in the future, only partly dampened by recent trends in recovery (Figs. 2 and 3B).

The structure and functioning of estuarine and coastal ecosystems has been fundamentally changed by the loss of large predators and herbivores, spawning and nursery habitat, and filtering capacity that sustains water quality (Fig. 3C and fig. S2). The erosion of diversity and complexity has slowly undermined resilience, giving way to undesirable algal blooms, dead zones, disease outbreaks, and invasions, and elevating the potential for disaster (*1–7*, *21*). Although declines in large vertebrates and habitat-providing species have slowed in the last 50 to 100 years, trends in small consumers, water quality, and species invasions continue to deteriorate (Figs. 2 and 3C). Together with the historical degradation of coral reefs (*4*), kelp forests (*23*), and an up-welling system (*24*), our results document severe, long-term degradation of near-shore marine systems worldwide. As human impacts spread rapidly from the coast to the shelf, open ocean, and deep sea (*25–27*), past trajectories in coastal zones may well forecast future changes in the entire ocean. Strong countermeasures are needed to reverse trends of expanding degradation (Fig. 3C).

Human impacts have pushed estuarine and coastal ecosystems far from their historical baseline of rich, diverse, and productive ecosystems. The severity and synchrony of degradation trends and the commonality of causes and consequences of change provide reference points and quantitative targets for ecosystem-based management and restoration. Overexploitation and habitat destruction have been responsible for the large majority of historical changes, and their reduction should be a major management priority. Eutrophication, although severe in the last phase of estuarine history, largely followed rather than drove observed declines in diversity, structure, and functioning. Despite some extinctions, most species and functional groups persist, albeit in greatly reduced numbers. Thus, the potential for recovery remains, and where human efforts have focused on protection and restoration, recovery has occurred, although often with significant lag times (*2*, *12*). Our study not only provides baselines on the extent of historical degradation, but also a vision for regenerating resilient estuarine and coastal ecosystems that can absorb shocks and disasters in an uncertain future.

References and Notes

1. J. B. C. Jackson *et al.*, *Science* **293**, 629 (2001).
2. H. K. Lotze, I. Milewski, *Ecol. Appl.* **14**, 1428 (2004).
3. H. K. Lotze *et al.*, *Helgol. Mar. Res.* **59**, 84 (2005).
4. J. M. Pandolfi *et al.*, *Science* **301**, 955 (2003).
5. W. N. Adger, T. P. Hughes, C. Folke, S. R. Carpenter, J. Rockström, *Science* **309**, 1036 (2005).
6. F. Danielsen *et al.*, *Science* **310**, 643 (2005).
7. E. Stokstad, *Science* **310**, 1264 (2005).
8. A. Balmford *et al.*, *Science* **307**, 212 (2005).
9. E. K. Pikitch *et al.*, *Science* **305**, 346 (2004).
10. Detailed methods are available as supporting online material on *Science* Online.
11. J. M. Broughton, *World Archaeol.* **34**, 60 (2002).
12. H. K. Lotze, *Helgol. Mar. Res.* **59**, 71 (2005).
13. M. X. Kirby, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 13096 (2004).
14. D. Pauly, V. Christensen, J. Dalsgaard, R. Froese, F. Torres Jr., *Science* **279**, 860 (1998).
15. J. E. Cloern, *Mar. Ecol. Prog. Ser.* **210**, 223 (2001).
16. K. S. Petersen, K. L. Rasmussen, J. Heinemeier, N. Rud, *Nature* **359**, 679 (1992).
17. G. M. Ruiz, J. T. Carlton, E. D. Grosholz, A. H. Hines, *Am. Zool.* **37**, 621 (1997).
18. N. K. Dulvy, Y. Sadovy, J. D. Reynolds, *Fish Fish.* **4**, 25 (2003).
19. D. A. Burney, T. F. Flannery, *Trends Ecol. Evol.* **20**, 395 (2005).
20. J. T. Carlton, J. B. Geller, M. L. Reaka-Kudla, E. A. Norse, *Annu. Rev. Ecol. Syst.* **30**, 515 (1999).
21. C. D. Harvell *et al.*, *Science* **296**, 2158 (2002).
22. H. S. Lenihan, C. H. Peterson, *Ecol. Appl.* **8**, 128 (1998).
23. R. S. Steneck *et al.*, *Environ. Conserv.* **29**, 436 (2002).
24. C. L. Griffiths *et al.*, *Oceanogr. Mar. Biol. Annu. Rev.* **42**, 303 (2004).
25. B. Worm, M. Sandow, A. Oschlies, H. K. Lotze, R. A. Myers, *Science* **309**, 1365 (2005).
26. D. Pauly *et al.*, *Science* **302**, 1359 (2003).
27. M. Pahlow, U. Riebesell, *Science* **287**, 831 (2000).
28. J. B. C. Jackson, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 5411 (2001).

29. We thank all colleagues for sharing data and insight and B. Worm and R. A. Myers for critical discussions. This work was initiated as part of the Long-Term Ecological Records of Marine Environments, Populations and Communities Working Group supported by the National Center for Ecological Analysis and Synthesis (funded by NSF grant DEB-0072909, the University of California, and the University of California, Santa Barbara). Additional funding was granted to H.K.L. by the Alfred-Wegener Institute for Polar and Marine Research, the Sloan Foundation (Census of Marine Life, History of Marine Animal Populations Program), and the Lenfest Ocean Program at the Pew Charitable Trusts.

Supporting Online Material

www.sciencemag.org/cgi/content/full/312/5781/1806/DC1
Materials and Methods
Figs. S1 and S2
Tables S1 to S8
References and Notes

29 March 2006; accepted 3 May 2006
10.1126/science.1128035

JETLAG Resets the *Drosophila* Circadian Clock by Promoting Light-Induced Degradation of TIMELESS

Kyunghee Koh, Xiangzhong Zheng, Amita Sehgal*

Organisms ranging from bacteria to humans synchronize their internal clocks to daily cycles of light and dark. Photic entrainment of the *Drosophila* clock is mediated by proteasomal degradation of the clock protein TIMELESS (TIM). We have identified mutations in *jetlag*—a gene coding for an F-box protein with leucine-rich repeats—that result in reduced light sensitivity of the circadian clock. Mutant flies show rhythmic behavior in constant light, reduced phase shifts in response to light pulses, and reduced light-dependent degradation of TIM. Expression of JET along with the circadian photoreceptor cryptochrome (CRY) in cultured S2R+ cells confers light-dependent degradation onto TIM, thereby reconstituting the acute response of the circadian clock to light in a cell culture system. Our results suggest that JET is essential for resetting the clock by transmitting light signals from CRY to TIM.

Travel across time zones often produces jet lag because it takes some time to resynchronize internal circadian clocks to the new day and night cycle. Although the molecular mechanisms for generating circadian rhythms through interlocking transcriptional feedback loops and posttranslational modifications have been characterized in some detail (*1*), few components of the light entrainment pathway are known (*2*). Photic entrainment in *Drosophila* can be mediated by the visual system and by CRY, a circadian blue-light photoreceptor expressed in clock cells (*3*). When the fly is exposed to light, CRY binds a core clock protein, TIM, which leads to subsequent ubiquitination and degradation of TIM by the proteasome pathway (*4–8*). Rapid, light-dependent degradation of TIM underlies the fly's ability to reset the circadian phase to reflect environmental fluctuations in light levels (*9*, *10*). However, the specific signals that drive the TIM response to light are not known.

In the course of characterizing rest:activity rhythms of various fly strains, we discovered a strain with anomalous activity patterns in constant light (LL). Whereas wild-type flies

---

Howard Hughes Medical Institute, Department of Neuroscience, University of Pennsylvania School of Medicine, Philadelphia, PA 19104, USA.

*To whom correspondence should be addressed. E-mail: amita@mail.med.upenn.edu