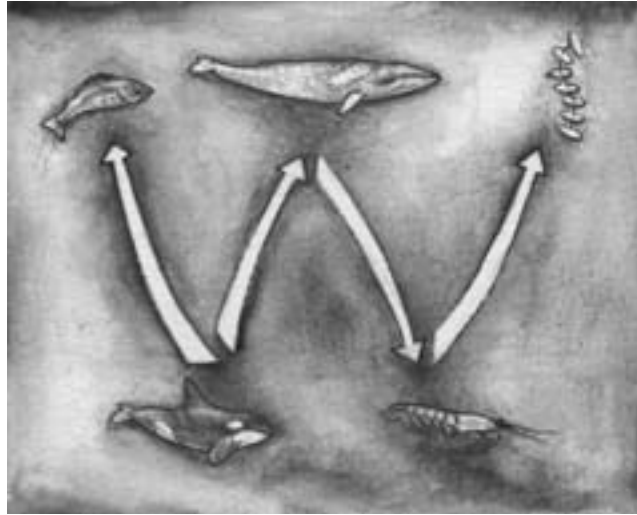# Whales, Interaction Webs, and Zero-Sum Ecology

ROBERT T. PAINE



Food webs are inescapable consequences of any multispecies study in which interactions are assumed to exist. The nexus can be pictured as links between species (e.g., Elton 1927) or as entries in a predator by prey matrix (Cohen et al. 1993). Both procedures promote the view that all ecosystems are characterized by clusters of interacting species. Both have encouraged compilations of increasingly complete trophic descriptions and the development of quantitative theory. Neither, however, confronts the issue of what constitutes a legitimate link (Paine 1988); neither can incorporate the consequences of dynamical alteration of predator (or prey) abundances or deal effectively with trophic cascades or indirect effects. Thus one challenge confronting contributors to this volume is the extent to which, or even whether, food webs provide an appropriate context for unraveling the anthropogenically forced changes in whales, including killer whales *(Orcinus orca)*, their interrelationships, and the derived implication for associated species.

A second challenge is simply the spatial vastness (Levin 1992) of the ecological stage on which whale demography and interactions are carried out. This bears obvious implications for the amount, completeness, and quality of the data and the degree to which "scaling up" is permissible. Manipulative experiments, equivalent to those that have proven so revealing on rocky shores and even more so in freshwater ecosystems, are clearly impossible. Buried here, but of critical

importance, is the "changing baseline" perspective (Pauly 1995, Jackson et al. 2001): Species abundances have changed, and therefore the ecological context, but by how much?

This essay begins with a brief summary of experimental studies that identify the importance of employing interaction webs as a format for further discussion of whales and ocean ecosystems. The concept, while not novel, was developed by Paine (1980) as "functional" webs; Menge (1995) provided the more appropriate term, *interaction web*. My motivation is threefold:

1. Such studies convincingly demonstrate that species do interact and that some subset of these interactions bear substantial consequences for many associated species.

2. The studies also reveal the panoply of interpretative horrors facing all dynamic community analysis: Individual species will have different, and varying, per capita impacts; nonlinear interactions are rampant; and indirect effects are commonplace.

3. The preceding two points raise another question: Are oceanic assemblages so fundamentally different from terrestrial, lentic, and shallow-water marine ones (perhaps because of an ecological dilution due to their spatial vastness) that different organizational rules apply?

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I next develop a crucial aspect of my argument that interaction webs provide a legitimate and useful framework. I call this aspect "zero-sum ecology." It invokes a mass balance equilibrium, implying that carbon is not being meaningfully sequestered from or released to global ecosystems over time spans appropriate to current whale ecology. It differs from Hubbell's (2001) similar perspective by focusing on energy rather than individual organisms. That is, the global cycling of organic carbon is more or less in balance, and thus all photosynthetically fixed carbon is returned to the global pool via bacterial or eukaryote respiration. Hairston et al. (1960) developed the same theme. Its primary implication is that removal of substantial biomass from one component of an ecosystem should be reflected in significant changes elsewhere, identified perhaps as increased (or decreased) biomass and population growth rates, alteration of diets as the spectrum of prey shifts, or changes in spatial distribution. Interaction webs are intended to portray these dynamics qualitatively and fit comfortably with multispecies models such as that of May et al. (1979).

The terminal section discusses a varied set of studies that collectively suggest that whales, including *O. orca*, at oceanic spatial scales could have played roles analogous to those demonstrated for consumers of secondary production in much smaller, experimentally tractable systems. Acceptance or denial of their relevance is at the crux of the question: Do whales and their interspecific interactions matter, or how might they, or could their consequences have been anticipated or predicted under an onslaught of anthropogenic forcing? The concluding paragraphs argue for an open-mindedness in addressing this question. Frankly, I do not *know* whether whales mattered (ecologically, not esthetically), but their large mass, physiology (homeothermy), and diminished numbers, even at characteristically huge spatial scales, implies that suggestion of significant roles in the ocean's economy should not be summarily dismissed or ignored. Resolution surely will involve an interplay between compilation and analysis of historical information (e.g., whaling records); modeling (e.g., using EcoSim/Ecopath; see Walters et al. 1997); newer data on demographic trends, density, diet, and so forth; and, equally, the degree to which analogy with data-rich exploited fish and shark populations proves relevant.

## Interaction Webs

Charles Darwin was an insightful experimentalist, and many of his tinkerings produced striking results, although the resolving power of such interventions in the organization of "nature" was unrecognized or underappreciated in his time. One kind of controlled manipulation is represented by [AUQ1] Darwin's (1859) grass clipping exercise or Paine (1966). Such studies identify phenomena such as changes in species richness, distribution pattern, or even production, and their results are often broadly repeatable despite minimal appreciation of the root mechanisms. Another kind of study involves manipulation of some variable such as density manipulation or specific nutrient inputs, with the goal of a much more precise understanding of how that segment of a system functions. Both kinds of study provide a basis for prediction, the former qualitative, the latter quantitative. Both also imply that species are dynamically linked and that changes in some species' density, prey or nutrient availability, or system trophic structure are highly likely to be reflected in changes elsewhere in the ecosystem.

These relationships constitute the domain of interaction webs. As identified earlier, such webs differ from the more descriptive linkage patterns and energy flow webs because they focus on the change subsequent to some manipulation rather than a fixed, seemingly immutable pattern. No standardized graphic protocols have been developed, and none are attempted here. On the other hand, an increasing number of review articles attest to a recognition that understanding the complexities of multispecies relationships is both a vital necessity and the handmaid of successful ecosystem management. Interaction webs provide the matrix in which such understanding can be developed.

An early review of experimentally induced alteration in assemblage structure (Paine 1980) introduced the term *trophic cascade* and provided a coarse taxonomy of food webs. That perspective was encouraged by a number of seminal studies, some of which described dramatic assemblage changes after an invasion (Brooks and Dodson 1965; Zaret and Paine 1973) or recovery of an apex predator (Estes and Palmisano 1974). Supplementing these results were manipulative experiments in which species of high trophic status were removed, excluded, or added (Paine 1966, Sutherland 1974, Power et al. 1985). Other studies employed experimental ponds (Hall et al. 1970) or their smaller cousins, "cattle tanks" (Morin 1983), and even whole lakes (Hassler et al. 1951, Schindler 1974). The foregoing references are but a small fraction of studies identifying the consequences of nutrient alteration, consumers jumbling the consequences of competitive interactions, or apex predators influencing whole community structure.

By 1990 this conceptual framework, already hinted at by Forbes (1887) and clearly visible in the work of Brooks and Dodson (1965), had been deeply explored in freshwater ecosystems (Carpenter et al. 1985, Carpenter and Kitchell 1993). The ecologically polarizing jargon of "top-down" (predator control) and "bottom-up" (production control) developed rapidly. An ecumenical review by Power (1992) established the obvious—that both forces exist, and it is their relative importance that should be evaluated. A majority of recent reviews concentrate on trophic cascades, a top-down forcing phenomenon and one easily produced in experimentally tractable assemblages and equally visible in large-geographic-scale, heavily fished systems. For instance, Sala et al. (1998), Fogarty and Murawski (1998), and Pinnegar et al. (2000) expand on fisheries' impacts in marine shallow-water, rocky-surface systems. Pace et al. (1999) identify cascades as widespread in a diversity of systems ranging from insect guts to open oceans; Shurin et al.

(2002), in an examination of 102 field experiments, found predation effects strongest in freshwater and marine benthic webs and weakest in marine plankton and terrestrial assemblages. Duffy (2002), Schmitz (2003), and Van Bael et al. (2003) have continued to develop an appreciation of the ubiquity, but not the generality, of top-down influences, as have Banse (2002) and Goericke (2002) for blue-water systems.

What is the relevance of small-scale, generally short-duration studies for whales, the biologists invested in their study, and even biological oceanographers investigating ecological events at spatial scales ranging from hundreds to thousands of square kilometers? With the exception of Estes's research (e.g., Estes and Palmisano 1974; Estes et al. 1998), we generally do not know. Those studies, conducted along the shallow shoreline of western North America, basically trace a predator-induced cascade from higher trophic levels to benthic algae attached to rocky surfaces, on which the relatively simple process of interference competition for space predominates. Is an understanding of such a dynamic transferable to open-water assemblages in which (presumably) exploitation competition occurs, in addition to the impacts of consumption by higher trophic levels? Again, we do not know. However, it appears shortsighted to reject top-down influences dogmatically, given their undisputed presence in some, though perhaps not all, other ecosystems.

## Zero-Sum Ecology

Hairston et al. (1960) based their seminal paper in part on a presumption that all photosynthetically fixed carbon was utilized. That is, natural gas, coal, and oil were not being deposited; globally, carbon fixed equaled carbon respired. In the short run, this appears to be correct, although increasing atmospheric $CO_2$ and uncertainty about carbon sources and sinks clouds the issue. The same might be said for methane ices or clathrates, $CH_4$ trapped in ice under known conditions of ambient pressure and temperature: There seems to be a balance between carbon in the sedimentary reservoirs and carbon fluxes (Kvenvolden 1998). Carbon atoms bound in rock (e.g., $CaCO_3$) are probably immaterial at the time scales considered here.

If these assumptions are correct, they have profound implications for interaction webs. What goes in must come out; a major alteration of living biomass and its maintenance requirements in one sector of a food web will surely be reflected by changes elsewhere. Because the rudimentary natural history outlining relationships known for more accessible systems is lacking, or minimized, for environments inhabited by whales, the prediction of and search for consequences have been hampered.

An analogy developed by Robert MacArthur catches the sense of the situation nicely. If a shelf is filled to capacity with books, every withdrawal permits an addition. On the other hand, on a shelf characterized by numerous gaps, removal (= extraction) or addition should be of small,

undetectable, or no consequence. A zero-sum ecological perspective implies that removals at the magnitude of suspected whale extractions must have had effects. Without knowing what these might have been, and in the absence of any serious attempt to document specific resultant changes, we must resort to inference or conjecture. The following section develops arguments that changes within oceanic ecosystems must have occurred.

## Consequential Interactions in Large, Open Ecosystems

We know that organisms interact, both from direct observation and as demonstrated by controlled manipulation at small spatial scales. As the spatial domain increases, however, our knowledge base diminishes accordingly—to the point, perhaps, where interactions at the community level (that is, beyond the obvious acts of feeding or being eaten) become uncertain and obscure. Various lines of evidence suggest that consequential interactions or interrelationships do exist in pelagic ecosystems. The examples that follow are hardly exhaustive; rather they indicate the kinds of natural or imposed phenomena that are capable of altering biological assemblages at large spatial scales. The absence of information on trophic responses is better viewed as lost opportunity rather than absence of effect. The majority of these examples have been categorized within the framework proposed by Bender et al. (1984) into pulse perturbations, which are relatively instantaneous impacts, and press experiments, in which the perturbation is maintained. Plagues and massive diebacks provide examples of the former, commercial fisheries of the latter.

### Pulse Perturbations

EEL GRASS DISAPPEARANCE. Between 1930 and 1933, a "wasting disease" caused the disappearances of about 90% of the eel grass *(Zostera marina)* in coastal waters of the north Atlantic (Short et al. 1987). *Zostera* is a major source of detritus and a food for birds. Its precipitious decline decimated populations of migratory waterfowl, led to loss of a commercial scallop fishery, impacted a lagoon's invertebrate assemblage, and generated the first documented extinction of a marine invertebrate: the limpet *Lottia alveus* (Carlton et al. 1991; Stauffer 1937).

DIADEMA DIEBACK. The catastrophic collapse of populations of the sea urchin *Diadema antillarum* provides a second example. Prior to 1983 this species was ubiquitous on coral reefs in the Caribbean basin. Within little more than a year, an epidemic of unknown cause had killed from 93% to nearly 100% of these urchins within a 3.5 million $km^2$ region (Lessios 1988). Community effects ranged from increases in benthic algal percent cover, increases in the rate of fish herbivory, decreases in bioerosion, reduced coral recruitment, and numerical increases in other urchin species, implicating previously unsuspected interspecific competition (Lessios

1988). Generalizations based on the demise of this single species are confounded by hurricane damage and overexploitation of large herbivorous fishes (Hughes 1994; Paine et al. 1998). Nonetheless, the lesson seems certain: The ecological consequences of mass, nearly instantaneous, mortality of an important grazer ramified throughout this ecosystem, and many of the resultant population shifts could have been predicted correctly a priori.

Catastrophic mortality events are not uncommon in marine near-shore ecosystems. The list of taxa involved ranges from corals and sponges to dolphins and seals. To the extent that single species are involved, these precipitous declines provide rare opportunities to probe the role a species plays in community organization. Do they occur in noncoastal oceans? We do not know. However, pulse perturbations at large spatial scales appear to retain the salient hallmarks characterizing small-scale experimental studies: dramatic community alteration, shifts in trophic structure, and important indirect consequences.

### Press Perturbations

Sustained industrial fishing operations in the world's coastal and central oceans can be considered press perturbations. Evidence for their effects is seen in the growing evidence for overexploitation of apex predators (Myers and Worm 2003) and an increasingly accepted metaphor of marine food webs being "fished down" (Pauly et al. 1998). The following examples only hint at the magnitude and complexity potentially induced when the density of apex predators is altered.

SHALLOW-WATER, BENTHIC SYSTEMS: SEA OTTERS. Trophic cascades occur when the addition or deletion of some higher-level consumer leads to major shifts in species composition at lower levels. One could consider keystone species effects (e.g., Paine 1966) as a muted cascade, although only two "trophic levels" were involved. A much clearer example, involving three and possibly four levels, has been developed by Estes et al. (1998). By the time (1911) sea otter exploitation was terminated, the species was locally extinct throughout much of its original range. The existence of a few local populations, however, led to the development of two contrasting states, providing the comparisons detailed in the classic study by Estes and Palmisano (1974). Although considering these regions as either two-level (without otters) or three-level (with otters) is a gross simplification, it has enabled a striking range of studies in this experimentally intractable system. For instance, Simenstad et al. (1978) illustrate that two- and three-state systems (excluding humans as a trophic level) characterize prehistoric Aleut middens and probably resulted from local overexploitation of sea otters. Duggins et al. (1989), by comparing islands with and without sea otters, quantified a range of indirect effects: At islands with otters, and therefore robust kelp populations, mussels and barnacles grow roughly twice as fast as they do at otterless islands. Stable carbon isotope analyses identified detrital kelp as the supplemental energy source. Estes and Duggins (1995) have demonstrated the geographic ubiquity of ecological transformation from a two- to three-level system as otter populations recovered and, in the process, promoted kelp bed development. Finally, Estes et al. (1998) have shown that the recent entry of killer whales into this food web, which added a fourth trophic level (comparable to the prehistoric Aleut impact), has generated the compositional shifts anticipated at all three linked lower levels.

I believe that otters at high population densities represent a sustained press perturbation just as, in their absence, sea urchins do. Furthermore, the results seem generalizable over thousands of kilometers of shoreline. Thus, while a trophic cascade and positive indirect effects on species not eaten by otters (barnacles) are clearly identified, it remains basically a shallow-water, benthic study system whose applicability to truly pelagic systems is open to question.

DEEP-WATER, BENTHIC SYSTEMS: ATLANTIC COD-SHRIMP INTERACTIONS. Commercial fisheries generate a wealth of data on fish abundances, often expressed as time series. Severely depleted Atlantic cod *(Gadus morhua)* stocks and those of their commercially valuable prey, the shrimp *Pandalus borealis*, have been subjected to meta-analysis by Worm and Myers (2003). These species represent a natural predator-prey coupling: Eight of nine analyses of mixed stocks in different geographic regions revealed significantly inverse abundances. When all north Atlantic regions are combined, cod catch statistics are also inversely related to catches of two large crustaceans (snow crabs and American lobsters). Such dominating top-down influences, expressed at a large geographic scale, are certain to have cascading effects on other benthic species (Worm and Myers 2003). Witman and Sebens's (1992) comparison of Western Atlantic seamounts supports this opinion. At offshore sites with abundant cod, crabs were scarce and brittle stars were subjected to significantly greater predation rates. The reverse pattern characterizes coastal sites with fishery-depleted cod populations. Since these invertebrates are themselves important predators, cascading impacts at still lower trophic levels, while difficult to measure, should have occurred.

Overexploitation of high-trophic-status predators such as cod can be anticipated to induce changes in community structures. The Worm and Myers (2003) analysis provides one striking example. The observation and small-scale experiments of Witman and Sebens (1992) substantiate that opinion. Nonetheless, these relationships, even if in deep water, are still firmly anchored to a benthic component, again calling into question their relevance to purely pelagic interactions. A variety of approaches to the latter are explored next.

OCEANIC, TOTALLY PELAGIC SYSTEMS: SHARKS, TUNA. Industrialized fishing occurs in the world's open oceans on almost unimaginable scales: purse seines two to three hundred meters in depth, baited lines in excess of 50 kilometers in length. They have extracted a toll on apex consumers (tuna, sharks) and have often been characterized by a substantial bycatch. Because of public concern about impacts on such charismatic species as albatross, turtles, and dolphins, as well as for fundamental management reasons, a

substantial database exists for some fisheries. For instance, Essington et al. (2002) and Schindler et al. (2002) employed bioenergetic models (Kitchell et al. 1977) that balance mean (population) metabolism and prey consumption to estimate the consequences of fishing effects on blue sharks and small tuna. One goal was to evaluate the efficiency of different fishing strategies. Both analyses employed what can be considered a hybrid food web modeling approach. Both concluded that commercial fisheries have strong effects on the character of trophic linkages in pelagic webs, that these effects may alter predator life history traits and have an impact on lower trophic level prey as well. Such a result is to be anticipated if "zero-sum" energy balances apply in the open ocean. Lack of both interest and a persuasive conceptual framework, and little or no funding for studies of tangential consequences, have constrained understanding of even minimal ecosystem effects of these press perturbations.

Similar interpretations involving a very different approach have been obtained by Stevens et al. (2000), who examined the effects of fishing on sharks and their allies employing the modeling technique EcoSim. For instance, their Table 1 summarizes the status of 17 stocks, of which 12 have collapsed or are in decline. The models compared the consequences of shark removal in three different ecosystems. In general, there were numerous surprises with respect to population trends, and many of the outcomes were not as predictable as anticipated. It seems impossible to know whether such trends reflect "reality" or whether, when "surprises" occur, they are due to unrealistic parameter estimates or incomplete knowledge of that particular food web.

Although none of the foregoing studies included whales, it is certain that species do not exist in an ecological vacuum, and therefore, interactions must be present. When the impact of diminished apex predator mass was evaluated in a food web context, population density of other food web members was found to change. Direct and indirect effects were implicated in these multi–trophic level simulations. In an earlier study employing linked differential equations in which whales were a key component, May et al. (1979) identified realistic population trajectories dependent on "treatment." That is, whether whales and/or krill were protected or exploited had identifiable consequences for seals and penguins. A variety of models, in fact, may provide the surest way to generate testable predictions in these large, open systems. As the quality and trophic extent of parameter estimates increases, the role of whales at even historic population levels might be evaluated. If modeling is to be effective, however, many of the attributes of interactions will have to be first identified and then quantified.

### Other Kinds of Interactions

Nature is highly variable—a condition confounded by anthropogenic forcing—so strict categorization of influences is difficult if not inappropriate. In addition to pulse and press

perturbations attributed to commercial overfishing, at least one other category producing ecological change exists. All species vary naturally in abundance in space through time. When these variations are haphazard (stochastic) in magnitude, timing, or place, they are frustratingly useless in an analytical sense. However, a few marine species vary in highly predictable ways. Shiomoto et al. (1997) have cautiously described the consequences of biannual variation in pink salmon catch in the subarctic North Pacific. This variation of slightly more than an order of magnitude translates in years of high salmon abundance to both fewer herbivorous zooplankton and a reduction of their predators (carnivorous macro-zooplankton), and increased concentrations of chlorophyll a, an index of phytoplankton abundance and primary production. When salmon were scarce, the pattern reversed. The implication of top-down dynamical consequence is inescapable.

Other quasi-cyclic variations exist—Pacific decadal oscillations, El Niño, and La Niña especially—but they are much too general in effect to provide the unambiguous, species-specific signals that most interaction webs, qualitative or quantitative, require.

### Conclusions

"Do or did whales matter?" is our primary issue. If global carbon flux is in equilibrium, at least to the extent that coal, oil, gas, and clathrates are not being deposited (which would signal no surplus of production over consumption), reducing the biomass of large-bodied consumers must have had effects on other elements of the food web. The experimental evidence for cascades (and ripples) from all kinds of ecosystems with a benthic component is unequivocal: Top-down influences are often important. Natural history detail, direct observation, and small-scale experimentation all substantiate this conclusion. Additional support comes from less tractable, larger systems, such as the Great Lakes (Madenjian et al. 2002) and the Northeast Pacific (Estes et al. 1998). A "weight of evidence" argument (National Research Council 2003) would support the view that whales did matter and that systematic exploitation, reducing their biomass and changing their spatial distribution, must have left an ecosystem imprint.

Sadly, there is little direct proof that this conjecture is correct, in part because of the spatial vastness of the whales' domain and in part to the near-total absence of trophic linkage detail and even taxonomy of the food web's membership. Probably the cleanest signal will come from predicting indirect consequences and then evaluating their robustness, much in the spirit of May et al. (1979) and Springer et al. (2003). However, it is almost certain that any confidence in the predicted consequences of whale removal will be compromised by both uncertainty about historic population sizes (Roman and Palumbi 2003) and concurrent overexploitation of other apex consumers. A more optimistic vision is that most whale stocks will recover eventually to sustainable levels. In that eventuality, again assuming zero-sum ecosystem

energetics and a sufficiently strong ecological signal, resurrection of these apex consumers will provide an important probe for understanding the organization of oceanic ecosystems at global scales.

## Acknowledgments

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[AUQ1] (Interaction Webs, first paragraph) Do you have a page number for the description of the grass clipping exercise in Darwin 1859?]

[AUQ2] (Literature Cited, Darwin 1859) The 1859 publication of *Origin of Species* was London: John Murray; it was the first edition. What are the date and edition of the Random House reprint?]