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Simulating community effects of sea floor shading by plankton blooms over the West Florida Shelf

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Abstract

Phytoplankton blooms are increasingly conspicuous along the world's coastlines, and the toxic effects of these blooms have become a major concern. Nutrient enrichment often causes phytoplankton blooms, which decrease water transparency, but little is known about the effects of such light regime changes on whole communities of the continental shelf. A series of simulations designed to evaluate the potential effects of shading by phytoplankton blooms on community organization were conducted using a balanced trophic model of the West Florida Shelf ecosystem and the Ecopath with Ecosim modeling approach. Many functional groups in the system were predicted to decline as benthic primary production was inhibited through shading by phytoplankton, especially when associated biogenic habitat was lost. Groups that obtain most of their energy from planktonic pathways increased when shading impact and associated structural habitat degradation were complemented by enhanced phytoplankton production. Groups predicted to decline as the result of shading by plankton blooms include seabirds, manatees, and a variety of demersal and benthic fishes and invertebrates. Some counterintuitive predictions of declines (mackerel, seabirds, and surface pelagics) resulted because these groups are somewhat dependent on benthic primary production. The overall effect of the simulated bloom-associated shading of benthic primary producers resembled a trophic cascade where the number of full cycles of biomass gains and losses was approximately equal to the number of trophic levels in the system (4.7).

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1. Introduction

Benthic primary production can be a significant portion of the overall primary production in a system, but the community effects of sea floor shading by plankton blooms is underemphasized despite an early recognition of the key role of water clarity (Verwey, 1931). Eutrophication and associated reductions of light penetration has long been known to decrease the maximum depth of macrophyte colonization in lakes (Maristo, 1941; Spence, 1982). Indeed, irradiance is the principle environmental characteristic determining depth distributions of marine and freshwater macrophytes (Sears and Cooper, 1978; Chambers and Kalff, 1985) as well as their seasonal and life history characteristics (e.g. Gomez, 2001). Examples of light reduction

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impacts on marine macrophytes are becoming common (e.g. Johansson and Snoeijs, 2002; Nielsen et al., 2002; Hauxwell et al., 2003).

Irradiance is presumably as crucial for 'microphytobenthic' primary producers as it is for macrophytes (e.g. Blanchard and Montagna, 1992; Daviescolley et al., 1992). Microphytobenthos consist of photosynthetic microorganisms on the sea floor and on lake and stream bottoms including cyanobacteria, benthic diatoms, euglenoid flagellates, and dinoflagellates (which include zooxanthellae—the photosynthetic endosymbionts of anthozoans). Enrichment of marine surface waters now appears to be the main mechanism inhibiting benthic photosynthesizers in coastal systems (e.g. Tomasko and LaPointe, 1994; Hall et al., 1999; Hillman et al., 1995; Meyercordt and Meyer-Reil, 1999).

Organic enrichment has been recognized for some time as a major cause of faunal change in marine systems (Pearson and Rosenberg, 1978), but it has been recognized for much longer that the penetration of light in water controls the depth of coral reefs (Verwey, 1931). Still, whole marine ecosystems have been considered somewhat immune to enrichment by nutrients and organic material due to their large size and potential for dilution. This immunity view began to lose popular credence with cases such as Kaneohe Bay, Hawai'i, where organic pollution caused profound changes to coral and algal assemblages and the system as a whole (Banner, 1974; Laws and Redalje, 1979; Hunter and Evans, 1995). There are now many examples of adverse effects of eutrophication and shading on coral reef systems (e.g. Loya, 1976; Rogers, 1979; Walker and Ormond, 1982; Tomascik and Sander, 1985, 1987; van Woesik et al., 1999). Only recently, however, have sunlight and water transparency been labeled as cornerstones of coral research based on findings that Florida corals exist at depths near their respiration-production compensation point (Yentsch et al., 2002). This implies that small changes in water transparency might cause broad ecological changes on continental shelves.

Fundamental ecological changes triggered by enrichment-related phytoplankton blooms are now evident in large coastal systems (e.g. Johansson and Snoeijs, 2002; Rabalais et al., 2002). 'Harmful algal blooms' (HABs) are common and increasing along much of the world's coastlines, and various toxicological, economic, and ecological effects are recognized. The growing concern is underscored by the recent development of broad-based scientific assessments and research programs (e.g. Boesch et al., 1997, CENR, 2000; NRC, 2000; Anderson et al., 2002; Conley et al., 2002). One notable program—ECOHAB—is a multidisciplinary research project designed to study the ecology and oceanography of HABs (Anderson, 1995). One result of this research is the realization that aeolian subsidies of iron from Saharan dust can trigger red tide events on the West Florida Shelf by stimulating nitrogen fixation by cyanophytes (Lenes et al., 2001; Walsh and Steidinger, 2001). Concerns surrounding nutrient enrichment and HABs have focused on human health (e.g. shellfish poisoning), economic impact of fisheries losses, and toxicological impact on marine life as the toxic effects propagate through the food web. One example, given by Landsberg and Steidinger (1998), is that a large bloom of the dinoflagellate *Karenia brevis* (formerly *Gymnodinium breve*) caused the deaths of large numbers (about 10%) of the remaining endangered Florida manatees (*Trichechus manatus latirostris*) in 1996.

Benthic primary production is underemphasized in marine ecosystems because phytoplankton is the main source of primary production in the world's oceans. In coastal settings however, macrophyte primary production has been recognized as an important component of overall primary production in coastal settings (Mann, 1972; Smith, 1981; Duggins et al., 1989; Vetter, 1994, 1995; Okey, 1997, 2003; Vetter and Dayton, 1998, 1999). Recent work has demonstrated that microphytobenthos can contribute a considerable portion of overall continental shelf primary production (Colijn and de Jonge, 1984; Cahoon and Cooke, 1992; Macintyre and Cullen, 1995; MacIntyre et al., 1996; Nelson et al., 1999). High rates of marine microphytobenthic primary production have been recognized for 30 years (e.g. Bunt et al., 1972; Sournia, 1976; Hartwig, 1978).

High production of microphytobenthos occurs on tropical and subtropical shelves where overlying water is relatively clear. The rate of primary production by microphytobenthos, as well as its biomass, is strongly limited by the light reaching the sediment (Hartwig, 1978). This light limitation is expressed in nature as a declining gradient of microphytobenthos production with increasing depth off Madagascar, for example

(Plante-Cuny, 1973 in Colijn and de Jonge, 1984), but also on the West Florida Shelf (Vargo, unpublished data) where these primary producers likely occur below the 200 m depth contour. Tropical and subtropical 'clear-water' shelf systems might in fact be particularly susceptible to the impacts of pollution that causes increased shading because sea floor primary production in these shelf areas can comprise a considerable portion of overall primary production, and because declines in the water transparency of these naturally oligotrophic systems might fundamentally shift patterns of energy flow as light fades below the minimum necessary thresholds of acclimated benthic primary producers. Many corals and foraminiferans rely on symbiotic zooxanthellae (i.e. intracellular microphytobenthos) to provide them with photosynthetic energy that is integral to the production and maintenance of tropical marine habitats and biodiversity. These organisms and habitats are degraded by transparency declines related to nutrient enrichment (Hallock and Schlager, 1986; Hallock, 1987, 1988, 2000; Hallock et al., 1993).

Microphytobenthic production is known to decrease when the biomass of overshading plankton increases, even though microphytobenthos can persist at low light levels (Cahoon and Cooke, 1992; Meyercordt and Meyer-Reil, 1999). This spatial and temporal primary production compensation by microphytobenthos should distribute primary production evenly across horizontal space and time, or at least moderate its overall variability. Similar compensation patterns are now emerging in other systems (e.g. Blanchard and Montagna, 1992; Clavier and Garrigue, 1999). Both horizontal and vertical distributions of microphotosynthesizers within sub-systems undoubtedly mediate the character of secondary and higher level production. As phytoplankton increases across a shelf, microphytobenthos tends to decrease.

Many organisms living over continental shelves utilize the primary production of microphytobenthos directly (Nelson et al., 1999) or indirectly. Shading by nutrient enrichment along coastal zones can, in theory then, shift communities from assemblages that rely on benthic primary production towards those that rely on planktonic primary production. This is consistent with simulations by Blanchard and Montagna (1995), which indicated that shading by phytoplankton blooms in Baffin Bay, Texas could profoundly decrease the production rate of microphytobenthos and the abundance of the benthic macrofauna supported by them. This shift along a benthos- to plankton-based continuum could have far reaching implications for community organization and benthic–pelagic coupling since a whole suite of organisms rely directly or indirectly on microphytobenthos.

Continental shelves cover about 8% of the world's ocean area, but produce almost one quarter of the world's plankton (Pauly and Christensen, 1995). Marine macrophytes on continental shelves add an additional 5% to the oceans' primary production, and make up fully two thirds of the oceans' plant biomass, despite inhabiting about one quarter of 1% of the total area inhabited by plankton (Smith, 1981). Benthic microflora on continental shelves adds even more to oceanic primary production. Shading related shifts in the assemblages of these continental shelf primary producers and dependent biological communities are especially important to humans because, for example, fisheries are concentrated near coasts. Of even greater concern than such pollution-induced shifts is the distinct possibility that such shifts might lead to degraded systems that are stable (i.e. do not recover). Not only could eutrophication and shading lead to large changes in flora and fauna, but certain changes in fauna (i.e. removal of filter feeders) could exacerbate cultural eutrophication in marine systems (Lenihan and Peterson, 1998; Lenihan, 1999; Jackson et al., 2001). Thus, positive feedbacks between nutrient enrichment and filter feeder degradation could potentially lead to 'alternate stability domains' in these marine systems (see Scheffer et al., 2001). In addition, Smith (1981) plausibly suggested that a good portion of the 9×10^8 tonnes of carbon captured annually by marine macrophytes could be entrained in marine carbon sinks because the fate of much of this material is unused detritus. Decreases in macrophyte production resulting from increases in shading by plankton could slow the flux to such a sink, thus slowing oceanic absorption of atmospheric carbon.

1.1. *The West Florida Shelf*

The West Florida continental shelf covers over 170,000 km^2 extending more than 200 km west from the intertidal zone to the 200 m isobath across a very gentle slope of ancient limestone platforms (slope $\ll 1^\circ$). These platforms are overlain with a veneer of old carbonate sediment and more recent riverine sediment. To the north, the shelf extends to DeSoto Submarine Canyon near the Alabama–Florida border, and to the south the delineation is drawn at our transition to the Florida Keys.

The nutrient content and optical properties of West Florida Shelf waters are strongly influenced by input from the Mississippi, Mobile, Apalachicola, Suwannee, and Caloosahatchee rivers (Muller-Karger et al., 1991; Gilbes et al., 1996; Del Castillo et al., 2000). Most Gulf waters are naturally poor in nutrients except adjacent to rivers and estuaries or when river flow is high, and except for seasonal patterns of upwelling and impingement of deeper nutrient-rich water from beyond the shelf break related to Loop Current frontal eddy intrusion and other forces (Paluszkiewicz et al., 1983; Weisberg et al., 1996, 2000; Meyers et al., 2001). Enrichment by riverine, estuarine, and upwelled nutrients is episodically complemented by aeolian deposits of iron from Sahara dust as mentioned previously.

Florida Bay lies at the inner edge of the Southwest Florida Shelf. Documented recent events in the Bay provide clues to the types of changes that might be occurring on the broader shelf. Since the middle to late 1980s, Florida Bay has undergone massive die-offs of several species of seagrasses. A reasonable explanation for this die-off is that increased nutrient inputs led to shading of these plants by macroalgal epiphytes (Fong and Harwell, 1994; Lapointe et al., 1994) and blooms of phytoplankton (Tomasko and LaPointe, 1994; Boyer et al., 1999; Fourqurean and Robblee, 1999; Hall et al., 1999). Phytoplankton blooms can increase water-column temperatures by absorbing solar radiation (Tomasko and LaPointe, 1994). Changes in salinity from freshwater diversion can influence the oxygen saturation in the water column (Gunderson, 2001). Furthermore, the die-off of seagrasses can increase sediment re-suspension in settings like Florida Bay, thereby causing more shading and seagrass die-off (Hall et al., 1999). Such a positive feedback can help explain the apparent shifts in stability domains in Florida Bay, in addition to the explanations presented by Gunderson (2001). Still another explanation that might have worked in concert with such scenarios is that sea turtle depletion led to outbreaks of epiphytes and diseases that kill seagrasses because naturally high densities of sea turtles cropped seagrass blades that would otherwise become susceptible (Jackson et al., 2001).

Whatever the exact mechanisms, the ichthyofauna of Florida Bay appears to have undergone a shift from benthic species toward more planktonic-feeding species during the same period (Thayer et al., 1999), and sponges also died in parts of the area (Butler et al., 1995). Similar changes have been observed in seagrass areas of Western Australia for apparently similar reasons (Hillman et al., 1995). Livingston (2001) has described the mechanisms behind such processes in Gulf Coast estuaries.

The widespread loss of seagrasses related to shading and related factors is a very conspicuous ecological change in Florida Bay, but analogous though less conspicuous changes might have occurred in deeper zones of the West Florida Shelf. An analysis of imagery from Advanced Very High Resolution Radiometry showed that reflectance and light attenuation increased between 1985 and 1997 in an area of the shelf west of Florida Bay (Stumpf et al., 1999). The present paper combines a new exploration of trends in water transparency over the West Florida Shelf with some preliminary dynamic simulations of broader community effects of shading using an up-to-date trophic model of the West Florida Shelf (Ecopath with Ecosim). Browder (1993) called for refinement of information about the Gulf of Mexico continental shelf after presenting a pilot model of the shelf using the Ecopath approach. Her preliminary modeling exercise indicated the existence of more benthos and higher benthic production than previously thought. The present exercise can be seen as following up on this, presenting results of a more recent synthesis of West Florida Shelf ecosystem information. The general questions addressed in this study were: (1) Are there multiyear trends in water transparency over the West Florida Shelf? (2) What proportion of the overall primary production on the West Florida Shelf is made up by microphytobenthos? (3) What broad community effects might result from nutrient enrichment and phytoplankton blooms?

A general trend of increasing phytoplankton production from the early 1970s to the early 1990s in the vicinity of the West Florida Shelf emerged during a literature survey, and was consistent with data collected during the Southeast Area Monitoring and Assessment Program (SEAMAP), which showed significant increases in chlorophyll and surface turbidity during the 1980s and 1990s in a pre-chosen area of the West Florida Shelf. Benthic primary producers were estimated to make up 35% of the overall primary production and 91% of the primary producer biomass on the West Florida Shelf, with microphytobenthos making up 10 and 11% of the respective totals (though the biomass and production of macroalgae might be underestimated in this analysis). The preliminary simulations indicated that broad community effects should be expected from a mechanism that decreases benthic primary production, such as shading by phytoplankton blooms.

2. Methods

This investigation consisted of two components: (1) exploration of trends in water transparency over the West Florida Shelf, and (2) simulations of community-wide effects of seafloor shading by phytoplankton blooms using a recently constructed balanced trophic model of the West Florida Shelf.

2.1. Trends in water transparency

Changes in water transparency were investigated with two approaches. The first was a review of phytoplankton production estimates from the vicinity of the West Florida Shelf. The second approach was to examine trends in water quality parameters in the SEAMAP data for a chosen portion of the West Florida Shelf. The examined area extends between 24 and 26°N and between 83 and 85°W, and is located just to the northwest of the Dry Tortugas. It was named the 'Hemingway Quadrant,' and was chosen because it encompassed an area of the seafloor covered by living coralline algal nodules (e.g. *Peyssonnelia rubra* and *Peyssonnelia simulans*; Phillips and Thompson, 1990) that can be used in the future as a proxy to document changes in shelf photosynthetic communities. The water quality data within this area were extracted from SEAMAP ichthyoplankton survey data collected during cruises in the Gulf of Mexico by the Florida Fish and Wildlife Conservation Commission (data held by C. Meyer and B. Mahmoudi, Florida Marine Research Institute, St. Petersburg). Temporal trends of chlorophyll at three depths, turbidity at three depths, and Secchi depth at the surface were analyzed with simple linear regression.

2.2. Modeling tools: Ecopath with Ecosim

Ecopath trophic models describe the state of energy flows in a food web. They are designed to include all biotic components of an ecosystem, and the most typical currency is biomass wet weight (used here). Polovina (1984) developed Ecopath to study coral reefs at French Frigate Shoals. A variety of dynamic capabilities have since been added (e.g. Christensen and Pauly, 1992; Walters et al., 1997, 1999; Christensen et al., 2000; Pauly et al., 2000). Scores of applications of Ecopath with Ecosim can be found at: http://www.ecopath.org/, along with the freely distributed software and documentation. Although the formulations and basic concepts are accessible in these venues, we summarize the general approach here.

The Ecopath master equation (Eq. (1)) expresses the law of conservation of mass or energy and indicates the basic parameters needed. This equation balances a group's net production (terms to the left of the equal sign) with all sources of mortality impacting on that group (terms to the right). More specifically, it states that the net production of a functional group equals the sum of (1) the total mass (or energy) removed by predators and fisheries, (2) the net biomass accumulation of the group, (3) the net migration of the group's biomass, and (4) the mass flowing to detritus.

$$B_i\left(\frac{P}{B}\right)_i \mathrm{EE}_i = Y_i + \sum B_j\left(\frac{Q}{B}\right)_j \mathrm{DC}_{ji} + \mathrm{BA}_i + \mathrm{NM}_i \qquad (1)$$

where, B_i and B_j are biomasses of prey (i) and predators (j), respectively; $(P/B)_i$ is the production/biomass ratio, equivalent to total mortality (Z) in most circumstances (Allen, 1971); EE_i is the ecotrophic efficiency; the fraction of the total production of a group that is utilized in the system; Y_i is the fisheries catch per unit area and time (i.e. $Y = F \times B$); $(Q/B)_j$ is the food consumption per unit biomass of j; and DC_{ji} is the contribution of i to the diet of j; BA_i is the biomass accumulation of i (positive or negative); NM_i is the net migration of I (emigration less immigration).

The thermodynamic constraints implied by Eq. (1) underscore the power of Ecopath models as a focal point for refinement of ecosystem information. The need to reconcile energy production and demand among components of the food web narrows the possible ranges of parameter estimates for particular groups. Inclusion of a biomass accumulation factor and migration factor in the general Ecopath algorithm distinguishes Ecopath modeling as an ‘energy continuity’ approach rather than a strictly ‘steady-state’ approach. Conservation of energy (*continuity*) is assumed for every identified component of the ecosystem, and the whole system. This basic constraint enables representation of changes in populations (i.e. functional groups) when expressed in dynamic form.

Ecopath was rendered even more useful by the dynamic simulation routines Ecosim and Ecospace (see Walters et al., 1997, 1999, 2000; Pauly et al., 2000). In Ecosim, information in a ‘snapshot’ Ecopath model is re-expressed in a dynamic formulation, viz.

$$\frac{\mathrm{dB}_i}{\mathrm{d}t} = f(B_i) - MB_i - F_i B_i - \sum_{j=1}^{n} c_{ij}(B_i B_j) \qquad (2)$$

where, $f(B_i)$ is a function of B_i if i is a primary producer or $f(B_i) = g_i \sum c_{ji}(B_i B_j)$ if i is a consumer, where g_i is the net growth efficiency, and $c_{ij}(B_i B_j)$ is the function used to predict consumption rates from B_i to B_j. Ecosim uses a function for c_{ij} derived from assuming possible spatial/behavioral limitations in predation rates (Walters et al., 1997). Prey vulnerabilities can be specified by essentially adjusting the proportion of prey in vulnerable and invulnerable states (pools). This simulates different types of trophic control (Lotka–Volterra type versus donor type control) as mediated by temporal or spatial refugia in a system or by the strength of physical organizing forces relative to trophic forces.

2.3. The West Florida Shelf model

The Ecopath model of the West Florida Shelf was constructed at the Florida Marine Research Institute during 2000 as an initiative by the Florida Fish and Wildlife Conservation Commission to synthesize existing ecosystem information in a format that would allow simulations of ecosystem dynamics related to living resource management along the Gulf coast of Florida (Mahmoudi et al., 2002). This model was constructed by combining extensive literature reviews of local, regional, and global information with a coordinated collaboration of marine scientists with expertise in West Florida Shelf biota. The basic parameters for the 59 functional groups in the West Florida Shelf Ecopath model are shown in Table 1. Diet compositions and full documentation of sources for all parameter estimates are available from the Florida Marine Research Institute (Okey and Mahmoudi, 2002).

2.4. Simulations

Seven scenarios were developed to investigate community-wide effects of shading interference of benthic primary producers by phytoplankton blooms:

1. Shade microphytobenthos
2. Shade macroalgae
3. Shade seagrasses
4. Shade all three benthic primary producer groups
5. Shade all three and include prey protection effects of biogenic structure
6. Shade all three and include enrichment of phytoplankton production
7. Shade all three; include refuge effects; include phytoplankton enrichment

Shading mortality was evenly increased from 0 to 50% of the production rate (P/B) for each of the three benthic producer groups between 2.5 and 10 years after the beginning of 30-year simulations. Scenario 5 added refuge effects of biogenic structure to the simulated shading of all three benthic primary producers. Seagrasses, macroalgae, drifting macrophytes, and sessile epibenthos benefit many prey organisms through refuge effects. Small fishes, for example, are less vulnerable to predators when they associate with this biogenic habitat structure, which is why they are found in higher abundances in such refugia (Holmquist, 1994; Levin and Hay, 1996). Ecosim allows specification of such a protective ‘mediation,’ such that prey organisms become more vulnerable to predators when their protective biogenic habitat declines. This is achieved by modifying the relationships within Ecosim’s algorithm by choosing or sketching a ‘shape’ of the relationship in the mediation interface representing how specified groups are impacted by changes in the biomass of a ‘mediating’ group. This protective effect was specified to be qualitatively equal for the four biogenic structures listed above, and was

Table 1
Basic parameters of the Ecopath model of the West Florida continental shelf

Group name	Trophic level	OI	Biomass (tonnes km^{-2})	*P*/*B* (per year)	Q/B (per year)	EE
Large oceanic piscivores	**4.7**	**0.313**	0.070	0.680	7.400	**0.845**
Pelagic oceanic piscivores	**4.5**	**0.266**	0.150	1.057	8.500	**0.829**
Dolphins	**4.4**	**0.283**	0.038	0.099	40.439	**0.082**
Coastal sharks	**4.3**	**0.732**	0.090	0.410	3.290	**0.909**
Large groupers	**4.3**	**0.252**	0.119	0.458	4.103	**0.880**
Pelagic coastal piscivores	**4.3**	**0.240**	0.230	0.640	10.230	**0.972**
Benthic oceanic piscivores	**4.2**	**0.331**	0.045	0.450	7.940	**0.961**
Mackerel (adult)	**4.2**	**0.097**	0.183	0.384	8.000	**0.938**
Mackerel (juvenile)	**4.2**	**0.051**	0.126	0.769	9.000	**0.970**
Nearshore-associated piscivores	**4.2**	**0.263**	**0.013**	1.057	7.670	**0.900**
Seabirds	**4.2**	**0.289**	0.001	0.100	80.000	**0.000**
Pelagic oceanic jelly eaters	**4.1**	**0.045**	2.200	1.560	8.071	**0.674**
Structure-associated coastal piscivores	**4.1**	**0.271**	0.220	0.630	5.400	**0.736**
Benthic coastal piscivores	**4.0**	**0.304**	0.245	0.550	8.386	**0.938**
Demersal coastal piscivores	**4.0**	**0.903**	0.120	0.642	6.334	**0.977**
Squid	**3.8**	**0.184**	1.100	3.000	35.000	**0.987**
Large oceanic planktivores	**3.7**	**0.305**	**0.043**	0.110	1.800	0.500
Rays and skates	**3.7**	**0.340**	0.238	0.380	7.720	**0.651**
Octopods	**3.6**	**0.400**	**0.074**	3.100	11.700	0.950
Benthic coastal invertebrate eaters	**3.5**	**0.129**	0.860	0.860	10.110	**0.991**
Benthic oceanic invertebrate eaters	**3.5**	**0.203**	0.190	1.200	15.780	**0.988**
Demersal coastal invertebrate eaters	**3.5**	**0.223**	1.400	0.654	7.920	**0.999**
Structure-associated coastal invertebrate eaters	**3.5**	**0.169**	1.200	0.748	7.330	**1.000**
Structure-associated coastal planktovores	**3.5**	**0.081**	0.050	2.000	10.000	**0.851**
Carnivorous jellyfish	**3.4**	**0.091**	0.265	40.000	80.000	**0.928**
Demersal oceanic invertebrate eaters	**3.4**	**0.069**	0.045	1.200	15.760	**0.971**
Lobsters	**3.4**	**0.246**	0.028	0.900	8.200	**0.858**
Other fishes	**3.4**	**0.225**	3.870	1.300	7.040	**0.950**
Pelagic oceanic planktivores	**3.4**	**0.509**	1.500	0.872	11.710	**0.949**
Stomatopods	**3.3**	**0.469**	0.994	1.335	7.432	**0.414**
Turtles	**3.3**	**0.639**	0.007	0.192	3.500	**0.417**
Nearshore planktivores	**3.2**	**0.262**	**2.215**	2.000	15.920	0.990
Large crabs	**3.1**	**0.189**	**0.705**	2.800	8.500	0.990
Sardine and herring	**3.1**	**0.471**	2.400	1.050	12.106	**1.000**
Carnivorous zooplankton	**3.0**	**0.171**	21.600	8.700	20.000	**0.250**
Adult shrimps	**2.9**	**0.443**	0.550	5.380	19.200	**0.987**
Demersal coastal omnivores	**2.9**	**0.490**	0.700	1.340	15.130	**0.784**
Ichthyoplankton	**2.9**	**0.427**	0.048	50.448	132.130	**0.748**
Surface pelagics	**2.9**	**0.859**	**0.099**	2.600	11.700	0.950
Other mesozooplankton	**2.6**	**0.277**	6.700	17.300	50.000	**0.851**
Structure assoc. coastal omnivores	**2.5**	**0.466**	**0.312**	1.329	24.370	0.980
Echinoderms	**2.4**	**0.347**	19.246	1.200	3.700	**0.277**
Meiofauna	**2.4**	**0.236**	13.000	12.500	25.000	**0.822**
Sessile epibenthos	**2.4**	**0.273**	219.000	0.800	9.000	**0.236**
Small mobile epifauna	**2.4**	**0.284**	**12.614**	7.010	27.140	0.950
Small infauna	**2.3**	**0.273**	19.032	4.600	15.900	**0.401**
Small copepods	**2.2**	**0.133**	8.300	17.300	50.000	**0.939**
Bivalves	**2.1**	**0.106**	48.596	1.209	23.000	**0.168**
Mullets	**2.1**	**0.101**	0.329	0.701	11.030	**0.512**
Manatees	**2.0**	**0.000**	0.001	0.100	36.500	**0.000**
Microbial heterotrophs	**2.0**	**0.000**	60.000	100.000	215.000	**0.235**
Dead carcasses	**1.0**	**0.421**	1.000	–	–	**0.906**

Table 1 (*Continued*)

Group name	Trophic level	OI	Biomass (tonnes km^{-2})	*P*/*B* (per year)	Q/B (per year)	EE
Drift macrophytes	**1.0**	**0.000**	2.659	–	–	**0.324**
Macroalgae	**1.0**	**0.000**	36.050	4.000	–	**0.396**
Microphytobenthos	**1.0**	**0.000**	29.778	23.725	–	**0.623**
Phytoplankton	**1.0**	**0.000**	25.000	182.130	–	**0.304**
Seagrasses	**1.0**	**0.000**	175.617	9.014	–	**0.017**
Sediment detritus	**1.0**	**0.274**	390.000	–	–	**0.884**
Watercolumn detritus	**1.0**	**0.347**	125.000	–	–	**0.910**

OI is the omnivory index, which is the variance of prey trophic levels; *P*/*B* and *Q*/*B* are the ratios of production (*P*) and consumption (*Q*) to biomass; EE is the ecotrophic efficiency, or the proportion of production consumed by predators or exported. Values in bold have been calculated by the Ecopath algorithm; other values are empirically based inputs, or values that were adjusted from empirically based values during balancing. An electronic file of the diet composition matrix is available from the corresponding author. Documentation of the derivations of these estimates is available in Okey and Mahmoudi (2002).

applied to predator–prey interactions for a variety of demersal and structure-associated fishes and other organisms in the system. This relationship was specified with a negative sigmoid function that was automatically scaled relative to Ecopath baseline inputs (see Christensen et al., 2000). Scenario 6 combines simulated shading of the three benthic primary producers with concomitant increases in surface phytoplankton at the approximate rate indicated by revealed trends in SEAMAP data (discussed later). Scenario 7 resembles bloom-related shading best in that it combines overall shading with both refuge effects (loss of refuge) and phytoplankton enhancement. The system-wide prey vulnerability setting for all scenarios was 0.4, representing a mix of Lotka–Volterra versus donor type control, or top down versus bottom up control.

3. Results

The literature review of phytoplankton production indicated general increases in the vicinity of the West Florida Shelf between the early 1970s and the early 1990s (Fig. 1). Consistent with this trend was significant increases in surface and middle-depth chlorophyll and surface turbidity in SEAMAP samples from

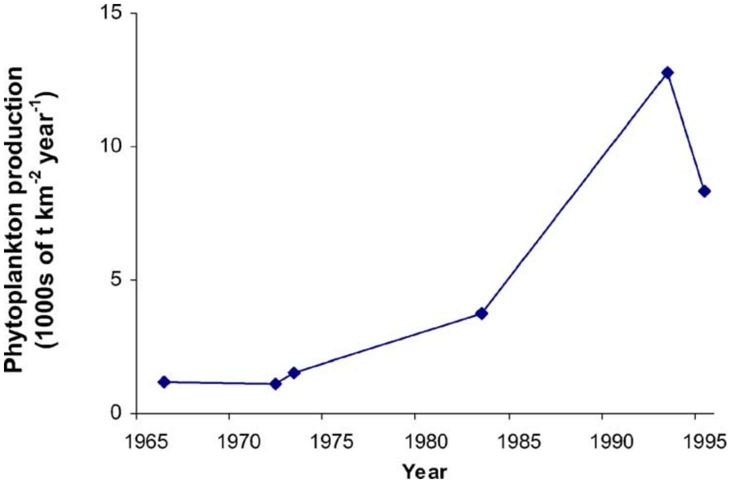

Fig. 1. Changes in estimates of phytoplankton production from 1966 until 1995 (from Kondratyeva and Sosa, 1966 in Vargo and Hopkins, 1990; El-Sayed, 1972; Steidinger, 1973 in Vargo and Hopkins, 1990; Yoder and Mahood, 1983 in Vargo and Meyers, 1991, Vargo, unpublished data in 1993, Brian Bendis, Florida Fish and Wildlife Conservation Commission, unpublished data from 1994 to 1996).

Table 2
Results of regressions of water column measurements against time in the Hemingway Quadrant of the West Florida Shelf

Water-column depths	Intercept *a*	Slope *b* ± *s.e.*	*n*	R^2	*P*
Chlorophyll					
Surface	−66	0.03 ± 0.01	210	0.05	0.001
Middle	−517	0.26 ± 0.11	33	0.16	0.02
Maximum	−34	0.02 ± 0.04	34	0.01	0.65
Turbidity					
Surface	−4663	2.37 ± 1.16	93	0.04	0.04
Middle	2572	−1.25 ± 1.28	93	0.01	0.33
Maximum	2181	−1.06 ± 1.34	93	0.01	0.43
Clarity (Secchi depth)					
Surface	395	−0.19 ± 0.15	89	0.018	0.208

the ‘Hemingway Quadrant’ (Table 2). These chlorophyll data spanned from the early 1980s to the late 1990s, data on the surface turbidity (the capacity of suspended particles in water to scatter light) spanned from 1993 to 1999; and data indicating the trend of declining clarity (Secchi depths) spanned from 1983 to 1997.

Benthic primary producers were estimated to comprise 35% of the overall primary production on the West Florida Shelf, with microphytobenthos accounting for 10%, macroalgae 2%, and seagrasses 23%, based on a literature review by Okey (2002). In contrast, benthic primary producers make up an estimated 91% of the shelf’s overall primary producer biomass, with microphytobenthos accounting for 11%, macroalgae 14%, and seagrasses 66% (Table 3). The distribution of flows at each trophic level is shown in Table 4.

Table 3
Estimated production and biomass of the four primary producers in the West Florida Shelf ecosystem[a]

Primary producer	Production (tonnes km^{-2} per year)	Biomass (tonnes km^{-2})
Phytoplankton	4553[b]	25.0[c]
Microphytobenthos	706	29.8
Macroalgae	144[d]	36.1[d]
Seagrasses	1583	175.6

[a] Estimates were chosen or derived based on a literature review by Okey (2002). Sources are indicated when chosen from a range of estimates, not derived.
[b] Steidinger (1973) and Tomas (1995).
[c] Steidinger (1973).
[d] Likely an underestimate for WFS.

The biomass of almost all functional groups in the system were predicted to decline when shading mortality on benthic primary producers was simulated without including concomitant refuge effects of biogenic structure or enhancement of phytoplankton (Fig. 2; the specified shading mortality of half the P/B values resulted in an approximate 50% reduction in the biomass of each or all of the benthic primary producers). Of the 55 living groups in the model, only phytoplankton, small copepods, ichthyoplankton, and carnivorous jellyfish never declined as the result of the specified simple seafloor shading mortalities. These were the only groups in the model whose food sources originated entirely with phytoplankton (and detritus).

Declines were generally more severe when refuge effects of benthic groups (biogenic habitat structure) were specified using the ‘mediation’ function

Table 4
Flows from primary production and detritus (tonnes km^{-2} per year)

Trophic level	From primary production				From detritus			
	Consumed	To detritus	Respiration	Throughput	Consumed	To detritus	Respiration	Throughput
VI	0	0	0	0	0	1	1	2
V	0	1	3	5	2	8	12	22
IV	5	15	18	38	22	91	71	184
III	38	138	83	259	184	952	393	1529
II	259	1109	540	1909	1529	8169	4854	14552
I	1907	5080	0	6987	14551	0	0	17164
Sum	2209	6344	645	9198	16289	9220	5332	33454

System imports and exports are not shown. Some flows reach trophic level six because some organisms within some functional groups are supported by energy that has traversed five links from primary producers.

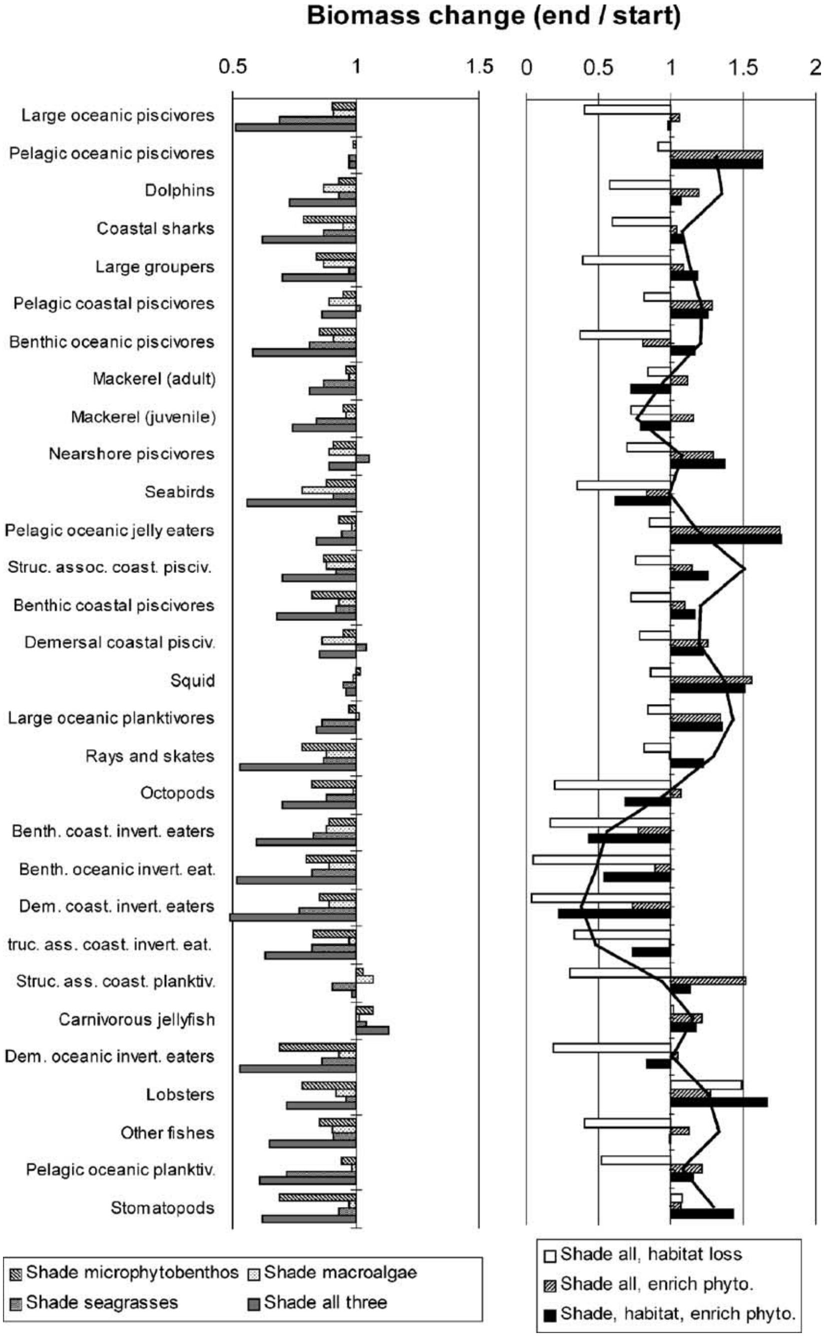

Fig. 2. Predicted biomass changes (proportional change relative to starting baseline) after the 30-year simulations for the 59 functional groups in the West Florida continental shelf ecosystem. Groups are organized by descending trophic level (from 4.7 to 1). The left panel shows the results of simulated shading of the three benthic primary producers (shading mortality equal to half the production rate). The right panel shows shading simulations with the refuge effect from biogenic habitat structure, with a concomitant enrichment of phytoplankton, and with all effects. The black line is a moving average (second period) of the predicted changes from these combined effects; it is added simply to show the general trend in the direction of biomass change at different trophic levels.

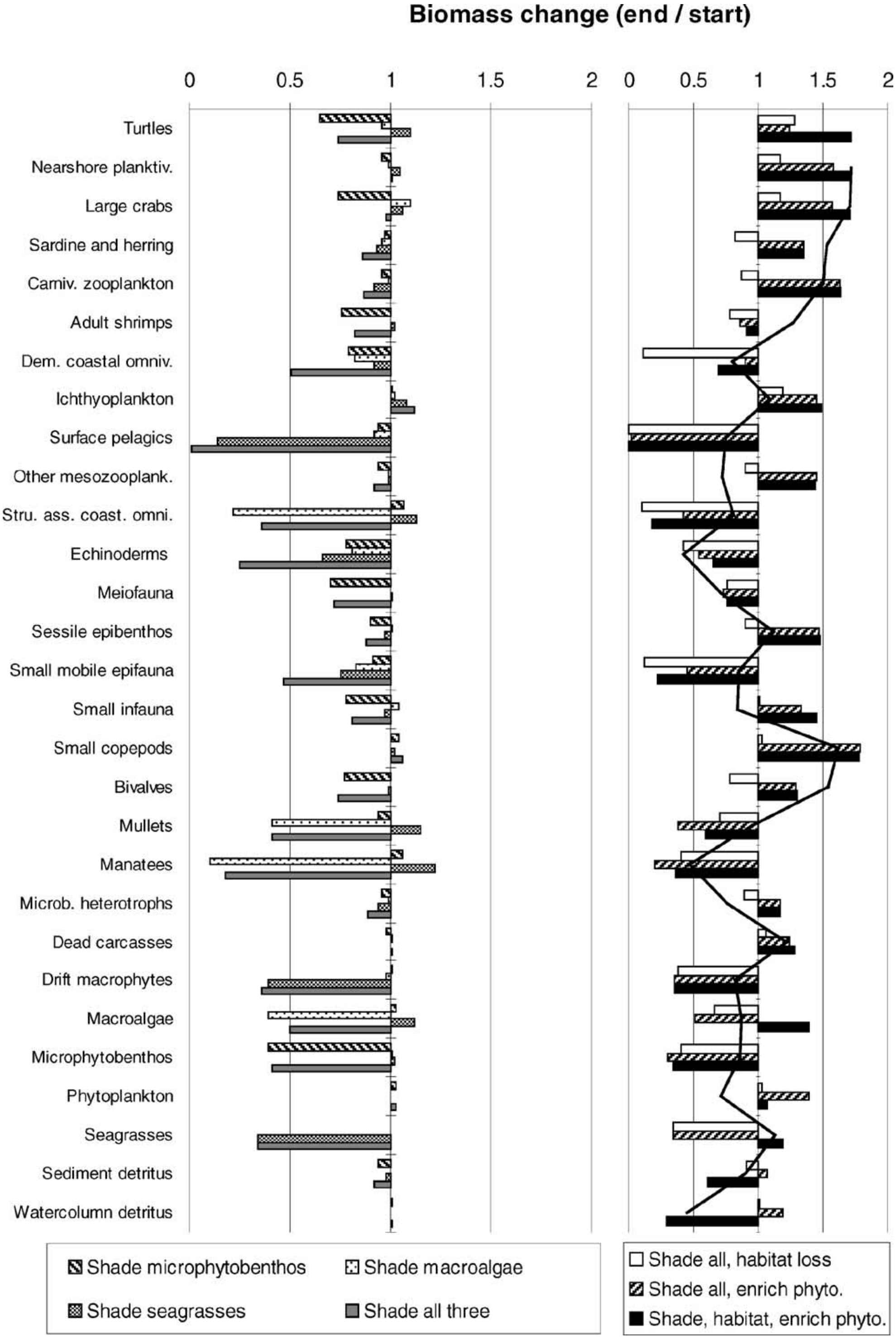

Fig. 2. (*Continued*).

in Ecosim. Most groups declined more as the now 'habitat-providing' benthic primary producers declined. This occurred whether or not a species directly benefited from these habitat structures. Five groups, however, increased as the habitat-providing benthic primary producers declined. These were lobsters, large crabs, stomatopods, nearshore planktivores, and turtles, all clustered between trophic levels 3.1 and 3.4. The addition of simulated phytoplankton enrichment to the shading and habitat scenarios led to predicted increases in groups that obtain most of their energy from phytoplankton pathways and decreases in groups that obtain most of their energy from benthic primary production. The direction of effects alternated regularly as they propagated to higher trophic levels. The number of full cycles of alternating effects appears to match the number of trophic levels in the system (4.7 trophic levels) (Fig. 2).

4. Discussion

4.1. The mechanism of community change via shading

The separate articulation of four primary producer groups in the West Florida Shelf Ecopath model (out of 59 functional groups) enabled exploration of the potential community effects of long-term declines of water-column transparency in this historically clear-water system. Three of these primary producers are benthic and one is pelagic (i.e. phytoplankton). The main assumption of this investigation is that benthic primary production by microphytobenthos, macrophytes, and seagrasses would decrease over this continental shelf as the result of shading by phytoplankton blooms. This assumption is supported by several empirical studies in marine and freshwater settings (e.g. Maristo, 1941; Spence, 1982; Meyercordt and Meyer-Reil, 1999; Nelson et al., 1999). Broad community changes result from sea floor shading because a considerable proportion of the energy used by species throughout the system originates with benthic primary production. Changes propagate through the system when benthic primary production is decreased not only because of the degradation of food pathways, but also because of shifts in the character and distribution of food production. The main prediction was that changes in primary production patterns and other changes related to shading (e.g. detritus deposition and DO declines) would shift the continental shelf community to a different assemblage with a proportionally greater reliance on water-column primary production and detritus deposition, and less of a reliance on benthic primary production and refuge value provided by associated biogenic structure. The modeling simulations were generally consistent with this prediction.

The West Florida Shelf is unique among continental shelves of North America. Historical water clarity has been so high that attached macroalgae in the region have been observed and collected at depths beyond the 200 m shelf break (Sylvia Earle, personal communication with Humm, 1973; also see Littler et al., 1985). More recent data suggest that enough light reaches 75 m depths to enable substantial photosynthesis of West Florida Shelf benthic microflora. Tomas (1995) pointed out that conventionally measured estimates of overall primary production should be considerably higher to account for the benthic microflora whose contributions are likely profound, though not well known, on the West Florida Shelf. The present Ecopath model is among the first to account for recent high estimates of benthic microalgae in nearshore marine systems, and this could partially explain the high overall primary production estimation (6987 tonnes ww km^{-2} per year) relative to previous estimates from the region when less information about benthic primary production was included (2619 tonnes ww km^{-2} per year from Browder, 1993 using conversions provided by Durbin and Durbin, 1998 and Parsons et al., 1977). The inclusion of this previously underestimated component of primary production helps resolve a long-standing dilemma typically encountered while attempting to balance whole food web models—the apparent lack of adequate energy to support higher trophic levels. The estimate for overall primary production for the West Florida Shelf model is merely 2.7% lower than the estimate for phytoplankton primary production in the Mississippi delta bight (7182 tonnes ww km^{-2} per year; from Sklar, 1976 using above conversion sources). Primary production is virtually equal in these two systems if phytoplankton in the Mississippi delta bight completely inhibits benthic primary production.

4.2. Indicated community changes

The most conspicuous pattern revealed in this series of simulations is a shift in community composition away from organisms that obtain most of their energy from benthic primary production pathways, and towards organisms that obtain most of their energy from planktonic primary production. This pattern is best revealed by examining the direction of change of particular species during the final simulation, which combines shading mortality, biogenic habitat structure effects, and enhancement of plankton production (Fig. 2, right panel). Also, the general match between the number of trophic levels represented in this food web and the full cycles of alternation in the direction of biomass change in the final simulation is reminiscent of the known alternating effects of trophic cascades in freshwater food chains (e.g. Carpenter, 1988; Power, 1990; Wootton and Power, 1993; Carpenter and Kitchell, 1996) and marine systems (e.g. Paine, 1966; Estes and Palmisano, 1974; Estes et al., 1974; Estes and Duggins, 1995; Steinberg et al., 1995). If this pattern reflects a true trophic cascade, it is a donor-controlled cascade in a complex aquatic food web, and is thus only partially consistent with Strong's (1992) premise that most true cascades are aquatic and donor controlled and that cascades occur only in simple systems.

The simulations that specified shading mortality of benthic primary producers without concomitant increases in phytoplankton and without refuge effects of biogenic structure were valuable because they indicated the relative support provided by benthic primary producers throughout the system (Fig. 2, left panel). These simulations indicated that 51 of 55 living groups (or 93% of living groups) in the West Florida Shelf system depend on benthic primary producers to a considerable extent, whether directly or indirectly. The lack of a predicted biomass decline in the ichthyoplankton group could be partially explained by this pooled group's lack of specified ontogenetic linkage to the various fish groups in this model iteration. Nevertheless, fish groups usually did not decline by more than 50% during these simulations so that spawning stock would presumably be maintained.

Some nearshore forage-fish assemblages and higher trophic levels responded to simulated phytoplankton blooms and shading in unexpected ways (i.e. negatively rather than positively), but this paradox was resolved when *a posteriori* examinations of diet compositions revealed the dependence of these groups on benthic production pathways. For example, the considerable and apparently counterintuitive declines of ‘surface pelagics’ to simulated enhancement of phytoplankton and inhibition of benthic primary production is explained by the group's species composition and specified diet. Halfbeaks (*Hemirhamphidae*) and flying fishes (*Exocoetidae*) make up this group and the specified diet is 47% seagrasses, 26% small mobile epifauna, 12% nearshore planktivores, 9% other fishes, 6% small infauna, and 1% mesozooplankton (based on halfbeak diets in Randall, 1967). This implies a near exclusive reliance on benthic production, and so the direction of their response is not surprising. However, flying fish diet and biomass information were not available, and it is possible that halfbeaks occasionally consume quantities of zooplankton surpassing 1% of their diet. The indicated declines of this group would be more moderate if phytoplankton food were a larger part of its diet.

Seabirds are also specified in the Ecopath model as being somewhat reliant on benthic primary production; they consume a variety of demersal and benthic fish species in addition to plankton-dependent sardine, herring, and nearshore pelagics (Vidal-Hernandez and Nesbitt, 2002). Adult and juvenile mackerel also rely on some demersal and benthic fishes in addition to planktivorous fishes. The alternating response of both of these species to the final two simulations (Fig. 2) reveals the diverse production origins of their diets. Predicted responses of such species look surprising only when our immediate assumptions about a group's diet composition do not match with the diet composition specified in the model. In Ecosim, diet compositions do change dynamically during simulations as predators target prey at rates proportional to the prey's relative abundance. However, some level of consumption of a prey by a predator must be specified for such shifts to occur. “Apparent prey switching” by predators results from particular prey spending less time foraging (i.e. less time in the ‘vulnerable’ pool) as they become less abundant. This is complemented by predator 'satiation,' which is represented by decreases in feeding time at high prey encounter rates, and through direct handling time effects (C. Walters, personal communication, November 12, 2001).

Predictions of increased biomass in five groups after the biogenic refuge effect was added to the shading simulation were initially surprising because three of these groups were specified as direct beneficiaries of biogenic habitat protection. The five groups were large crabs, lobsters, stomatopods, nearshore planktivores, and turtles. This apparent paradox was resolved by examining changes in the predicted biomasses of their main predators. Declines in these main predators (mostly benthic and demersal fish predators) were more pronounced when the biogenic structure effect was added to the combined shading simulation. The resulting release in predation pressure on the five groups in question allowed them to increase above baseline levels despite decreases in available refugia and benthic primary production.

These opposing forces are integrated in the Ecopath model and the Ecosim simulation; the decline in predators was expressed as a relatively stronger effect than the decline in refugia (and benthic primary production). This result indicates only that these opposing forces exist. For application to lobster or crab policy development, the model should be refined to emphasize the articulation and relative strengths of protective effects of habitat and other related questions. For example, Butler et al. (1995) observed that the widespread decline of sponges in parts of Florida Bay (related to cyanobacteria blooms) had a dramatic impact on the abundance and distribution of juvenile lobsters. Splitting lobsters into ontogenetically linked functional groups would better capture the energetic dynamics of the protective effects of sponges on juvenile lobsters, and thus the whole population, but the current West Florida Shelf model contains only one lobster group because the emphasis of the current exercise is on the whole system.

Forces other than shading can, of course, shift systems from benthic to pelagic, or otherwise considerably restructure marine communities. These include fishing impacts that can preferentially remove benthic target organisms (e.g. Overholtz et al., 1999) or benthic nontarget organisms as in trawling (e.g. Jennings et al., 2001a,b; Koslow et al., 2001).

4.3. Some potential consequences of benthic–pelagic shifts in community organization

Shifts from benthic to pelagic modes of production might be occurring in coastal marine ecosystems worldwide. The example that follows helps reveal specific processes of change in coastal systems relating to changes in water-column transparency and benthic–pelagic shifts of production pathways, in this case related to fisheries interests. Two questions regarding to the dynamics of forage fishes and other middle and high trophic level groups can be addressed by examining a benthic portion of the West Florida Shelf food web (Fig. 3): (1) Does the fisheries removal of shrimps and crabs increase the number of forage fishes produced through benthic pathways, or would the habitat modifications of shrimp trawling offset such benefits? (2) Can the presence of a keystone predator, such as stomatopods, lead to more forage fish being produced through benthic pathways?

The third trophic level depicted in Fig. 3 shows the alternate pathways of benthic production through forage fishes or higher crustaceans. Flow of benthic production to forage fishes might be facilitated by the presence of stomatopods—a possible keystone predator. Intense fisheries on one of the pathways might similarly facilitate the flow of benthic production up the alternate pathway, but water quality degradation (i.e. transparency declines) could decrease the flow of benthic primary production up both pathways. However, a shift to relatively higher planktonic primary production would lead to higher detritus fallout to the benthos (not shown) thereby increasing benthic detritus pathways. Such questions can be explicitly addressed using modeling approaches such as Ecopath with Ecosim when linkages between benthic and pelagic components are adequately represented.

Notwithstanding the potential for such keystone mediation in community dynamics, seafloor shading should shift the composition of benthic communities rather than decrease the overall benthic biomass because plankton blooms should result in increased detritus deposition. Benthic primary consumers should thus shift from away from herbivory and towards detritivory. Such compensation might partially explain the high resiliency of Gulf of Mexico shrimp populations to fishing pressure (Cushing, 1984) because shrimp trawling can decrease the standing biomass

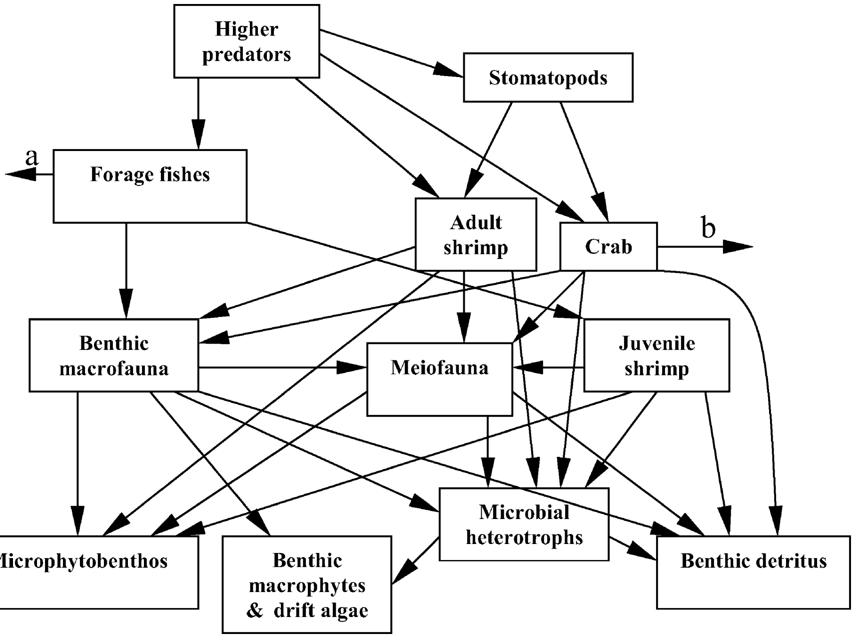

Fig. 3. Generalized predatory interactions in a simplified benthic food web of the West Florida Shelf (expanded from Walsh's example in Cushing, 1984). Arrow (a) represents fishes feeding on plankton and arrow (b) represents crabs feeding on clams, which eat detritus and phytoplankton. Other major components of the West Florida Shelf benthos have been excluded here for simplicity.

of benthic primary producers but increase the input of detritus (e.g. discards), possibly providing a feedback that promotes shrimp production, especially in situations of moderate hypoxia. Lowered dissolved oxygen would result not just from microbial decomposition of increased organic material reaching the marine sediment, but also from decreases in benthic photosynthesis. Even extreme examples of hypoxia in marine systems, such as the "dead zone" associated with Mississippi River inputs (e.g. Malakoff, 1998), might have resulted, in part, from the loss of benthic photosynthesis related to sea floor shading.

4.4. Sources of underestimation of shading effects

The West Florida Shelf contains considerable areas of hard substrate on which benthic macroalgae can attach and grow (hard bottom is ∼35% of the total shelf area; Phillips et al., 1990; Phillips and Thompson, 1990). Some evidence suggests that the biomass and production of macroalgae on the West Florida Shelf as a whole are higher than the conservative estimates used in this analysis (Table 3). For example, Phillips and Thompson (1990) indirectly imply that the macroalgal biomass on the overall West Florida Shelf is 45% higher than the value used here. Zieman et al. (1999) estimated that macroalgae biomass was equal to 118 tonnes km^{-2} in Florida Bay, an area of high macroalgal biomass that does not necessarily represent this shelf as a whole. Information on macroalgae of the West Florida Shelf stands out as the most uncertain among other primary producers (notwithstanding work by Earle, 1972), and underestimation of its biomass and production in this analysis would underestimate the effects of shading. Furthermore, Luning's (1990) ratio of production to biomass (P/B) that was used for macroalgae (4 per year) might be conservative.

One of the authors (Vargo) used extinction coefficients, irradiance, and the Blanchard and Montagna (1995) model to derive Pmax and alpha values that were used in a simple hyperbolic model to calculate benthic productivity. This was multiplied by the measured benthic chlorophyll to derive a benthic production rate of 180 g C m^{-2} per year (∼4860 tonnes ww km^{-2} per year) after averaging over all depth ranges examined on the shelf. This benthic production rate is equivalent to the average water-column production rates of 165 g C m^{-2} per year (∼4455 tonnes ww km^{-2} per year) in Vargo and Meyers (1991), 150 g C m^{-2} per year (∼ 4050 tonnes ww km^{-2} per year) in Yoder and Mahood (1983), and the low end of the range for a 1-month long red tide (∼183 g C m^{-2} per year in Vargo et al., 1987; ∼4941 tonnes ww km^{-2} per year). The implication that benthic primary production could be approximately equivalent to water-column primary production on the West Florida Shelf is in line with other recent studies (Cahoon and Cooke, 1992; MacIntyre et al., 1996; Miller et al., 1996) and indicates that the current analysis could greatly underestimate the impacts of shading. Sediment chlorophyll alone has been shown to exceed water-column chlorophyll considerably in some settings (Cahoon et al., 1990; Nelson et al., 1999).

4.5. *Is it really happening?*

The trend of increasing phytoplankton production in Fig. 1 might simply reflect an evolution of detectability from 1965 until the early 1990s, or it might reflect a chance sequence related to differences in sampling areas throughout the region. Alternatively, it could indicate widespread ecological changes on the West Florida Shelf that have gone unnoticed. El-Sayed's (1972) measurements were made close to the shelf break in more oligotrophic waters than the later 'mid-shelf' samples, which could have been more influenced by riverine enrichment (Gilbes et al., 1996; Del Castillo et al., 2000). Such measurements should only be compared for similar water types (Vargo and Meyers, 1991). Even when considering these sources of error, the El-Sayed (1972) estimate is still low relative to current measurements. The trends in Table 2 support the notion that water-column transparency has been declining and that those declines have been caused by phytoplankton blooms in surface waters. These trends result from aggregation of sampling locations that shifted spatially among sampling dates throughout the Hemingway Quadrant (e.g. it is possible that a 'temporal' trend might simply represent spatial differences within the area because sites were not re-visited). However, sampling bias was minimized by the systematic sampling design, the large number of samples, and the effectively haphazard placement of the Hemingway Quadrant, which is equivalent to random placement when one cannot 'see' the system being sampled (Fager, 1968).

Phytoplankton production rates per unit area are very high in the region's estuaries where nutrients are more concentrated. Livingston (1984) found that phytoplankton productivity of the Apalachicola Bay estuary system during the 1970s and 1980s ranged from 63 to 1694 mg C m^{-2} day^{-1}. Eastbrook (1973 in Livingston, 1984) estimated the annual phytoplankton production of the Apalachicola estuary to be 371 g C m^{-2}, which is equivalent to 15,426 tonnes km^{-2} per year. Thus, phytoplankton production for the region's estuaries can be over three times higher than the phytoplankton production (per unit area) for the overall West Florida Shelf. Increases in nutrients in the waters of the greater shelf can only increase the efficacy of the shading effect explored here.

The broad shifts in benthic primary producers and the organisms they support might indeed be occurring on the West Florida Shelf, given the order-of-magnitude increases in terrestrial-origin nutrient loads in nearshore waters during the last two decades (Paul Carlson, Florida Marine Research Institute, personal communication, 2000). A community shift from distinctly benthic-based production to one characterized by more pelagic primary production occurred in Florida Bay during the early 1990s (Hall et al., 1999; Zieman et al., 1999) when turbidity increased dramatically (Boyer et al., 1999). The results of the present analysis of the broader West Florida Shelf are consistent with these empirical findings.

The ecology of the West Florida Shelf might well hinge on basic water quality, since decreases in transparency could shift the predominant energy flow pathways along a benthic to pelagic (sea floor to water column) continuum (e.g. Thayer et al., 1999). Such a change in water quality might also shift and compress low-light-adapted photosynthetic organisms into shallower zones (in cases where appropriate substrate is available).

Sears and Cooper (1978) recognized the potential importance of shading on continental shelf communities when they suggested that observed changes in the extinction depth of benthic macroalgal assemblages could be used as a bioassay for evaluating water conditions. The West Florida Shelf provides a good opportunity for applying this methodology because a unique 'deep-water' (70–100 m depth) algal nodule habitat was documented using geo-referenced video and photographs during MMS surveys during the mid-1980s (ESE et al., 1987). The question of whether microphytobenthos production or benthic primary production in general has declined over the West Florida Shelf during the last 20 years could be indirectly addressed by choosing such a measurable proxy, based on Littler et al.'s (1991) and Steller and Foster's (1995) descriptions of algal nodule habitats and their potential uses for exploration of long-term ecological changes.

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