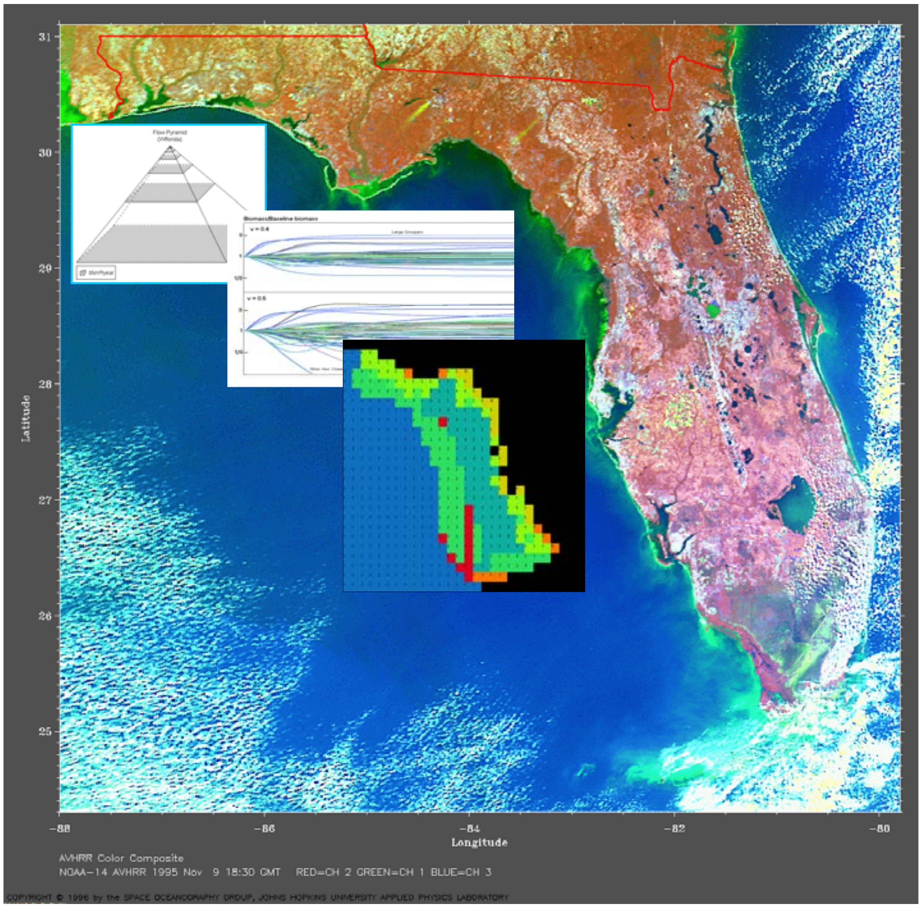
An Ecosystem model of the West Florida Shelf for use in Fisheries Management and Ecological Research:

Volume II. Model Construction



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An Ecosystem Model of the West Florida Shelf for use in Fisheries Management and Ecological Research:

Volume II. Model Construction

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Preface

In 1999, the Florida State Legislature provided funds to the Florida Fish and Wildlife Conservation Commission / Florida Marine Research Institute (FWC/FMRI) to conduct research on the role of forage fish populations in Florida's coastal marine ecosystem, and to assess the health of these populations. Sardine and herring, conspicuous forage fishes of the West Florida Shelf, support a number of Florida's commercial and recreational fisheries either directly or indirectly. Such 'bait fish' play a critical role in the coastal ecosystem by linking apex predators with plankton production. For example, changes in the abundance of the sardine/herring complex should cause subsequent changes throughout the biological community across the West Forida Shelf. The trophic modelling approaches described in this volume, and the companion volume, were employed to provide a quantifyable method to investigate the roles and health of these types of forage fishes, as well as to investigate and address other pressing ecological dilemmas. The methodologies described herein represent the first real steps towards an ecosystem-based approach to managing and protecting Florida's marine resources. Such an ecosystem-based approach is necessary to enable the most broad and risk-averse uses of Florida's living marine resources.

Scientists and managers from the FWC/FMRI Division of Marine Fisheries, and scientists from other institutions, reviewed several modelling techniques during a two-day workshop held in November 1999 in St. Petersburg. *Ecopath/Ecosim/Ecospace* modelling techniques emerged as the most useful approach given the available data and questions. Researchers from the University of British Columbia's Fisheries Centre worked with scientists from the Florida Fish and Wildlife Conservation Commission / Florida Marine Research Institute (FWC/FMRI), the University of South Florida, the National Marine Fisheries Service (NMFS, SEFC), and other institutions to construct the present trophic model of the West Florida Shelf. The electronic version of the model is available from the FMRI to any interested parties. The EwE software can be freely downloaded from www.*Ecopath*.org.

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Summary

This volume documents the derivation of input parameters for the construction of a mass-balanced food web model of the West Florida Shelf. A broad collaboration of experts on the marine biota of the region used a broad literature and information base to derive input parameters and construct this model using trophic modelling approach *Ecopath with Ecosim* (EwE). The resulting model is an integrated, whole-system view of the West Florida Shelf biological community during the late 1990s. This model was made exceptionally transparent by the easy-to-use ‘windows-based’ EwE software, and the present document. The model was constructed to complement current research in the region with cutting-edge food web analysis and dynamic simulation techniques to address pressing ecological and fisheries dilemmas. It holds considerable potential for education, in addition to its uses in scientific research, management, and policymaking. The companion volume (Mahmoudi et al. 2002) presents examples of dynamic simulation analyses supported by the model documented here.

Literature Cited (Summary)

Mahmoudi, B., Mackinson, S., Vasconcellos, M., Vidal-Hernandez, L., Okey, T.A., 2002. An ecosystem model of the West Florida Shelf for use in fisheries management and ecological research: Volume I: summary and analyses. Florida Marine Research Institute-Fish and Wildlife Conservation Commission, St. Petersburg, 39p.

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1. The *Ecopath* approach

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1.1 WHAT IS *ECOPATH*?

An *Ecopath* model is a quantitative description of biomass flows in a food web (i.e., energy flows). These computer models are constructed by defining a model area and time, organizing species (and detritus) into convienient functional groupings, and estimating the biological (i.e., energy) characteristics of each grouping. *Ecopath* models and their defined components are then 'balanced' in terms of mass or energy to gain insights into ecosystem and its biotic components, and to obtain a whole-system view of the biological community. The *Ecopath* mass-balance approach was initially developed by Polovina (1984). Since that initial application, over 100 *Ecopath* models have been constructed, mostly in marine ecosystems, and the approach has been refined considerably (see http://www.*Ecopath*.org).

Ecopath models can be analyzed in their static form (Christensen and Pauly 1992), but the the dynamic simulation routines *Ecosim* and *Ecospace* (Walters et al. 1997, Walters et al. 1999) expanded the utility of the approach considerably. These dynamic routines use the information in *Ecopath* models to simulate the potential responses of a system's biota to changes in fisheries harvest strategies or disturbance regimes (*Ecosim*), and such analyses can be conducted in a habitat-based context (*Ecospace*). *Ecosim* also enables exploration of social, economic, and ecological trade-offs in harvest strategies.

These complimentary approaches, *Ecopath* and *Ecosim*, provide a rigorous and relatively simple framework to provide testable insights into the causes of ecosystem changes. Most importantly, they can be used to implement ecosystem-based management by aiding in the design of policies that account for indirect impacts of human activities. The relative importance of factors that shape communities can be explored by comparing (temporal and spatial) simulations to empirical information about such changes. Simulation results are often consistent with ecological theory (Christensen 1995, Vasconcellos et al. 1997), but they can be even more useful when simulation results are counterintuitive. Either way, *Ecopath with Ecosim* analyses can provide useful insights into marine ecosystem organization and functioning.

Physical forces are not explicitly included in the parameterization of *Ecopath* models, though they can be included in the *Ecosim* routine to distinguish the relative roles of trophic and physical forces. Approaches such as physical forcing, trophic mediation, and time-series fitting are available to compare and combine simulated biological and physical forces. These approaches are discussed by Christensen et al. (2000).

Ecopath models are never final because ecosystem knowledge is never complete. The usefulness of such models can improve considerably, however, through iterative combinations of simulation and empirical research in a whole ecosystem context (Pauly et al. 2000).

1.2 THE *ECOPATH* MASTER EQUATION

The parameters necessary for the construction of an *Ecopath* model are found in the *Ecopath* master equation (Equation 1.1):

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \Sigma\, B_j \cdot (Q/B)_j \cdot DC_{ji} + BA_i + NM_i \qquad \text{Equation 1.1}$$

where,

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

This equation expresses a balance between a group's net production (terms to the left of the equal sign) with all sources of its mortality (terms to the right). 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 group's total natural senescence (i.e., flow to detritus), (3) the net biomass accumulation of the group, and (4) the net migration of the group's biomass.

The thermodynamic constraints implied by Equation 1.1 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.

The law of conservation of mass or energy is expressed in this master equation, but the biomass accumulation and migration terms distinguishes this 'energy continuity' approach from a strictly 'steady state' approach. This basic 'continuity' constraint enables representation of changes in populations (i.e., functional groups) when expressed in dynamic form (not discussed here).

Because the *Ecopath* model of the entire system is a set of these linear (master) equations solved simultaneously, the *Ecopath* routine can solve for any of the four basic input parameters; B, P/B, Q/B, and EE (Christensen and Pauly 1992). These along with diet compositions, are the main parameters derived in Sections 4 – 13 of this report. Other information such as spatial and temporal distributions, habitat preferences, assimilation efficiencies, detritus fate, and other pertinent information are also covered in these parameter estimation sections.

Literature cited (The *Ecopath* approach)

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Walters, C.J., Christensen, V. and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7(2):139-172.

Walters, C. J., Pauly, D., and Christensen, V., 1999. *Ecospace*: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2:539-554.

2. Model construction

2.1 PROCEDURE FOR MODEL CONSTRUCTION

General protocol

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Procedures for deriving model input parameters and constructing *Ecopath* models include literature reviews by individuals or a small groups, empirical studies by individuals or groups, or coordinated approaches by broad collaborations of experts (e.g., Okey and Pauly 1999). The West Florida Shelf model was was constructed by a core group of researchers based on contributions by expert collaborators. These regional and topical experts contributed written sections to this compendium describing basic parameter derivations for each functional group. Inputs to this model were based on the latest available information on the entire suite of biotic components of the West Florida Shelf. Appendix 1 lists these contributors with their contact information, and authors of each section are specified.

Eight steps can be taken to construct an *Ecopath* model:

1. **Define the ecosystem in space and time** – the spatial extent of the system and the represented time period must be clearly defined. Parameter estimates are expressed in annual units, but any time period can be represented.
2. **Define functional groups** – Myriad species comprise interaction webs, but these species must be aggregated into related groupings that make sense in terms of ecological function, and the types of questions of interest. Fifty-nine functional groups comprise the West Florida Shelf model.
3. **Estimate basic parameters** for each functional group. These parameters are listed in Section 1.2, and documenting these derivations makes up the bulk of this volume.
4. **Estimate fisheries information** – Landings, discards, discard fates, and economic information can be entered for each fisheries gear type.
5. **Estimate additional *Ecopath* parameters** – detritus fates, assimilation rates, multi-year trends, spatial and temporal distributions, and habitat associations.
6. **Enter parameters** into the windows-based input interfaces (see www.*Ecopath*.org).
7. **Characterize model pedigree** by ranking parameter quality (i.e., confidence).
8. **Balance the model** according to thermodynamic constraints.

The biological components of the ecosystem are generally represented in *Ecopath* using average values, or other meaningful measures of central tendency that take into account both annual (seasonal) changes and ontogenetic changes. Production rates, consumption rates, and diet compositions vary among seasons and life histroy stages for most species in aquatic systems. However, explicit inclusion of seasonal information into *Ecopath with Ecosim* modelling merely makes answers messy rather than changing the basic results of analyses (based on experience with a large number of *Ecopath* models; C. Walters, pers. comm.).

Ontogenetic changes can be incorporated using *Ecopath with Ecosim* using two approaches. First, groups can be split into adult and juvenile 'pools' that are linked through and age structured growth and recruitment parameters; Second, numerous ontogenetic 'stanzas' can be specified for an integrated calculation of a given *Ecopath* parameter. This latter approach in particular enables real-time incorporation of variable growth, production, or consumption models into the representation of *Ecopath* parameters (C. Walters, UBC Fisheries Centre, pers. comm.).

Still, the assumption of 'average' representation of parameters is a useful convenience for modelling at the scale of entire systems because these values describe the basic interaction and energy structure of a food web. 'Energy continuity' offers a powerful mass-balance-type constraint to model parameterization and construction. Section 3 describes the balancing methodology employed for the West Florida Shelf model.

Additional parameters

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(i) Unassimilated / Consumption

Only a fraction of the food eaten by organisms is assimilated to the body; non-assimilated food is expelled. Proportions of unassimilated food must be specified in *Ecopath*, and this fraction flows to specified detritus pools. A default value of 0.2 was used for carnivorous fish groups (Winberg 1960) since assimilation efficiency information for particular fish species was scarce. This means that 80% of the food was considered assimilated. Values of 0.4 and 0.3 were applied to herbivores and planktivores since these groups preying on harder-to-digest food.

(ii) Detritus Fate

The fate of detritus is the defined pool of detritus that unasimialted food and dead organisms are specified to flow in to. A portion of the dead and decaying animals falling through the water column (including fishery discards) is directed to 'dead carcasses.' The specific proportions are assumed based on a subjective judgment relating to the habitat and niche of the various organisms (Apendix 2). The majority of detritus from non-assimilated food is directed to water column detritus and sediment detritus, but these ratios vary depending on the types of organisms. Approximately 50% of the detritus from birds is considered to be exported from the system (i.e., corpses and feces end up on land). All dead and decaying macroalgae and seagrasses contribute to the drift macrophytes detritus pool. Ultimately, detritus from the 4 detritus groups flow to the sediment detritus pool which is then exported from the system as sediment detritus is buried and rendered unavailable to the system.

2.2 ESTIMATING AREAS OF WFS DEPTH ZONES

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Estimating biomass of species occuring on the West Florida Shelf often requires calculating the areal extent over which organisms are distributed. To derive these areal estimates, bathymetry data, digitized from NOAA Nautical Charts ranging in scale from 1:450,000 to 1:1,200,000, were compiled along with detailed shoreline data provided by FMRI. Using De Soto Canyon as the northernmost limit, and the northern boundary of the Florida Keys as the southernmost limit, the study area was stratified into depth zones based on the contours defined by NOAA (Figure 2.1). Estimates of area covered by different depth strata are given in Table 2.1.

Table 2.1. Surface areas of depth strata for the West Florida Shelf.

Depth Stratum (m)	Area (km^2)	Percent of area	Cumulative area (km^2)
0-5*	5,629	2.6	5,629
5-9*	2,900	1.4	8,529
9-18	36,151	16.9	44,680
18-37	44,084	20.6	88,764
37-91	50,915	23.8	139,679
91-183	22,848	10.7	162,527
183-366	20,417	9.6	182,944
366-1,829	30,845	14.4	213,789
Total	213,789	100.0	

* Depth strata 0-5 m and 5-9 m were calculated for the Big Bend area only, which extends from Lighthouse Point in the north to North Anclote Key in the south (see Figure 2.1).

The limit of the West Florida Shelf was defined as the 200m isobath. Based on the areal measurements given in Table 2.1, the total area was taken as being 170,000 km^2. This value was used in biomass calculations where appropriate.

Literature cited (Model construction)

Allen, R.R. 1971. Relation between production and biomass. J. Fish. Res. Board Can. 28:1573-1581.

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Winberg, G.G. 1960. Rate of metabolism and food requirements of fishes. Fish. Res. Bd. Can. Translation series No. 194.

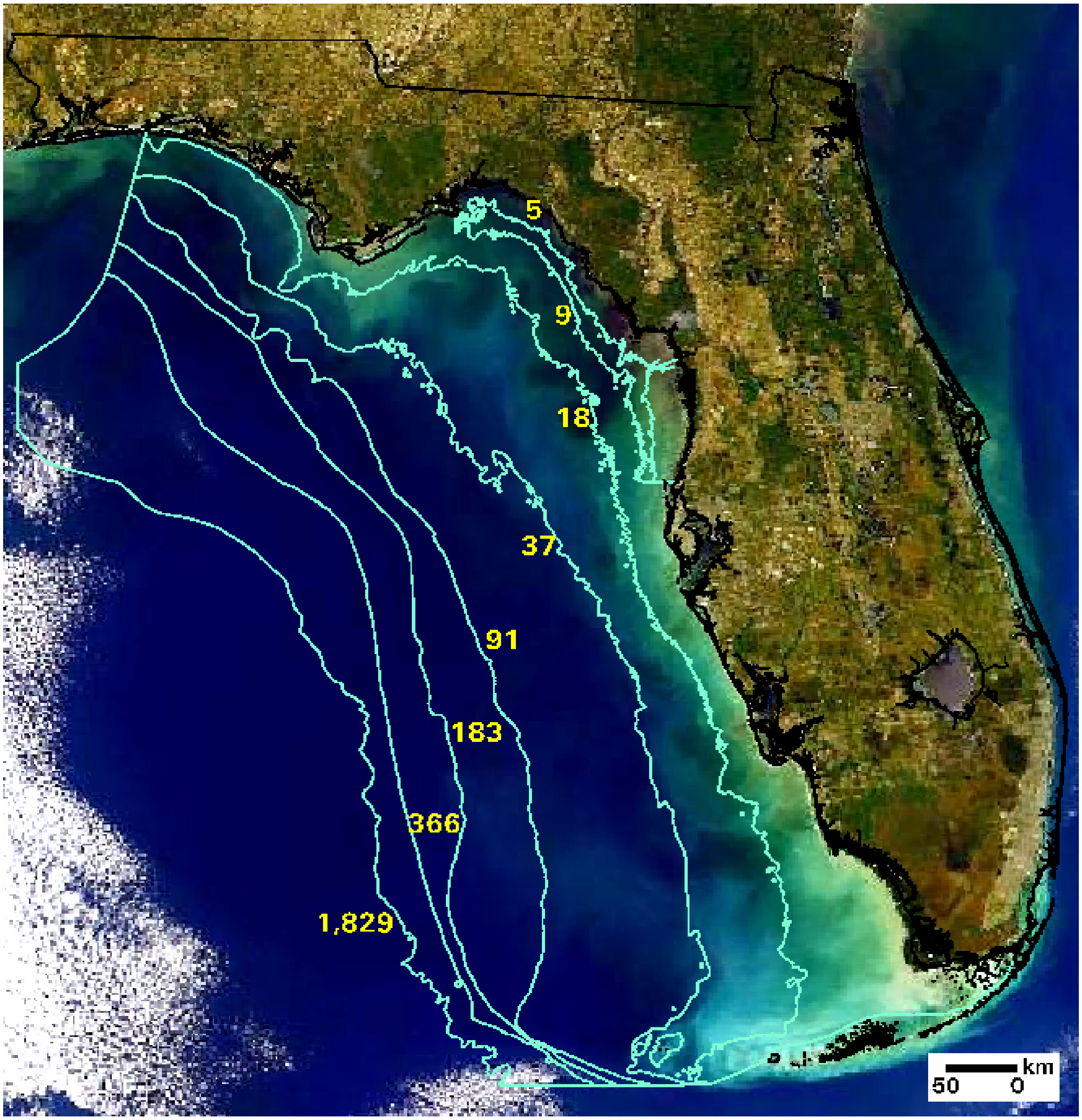

Figure 2.1. Depth strata for the West Florida Shelf (Meters). (SeaWiFS natural color satellite image provided by the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE.)

2.3 BASIC INPUT PARAMETERS OF THE WFS MODEL

Basic input parameters estimated for each of the functional groups in the West Florida Shelf model are shown in Table 2.2 with ranges of estimates, or reasonable confidence ranges, when available. These values represent independently-derived estimates contributed by experts prior to the construction and balancing of the model. Examples of diet compositions and other input parameters are provided in Section 3, and in parameter estimation sections (Sections 4 – 13). Fisheries catch and discard information is provided in Section 13; the final input parameters of the balanced model are presented in Section 3.5; the diet matrix for the West Florida Shelf model is provided in Appendix 2; detritus fate information is provided in Appendix 3; and the market value of harvested groups is shown in Appendix 4.

The relative confidence in the parameter estimates for each functional group depends on several factors. For example, the behavior and habitat of some species reduces their availability to trawl sampling, and thus their abundance is underrepresented. For other groups, the general paucity of data insists that for the time being, parameters are borrowed from similar species and settings.

Table 2.2. Best estimates used as initial inputs for the West Florida Shelf model.

Functional group	**Biomass ($t\cdot km^{-2}$)**			**P/B ($year^{-1}$)**			**Q/B ($year^{-1}$)**		
	Best	**Max**	**Min**	**Best**	**Max**	**Min**	**Best**	**Max**	**Min**
Whales and dolphins							40.86		
Sea birds				3.00			80.00		
Turtles				0.15			3.50		
Manatees	0.001			0.10			36.50		
Large oceanic piscivores	0.079	0.077	0.079	0.68	1.64	0.66	10.56	12.76	8.54
Large ocean planktivores				0.11			1.80		
Coastal sharks	0.038			0.41	0.42	0.31	3.29	4.10	3.61
Rays and skates	0.239	0.568	0.075	0.38	0.38	7.43	7.72	7.72	0.37
Pelagic oceanic piscivores	0.150	0.845	0.150	1.06			25.54		
Pelagic coastal piscivores	**0.097**	0.131	0.036	0.64	0.67	0.61	11.53	14.02	10.23
Mackerels adult	0.183	0.267	0.023	0.38	0.89	0.53	9.49	25.70	8.95
Juvenile mackerels	0.124			0.77	1.78	1.06	18.97	51.40	17.00
Sardine/Herring	0.457	6.076	0.033	1.18	1.18	1.05	12.11	12.58	10.49
PelOceJelly/eaters	2.693	2.693	0.185	1.59	1.59	1.56	8.07	23.78	8.08
PelOcePlanktivores	3.139	4.559	0.076	0.87	0.87	0.83	11.78	12.97	11.71
DemOceInvert/eaters	0.041	0.084	0.041	**2.17**			15.76		
DemCoasPisc	0.067	0.126	0.030	0.64			6.33	6.75	6.24
DemCoasInvert/eaters	2.713	5.300	0.244	0.65	0.65	0.57	8.06	9.15	7.92
DemCoasOmniv	1.429	2.036	0.271	1.60	1.60	1.34	15.13	15.04	10.71
BentOcePisc	**0.109**	**0.217**	**0.055**	**0.30**	**0.75**	**0.30**	**7.94**	**8.86**	**7.94**
BentOceInvert/eaters	0.121	0.148	0.055	**2.24**	2.24	2.44	15.78	15.78	15.79
BentCoasPisc	0.262	0.368	0.028	0.30			8.39	8.38	8.34
BentCoasInvert/eaters	1.669	2.329	0.436	1.16	1.23	0.86	12.21	12.20	10.11

SurfacePelagics	**0.0003**			2.60			11.70	96.73	11.70
StrucAssCoasPisc	0.722	1.038	0.224	0.63	0.63	0.55	7.81	8.60	5.40
LgGroupers	0.119	0.149	0.031	0.46	0.47	0.40	4.10	4.79	2.59
StrucAssCoasInvert/eaters	1.345	1.969	0.192	0.75	0.77	0.54	8.34	8.36	7.33
StrucAssCoasOmniv	0.060	0.066	0.035	1.33	1.33	1.32	29.15	29.25	24.37
StrucAssCoasPlank	**0.003**			**2.60**			**10.00**		
NearshAssPisc	0.005			1.06			7.67	17.25	7.67
Mullets (all)	0.329	0.329	0.0006	0.70	0.90	0.79	11.03	11.03	10.37
NearshPlanktivores	**0.181**	0.186	0.010	0.60	1.32	0.60	15.91	16.42	14.54
Other fishes	**3.877**	**5.806**	**0.271**	**0.70**			**7.04**		
Squid	**0.267**			2.67	3.16	1.70	36.50		
Adult shrimps	0.086	0.627	0.020	4.08	5.38	4.08	19.20		
Lobsters	**0.007**	**0.035**	**0.007**	0.90			8.20		
Large crabs	**0.088**	**0.445**	**0.089**	1.38	2.80	1.38	8.50		
Octopods				3.10	3.10	1.12	7.30	7.30	3.56
Stomatopods	0.994	1.890	0.099	1.34			74.32	74.32	0.9944
Echinoderms/large gastro. rggstgastropods	**19.246**	**28.869**	**19.246**	1.20	1.50	1.20	3.70	4.00	3.70
Bivalves	**48.598**	**145.790**	**16.190**	1.21	1.20	1.00	**23.00**		
Sessile epibenthos	**219.00**	**472.500**	**219.000**	0.80			9.00		
Small infauna	9.923	20.000	6.960	4.60	6.49	2.75	15.90	25.00	7.00
Small mobile epifauna				7.01	7.38	5.62	27.14	27.14	18.73
Meiofauna	**2.051**			12.50	12.50	5.33	25.00	42.15	25.00
Small Copepods	8.300	8.200	16.800	17.30	22.12	17.30	57.67	116.48	57.67
Other mesozooplankton	6.700	7.100	12.800	17.30	22.12	17.30	57.67	116.48	57.67
Carnivorous zooplankton	21.600	41.700	22.800	8.70	15.00	8.70	29.00	110.00	29.00
Ichthyoplankton	**0.047**	**0.095**	**0.024**	50.45	75.67	33.63	132.13	198.20	88.09
Carnivorous jellyfish	0.221	0.402	0.040	40.15			80.00		
Microbial heterotrophs	**60.000**	**120.000**	**30.000**	**100.00**			**215.00**		
Macroalgae	**36.050**	**108.200**	**12.000**	4.00			N/A	N/A	N/A
Microphytobenthos	29.780	47.000	17.000	23.73	55.60	12.68	N/A	N/A	N/A
Phytoplankton	25.000	73.000	11.000	182.13	516.00	108.00	N/A	N/A	N/A
Sea grasses	175.620	263.430	117.080	9.01	13.52	6.01	N/A	N/A	N/A
Dead carcasses	**0.001**			N/A	N/A	N/A	N/A	N/A	N/A
Sediment detritus	390.000	585.000	260.000	N/A	N/A	N/A	N/A	N/A	N/A
Watercolumn detritus	125.000	187.500	83.330	N/A	N/A	N/A	N/A	N/A	N/A
Drift macrophytes	**2.659**	**7.9770**	**0.886**	N/A	N/A	N/A	N/A	N/A	N/A

Note: Values within given ranges were prefered during balancing. Bolded values are very uncertain.

3. “Balancing” the model

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3.1 THE MEANING OF “BALANCING”

Ecopath models must be ‘balanced’ in the sense of achieving continuity among energy fluxes in the defined ecosystem, not in the sense of ‘static equilibrium.’ Continuity of energy fluxes must likewise be achieved for each particular group within the overall system, as discussed in Section 1.2.

Because an attempt is made to account for all fluxes, *Ecopath* models do not inherently assume ‘steady state.’ If the total combined demand of energy on a particular group exceeds the production of that group (plus the energy needed for respiration), the group is commonly said to be out of ‘balance,’ in the sense of energy discontinuity. *Ecopath* models constructed with good information for most or all components in a system tend to require minimal ‘balancing.’ This is because energy continuity is a true property of real world ecosystems.

The degree of discontinuity, or “imbalance,” in each functional group is revealed by the calculated ‘ecotrophic efficiency’ values. Ecotrophic efficiency (EE) is the proportion of the net production of a group that is consumed by predators or fisheries (or directly exported). These EE terms are calculated after initial input parameters have been derived and entered. An ecotrophic efficiency value of greater than one is impossible, as it indicates that total energy demand on a functional group exceeds total production and maintenance of that group. EE values greater than one are thus used as diagnostic indicators of model discontinuity or “imbalance.” This is the handle for balancing, and changes in these values are monitored while adjusting model inputs.

3.2 MODEL BALANCING STRATEGIES

Strategic approaches are implemented when balancing *Ecopath* models to optimize the representation of the system, and to avoid erosion of contributed information. For example, adjustments to input parameters are best made after prioritization according to ‘degree of imbalance,’ ‘quality of estimates,’ or other criteria applicable to the system at hand. The quality of estimates can be characterized by specified confidence bounds for each parameter (Table 2.2) or by ranking the data ‘pedigree’ of parameters (Section 3.3).

Some experienced *Ecopath* modelers suggest that model balancing should focus on diet composition adjustments because diet composition data tends to be very high relative to other parameters (V. Christensen, UBC Fisheries Centre, pers. com., 7 November 2000). However, this relative uncertainty among parameters should be assessed on a case-specific basis. Indeed, for some functional groups, the uncertainty of input parameter estimates such as biomass might rival or surpass uncertainties associated with diet compositions. Finally, model users can introduce bias into the model through a one sided approach to balancing. For example, a model can be erroneously inflated by increasing prey biomasses, or production rates, or both, rather than taking a balanced approach by including the reduction of predator consumption rates, or by re-allocating diet compositions.

Commonly, ‘top-down’ balancing strategies have been applied to balancing *Ecopath* models, in that the production and/or biomass estimates of lower trophic levels (where uncertainty can be more common) is increased to meet the demands of upper trophic levels. The result of such a method is that the biomass or production rates at the lower trophic levels can be inflated unrealistically to achieve a balanced model (T. Dean in Okey and Pauly 1999). Clearly, such a result is unrealistic and this potential interjection of bias points to the need to make a conscious effort to apply a more evenhanded approach during balancing. Not only should the accounts tally, but more importantly they should stay within the specified bounds of confidence and make intuitive sense in terms of ecological interactions. The fundamental importance of the balancing procedure as a crucial bridge to the ecology of a system must be emphasized to users who might otherwise view the balancing step as merely a necessary technical modeling procedure.

3.3 PARAMETER PEDIGREE ASSESSMENT

Parameter ‘pedigree’ index values can be assigned to each input parameter of an *Ecopath* model. *Ecopath*’s parameter pedigree routine is an approach to convert qualitative rankings of parameter quality to quantitative confidence intervals (See Appendix 5). The output of this routine can be used during manual balancing, automated balancing and analysis routines, such as the Monte Carlo routine ‘*Ecoranger*,’ or in meta-analyses that compare various models in terms of relationships between model attributes and overall data pedigree. Assigning pedigree values to functional groups whose parameters are derived from combined estimates from many data sources of varying quality is a subjective task, but nevertheless instructive. In a more general sense, it is informative to future users of the model to be as explicit as possible about the level of confidence in input parameters. The parameter pedigree routine thus inhances model transparency beyond a description of of parameter derivation.

The pedigree index value represents the quality or relative confidence assigned to each parameter estimate. Pedigree index values assigned to West Florida Shelf model parameters are shown in Table 3.1.

Table 3.1. Assigned pedigree index values

	Functional Group	B	P/B	Q/B	Diets	Catches
1	Whales and dolphins	0.7	0.2	0.2	0.7	
2	Sea birds	0.4	0.2	0.2	0.7	

3	Turtles	0.7	0.2	0.2	0.5	
4	Manatees	1	1	1	1	
5	Large oceanic piscivores	0.4	0.6	0.6	0.7	1
6	Large ocean planktivores	0	0.2	0.2	0.2	
7	Coastal sharks	0.4	0.6	0.6	0.7	1
8	Rays and skates	0.7	0.6	0.6	0.7	1
9	Pelagic oceanic piscivores	0.7	0.6	0.6	0.2	1
10	Pelagic coastal piscivores	0.4	0.6	0.6	0.7	1
11	Mackerels adult	1	1	0.7	1	
12	Juvenile mackerels	1	1	0.7	1	
13	Sardine/Herring	0.4	0.8	0.7	1	1
14	PelOceJelly/eaters	0.4	0.5	0.5	0.2	1
15	PelOcePlanktivores	0.4	0.7	0.7	0.7	1
16	DemOceInvert/eaters	0.4	0.6	0.6	0.7	1
17	DemCoasPisc	0.7	0.6	0.6	1	1
18	DemCoasInvert/eaters	0.7	0.6	0.6	0.7	1
19	DemCoasOmniv	0.7	0.6	0.6	0.7	1
20	BentOcePisc	0.4	0.1	0.1	0.2	
21	BentOceInvert/eaters	0.4	0.1	0.6	0.7	1
22	BentCoasPisc	0.7	0.6	0.6	0.7	1
23	BentCoasInvert/eaters	0.7	0.6	0.6	0.7	1
24	SurfacePelagics	0	0.5	0.5	0.7	
25	StrucAssCoasPisc	0.7	0.6	0.6	0.7	1
26	LgGroupers	0.7	0.6	0.6	0.7	1
27	StrucAssCoasInvert/eaters	0.7	0.6	0.6	0.7	1
28	StrucAssCoasOmniv	0	0.6	0.6	0.7	1
29	StrucAssCoasPlank	0	0.1	0.1	0.7	1
30	NearshAssPisc	0	0.6	0.6	0.7	1
31	Mullets	0.7	0.6	0.6	0.7	1
32	NearshPlanktivores	0	0.5	0.5	0.7	
33	Other fishes	0.4	0.1	0.1	0.2	1
34	Squid	0.4	0.8	0.8	0.7	
35	Adult shrimps	0.4	0.6	0.6	0.5	
36	Lobsters	0	0.6	0.2	0.5	
37	Large crabs	0	0.6	0.6	0.5	
38	Octopods	0	0.6	0.6	0.7	
39	Stomatopods	0.7	0.8	0.8	0.7	
40	Echinoderms/large gastro.	0.7	0.6	0.6	0.5	
41	Bivalves	0.7	0.5	0.5	0.7	
42	Sessile epibenthos	0.7	0.6	0.6	0.7	
43	Small infauna	0.7	0.6	0.6	0.7	
44	Small mobile epifauna	0	0.6	0.8	0.5	
45	Meiofauna	0.7	0.7	0.7	0.7	
46	Small Copepods	1	1	1	1	
47	Other mesozooplankton	1	1	1	1	
48	Carnivorous zooplankton	1	1	1	1	
49	Ichthyoplankton	0.7	0.6	0.6	0.7	
50	Carnivorous jellyfish	0.7	0.8	0.8	0.7	
51	Microbial heterotrophs	0.4	0.6	0.6	0.5	
52	Macroalgae	0.4	0.8			
53	Microphytobenthos	0.4	0.8			
54	Phytoplankton	1	1			

55	Sea grasses	0.7	1
56	Dead carcasses	0	
57	Sediment detritus	0.7	
58	Watercolumn detritus	0.7	
59	Drift macrophytes	0	

Notes: Pedigree index values represent relative data quality of parameter estimates. Appendix 5 presents confidence intervals associated with pedigree index values.

3.4 BALANCING THE MODEL

We took an iterative and manual approach to balancing the the West Florida Shelf model. Our approach was largely based on the pedigree rankings assigned to each parameter, as well as more detailed and parameter-specific considerations. This ensured incorporation of 'best judgement' and common sense during thermodynamic balancing. It also provided maximum insights into ecosystem function.

A number of groups were unbalanced when output parameters were first estimated (Ecotrophic Efficiency' values were greater than 1). This indicated the impossible situation that the biomass 'demand' from several functional groups was greater than their 'supply.' Such unbalance is common (and expected) when whole food web models (e.g., *Ecopath*) are constructed due to the error inherent in estimating biological parameters. This unbalance is a tangible impetus for refinement of estimates, and the model thus serves as a vehicle for refinement of ecosystem knowledge.

In light of this unbalance, initial parameter estimates were re-evaluated and refined after dialogue and negotiation among coordinators regarding the limits of possibilities for their parameters. The process of balancing the model involved two iterations. The first iteration strived to achieve a preliminary 'mass-balance' using our initial input parameter estimates leaving some parameters to be estimated by *Ecopath*. The balancing procedure integrated an assessment of uncertainty and the relative degree on 'imbalance' for all groups. Assignments of pedigree values provided one basis for this prioritization. Another key aspect of the procedure was determining the most sensitive parameters. Balancing was then conducted by making adjustments from both 'top down' and 'bottom up,' such that predator demands were met by realistic prey productivity. For example, we opted to reduce the biomass and or consumption of predators in cases where predator demands on prey groups were very high and inflation of prey groups would have exceeded confidence bounds for those groups.

To guide the model balancing procedure we established ecological 'anchor' groups, each of which was positioned at different trophic levels. These groups were considered to have strong connections throughout the food web, and their parameters were thought to be of good quality. Mackerel and sardine-herring were our main anchor groups. We held constant the parameter estimates for these anchor groups while adjusting less robust values for other groups. The sardine-herring component was considered to be a particularly good anchor, since it is a crucial channel of energy from primary producers to top predators. This group occurs at a mid trophic level, and has a substantial estimated biomass. The collaborative team effort to 'balance' the model resulted in negotiation among specialists on different trophic realms, and this resulted in a toggling between 'top down' and 'bottom up' adjustments during more than 30 minor iterations as parameters were adjusted around anchor points based on these 'taxo-trophically' different perspectives.

Two common problems encountered during this preliminary balancing process were *Cycles*, where two groups are the main consumers of each other, and *Cannibalism*, when aggregation of interacting species into a single group increases the proportion of the diet that comes from within the group. These problems were corrected by, for example, reducing cannibalism to 1-2% for most groups, and spreading the diet proportionally among other prey.

Gross food conversion efficiency (GE), or the ratio of total production to total food consumption, was used as a biological 'cross check.' This ratio ranges from 0.05 to 0.25 for most vertebrate groups, but can be higher for some groups of small invertebrates and fish larvae (e.g. for coral reefs, bacteria, nauplii, fish larvae and other small, fast-growing organisms). Empirically-derived GE (P/Q) estimates were available for some groups, and values were maintained at taxonomically reasonable levels for each group.

The preliminary balanced model was reviewed by the architect of *Ecosim*, Dr. Carl Walters. His analysis indicated unrealistically high production rates for several fish groups (making them overly resilient to disturbance). It also indicated that the fishing mortality rate estimate for shrimp was considerably lower than typical, implying that shrimp biomasses were overestimated (fishing mortality = catch / biomass). The same fishing mortality rate problem also applied to some fish groups, a consequence again of aggregation into functional groups (see Section 14.3).

A second iteration of model balancing then commenced in response the inconsistencies pointed out during this review, and additional information. Parameter estimates were then revised using these additional data. The model was refined and 'balanced' according to four criteria:

1. Parameter estimates are based on the best and most recent available data;
2. Estimates are within acceptable ranges based on the present available data;
3. The model generally represents the West Florida Shelf ecosystem;
4. The model enables 'useful' simulations to explore policy alternatives;

3.5 PARAMETERS OF THE BALANCED MODEL

Table 3.2 reveals that departures of final (balanced) input parameters from the best estimates are reasonably small. Appendix 2 presents the diet matrix of the balanced model.

Table 3.2. Basic parameters of the balanced West Florida Shelf model.

Group name	Biomass	P/B	Q/B	EE	P/Q	Unass	Trophic

		(t/km²)	**(year^{-1})**	**(year^{-1})**			**/ cons.**	**level**
1	Dolphins	0.038	0.10	40.44	[0.082]	[0.002]	0.2	[4.35]
2	Seabirds	0.001	0.10	80.00	[0.000]	[0.001]	0.2	[4.23]
3	Turtles	0.007	0.19	3.50	[0.417]	[0.055]	0.2	[3.30]
4	Manatees	0.001	0.10	36.50	[0.000]	[0.003]	0.4	[2.00]
5	LgOcePisc	0.07 (0.078c,a)	0.68	7.4 (8.54c)	[0.845]	[0.092]	0.2	[4.72]
6	LgOcePlank	[0.043]	0.11	1.80	0.500	[0.061]	0.3	[3.74]
7	Coastalsharks	0.09 (0.038b,a)	0.41	3.29	[0.909]	[0.125]	0.2	[4.30]
8	Rays/sharks	0.238	0.38	7.72	[0.651]	[0.049]	0.2	[3.65]
9	PelOcePisc	0.150	1.06	8.5 (25.5a)	[0.829]	[0.124]	0.2	[4.55]
10	PelCoasPisc	0.23 (0.13b)	0.64	10.23	[0.972]	[0.063]	0.2	[4.26]
11	MackerelAdul	0.183	0.38	8 (8.95c)	[0.938]	[0.048]	0.2	[4.25]
12	MackerelJuv	0.126	0.77	9.00	[0.970]	[0.085]	0.2	[4.33]
13	Sardine/Herring	2.40	1.05	12.11	[1.000]	[0.087]	0.3	[3.11]
14	PelOceJelly/eaters	2.20	1.56	8.07	[0.674]	[0.193]	0.2	[4.13]
15	PelOcePlanktivores	1.50	0.87	11.71	[0.949]	[0.074]	0.3	[3.43]
16	DemOceInvert/eaters	0.045 (0.041b,a)	1.2 (2.17c,a)	15.76	[0.971]	[0.076]	0.2	[3.42]
17	DemCoasPisc	0.120	0.64	6.33	[0.977]	[0.101]	0.2	[3.99]
18	DemCoasInvert/eaters	1.40	0.65	7.92	[0.999]	[0.083]	0.2	[3.52]
19	DemCoasOmniv	0.70	1.34	15.13	[0.784]	[0.089]	0.2	[2.92]
20	BentOcePisc	0.045 (0.055c)	0.45	7.94	[0.961]	[0.057]	0.2	[4.24]
21	BentOceInvert/eaters	0.19 (0.148b)	1.2 (2.24c,a)	15.78	[0.988]	[0.076]	0.2	[3.51]
22	BentCoasPisc	0.245	0.55 (0.3 b,a)	8.39	[0.938]	[0.066]	0.2	[4.03]
23	BentCoasInvert/eaters	0.860	0.86	10.11	[0.991]	[0.085]	0.2	[3.50]
24	SurfacePelagics	[0.099]	2.60	11.70	0.950	[0.222]	0.2	[2.92]
25	StrucAssCoasPisc	0.22 (0.224c)	0.63	5.40	[0.736]	[0.117]	0.2	[4.09]
26	LgGroupers	0.119	0.46	4.10	[0.880]	[0.112]	0.2	[4.28]
27	StrucAssCoasInvert/eaters	1.20	0.75	7.33	[1.000]	[0.102]	0.2	[3.55]
28	StrucAssCoasOmniv	[0.312]	1.33	24.37	0.980	[0.055]	0.2	[2.48]
29	StrucAssCoasPlank	0.05 (0.0026c,a)	2 (2.6c,a)	10.00	[0.851]	[0.200]	0.3	[3.50]
30	NearshAssPisc	[0.013]	1.06	7.67	0.900	[0.138]	0.2	[4.16]
31	Mullets	0.329	0.70	11.03	[0.512]	[0.064]	0.2	[2.07]
32	NearshPlanktivores	[2.215]	2 (1.32b)	15.92	0.990	[0.126]	0.3	[3.25]
33	Other fishes	3.87	1.3 (0.7b)	7.04	[0.950]	[0.185]	0.2	[3.37]
34	Squid	1.1 (0.267a)	3.00	35 (36.5a)	[0.987]	[0.086]	0.35	[3.78]
35	Adult Shrimps	0.55	5.38	19.20	[0.987]	[0.280]	0.4	[2.89]
36	Lobsters	0.028	0.90	8.20	[0.858]	[0.110]	0.35	[3.36]
37	Large Crabs	[0.705]	2.80	8.50	0.990	[0.329]	0.35	[3.07]
38	Octopods	[0.074]	3.10	11.70	0.950	[0.265]	0.13	[3.58]
39	Stomatopods	0.994	1.34	7.43	[0.414]	[0.180]	0.3	[3.27]
40	Echinoderms/Lg gastropods	19.246	1.20	3.70	[0.277]	[0.324]	0.56	[2.40]
41	Bivalves	48.596	1.21	23.00	[0.168]	[0.053]	0.5	[2.11]
42	Sessile epibenthos	219	0.80	9.00	[0.236]	[0.089]	0.6	[2.39]
43	Small infauna	19.032	4.60	15.90	[0.401]	[0.289]	0.5	[2.31]
44	Small mobile epifauna	[12.614]	7.01	27.14	0.950	[0.258]	0.45	[2.35]
45	Meiofauna	13 (2.05 a)	12.50	25.00	[0.822]	[0.500]	0.45	[2.36]
46	Small Copepods	8.3	17.30	50 (57.7c,a)	[0.939]	[0.346]	0.5	[2.15]
47	Other Mesozooplankton	6.7	17.30	50 (57.7c,a)	[0.851]	[0.346]	0.5	[2.55]
48	CarnivZooplank	21.6	8.70	20 (29c,a)	[0.250]	[0.435]	0.4	[2.96]
49	Ichthyoplankton	0.048	50.45	132.13	[0.748]	[0.382]	0.4	[2.94]
50	CarnivJellyfish	0.265	40.00	80.00	[0.928]	[0.500]	0.1	[3.39]
51	Microbial Heterotrophs	60	100.00	215.00	[0.235]	[0.465]	0.2	[2.00]
52	Macroalgae	36.05	4.00	-	[0.396]	-	-	[1.00]
53	Microphytobenthos	29.78	23.73	-	[0.623]	-	-	[1.00]

54 Phytoplankton	25.0	182.13	-	[0.304]	-	-	[1.00]
55 Sea grasses	175.62	9.01	-	[0.017]	-	-	[1.00]
56 Dead carcasses	1.0	-	-	[0.906]	-	-	[1.00]
57 Sediment Detritus	390	-	-	[0.884]	-	-	[1.00]
58 Watercolumn Detritus	125	-	-	[0.910]	-	-	[1.00]
59 Drift Macrophytes	2.66	-	-	[0.324]	-	-	[1.00]

Note: Values that fall outside of the range of derived estimates (Table 2.1) have nearest estimate adjacent in (brackets). The derived best estimates are marked with a, maximum estimates are marked with b, and minimum estimates are marked with c. Values in [square brackets and red] are estimated by *Ecopath*.

Model inputs (Sections 4 – 13)

The following sections document the derivation of input parameters for the 59 functional groups in the West Florida Shelf model. Functional groups are organized into nine 'taxo-trophic' realms to organize this document: primary producers, detritus, microbial heterotrophs, zooplankton, benthic invertebrates, fishes, seabirds, sea turtles, and marine mammals.

The format of most of the parameter derivation sections is standard. Each section begins with a definition of the functional group and a brief description of their taxonomy, distributions, and life history. After the group introduction, detailed approaches to estimating biomass, P/B, Q/B, and diet compositions are presented. Other information such as food assimilation efficiency, gross efficiency, ecotrophic efficiency, multi-year biomass accumulation trends, and migration information are included in these sections when available and appropriate. Section 9 (Fishes), the exception to this format, features an integrated approach to parameter estimation. Section 13 provides information on fisheries landings and discards.

4. PRIMARY PRODUCERS

4.1 Phytoplankton

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The phytoplankton of the West Florida Shelf consists mainly of diatoms and dinoflagellates. Diatoms are photosynthetic, single-celled protists (division Chrysophyta) with silicified cell walls, which take the form of lid-like valves of a protective 'frustule' (Wetzel 1983). Dinoflagellates are protozoans (subphylum Mastigophora) that are autotrophic (photosynthetic). These proto-animals propel themselves with flagella, but they are treated as algae by phycologists because they contain chlorophyll and to not feed hererotrophically (Barnes 1987). Phytoplankton is an important component of primary production on the West Florida Shelf, and they mediate the abundance and production of benthic primary producers by interfering with light penetration. Ultra-microscopic bacterioplankton (e.g., cyanobacteria) are thought to produce 10 – 60 times the as much as the larger phytoplankton constituents. The estimates included herein, however, incorporate this bacterioplankton component as biomass measurements are based on chlorophyll *a* concentrations.

Although the global biomass of marine phytoplankton is relatively low (about three orders of magnitude lower than the global biomass of terrestrial plants), their production rates are so high that the global primary production of marine plankton is almost equal to that of terrestrial plants (Smith 1981). This fast production rate allows a relatively low biomass of marine primary producers to support relatively high biomasses of organisms in upper trophic levels. Marine food webs maintain their dynamic stability by switching to alternate food sources as ephemeral primary producers fluctuate in response to physical forces in the system. The ephemeral nature of these fast producers, however, presents a challenge when attempting to represent these highly productive marine ecosystems, underscoring the importance of understanding the dynamics of these producers and the processes of their utilization.

The planktonic flora of the West Florida Shelf was very poorly known prior to 1964, despite the central importance of phytoplankton to Gulf of Mexico food webs (El-Sayed 1972). A number of studies have been conducted since that time (Tables 4.1 and 4.2), but most are basic descriptions rather than focused analyses of the ecological implications of phytoplankton dynamics.

The seasonal fluctuations of phytoplankton biomass and production on the West Florida Shelf necessitate careful scrutiny of estimates when characterizing the annual state of the system with measures of central tendency. Tables 4.1 and 4.2 provide a spectrum of estimates within which grand central measures can be chosen.

Table 4.1. Estimates of phytoplankton biomass over the West Florida Shelf.

Value	Provided unit	Source	Region	Biomass ($t \cdot km^{-2}$)
0.392 [a]	ug chl a / litre	Vargo 1995	West Florida Shelf, spring -fall	73
13.25 [b]	mg chl *a* /m2	Steidinger 1973 [d]	Inshore gulf waters	**25**
0.15 [c]	mg chl *a* /m3	El-Sayed and Turner 1977 [d]	Stations in Gulf of Mexico	28
5.92	mg chl a /m2	Cahoon et al. 1990	Onslow Bay, North Carolina	11
8.2	mg chl a /m2	Cahoon and Cooke 1992	Onslow Bay, North Carolina	15

Notes: Values in bold are those chosen to represent the West Florida Shelf; [a]grand mean of spring, summer, and fall data; [b]median value of provided range, 10 – 16.5; [c]median value of provided range, 0.1 – 0.2; [d]Vargo and Hopkins 1990.

Table 4.2. Estimates of phytoplankton production over the West Florida Shelf.

Value	Provided unit	Source	Region		Production ($t \cdot km^{-2} \cdot y^{-1}$)
Coastal phytoplankton					
0.3 [f]	$kg\ C \cdot m^{-2} \cdot year^{-1}$	Valiela 1984 [a]	General coastal phytoplankton		12474
200 [g]	$g\ C \cdot m^{-2} \cdot year^{-1}$	B. Bendis [b]	Florida Bay, 1994-1996		8316
27.4	$mg\ C \cdot m^{-2} \cdot hr^{-1}$	Cahoon and Cooke 1992	Onslow Bay, North Carolina		4990
0.3 [f]	$g\ C \cdot m^{-2} \cdot day^{-1}$	Thomas 1995	West Florida shelf and loop current		**4553**
90	$g\ C \cdot m^{-2} \cdot year^{-1}$	Yoder & Mahood 1983 [c]	West Florida shelf and loop current		3742
0.1	$g\ C \cdot m^{-2} \cdot day^{-1}$	Steidinger 1973 [d]	Inshore Gulf of Mexico waters		1518
28	$g\ C \cdot m^{-2} \cdot year^{-1}$	Kondratyeva & Sosa 1966 [d]	NW Cuban coastal waters		1164
27	$g\ C \cdot m^{-2} \cdot year^{-1}$	El-Sayed 1972 [e]	Gulf of Mexico coastal		1123
0.09 [h]	$g\ C \cdot m^{-2} \cdot day^{-1}$	Bunt et al. 1972	Florida waters and Caribbeaan		1366
Oceanic phytoplankton					
0.2	$kg\ C \cdot m^{-2} \cdot year^{-1}$	Valiela 1984 in Dawes 1998	General		8316
160	$g\ C \cdot m^{-2} \cdot year^{-1}$	Kondratyeva & Sosa 1966 [c]	Oceanic waters off Cuba		6653
318 [i]	$mg\ C \cdot m^{-2} \cdot day^{-1}$	El-Sayed and Turner 1977 [d]	Stations in Gulf of Mexico		4826
Seasonal patterns					
0.8397 [j]	$g\ C \cdot m^{-2} \cdot day^{-1}$	Vargo 1995	W. Fla shelf; 92-93	spring to fall	12744
15 [k]	$mg\ C \cdot m^{-2} \cdot hr^{-1}$	Ortner et al. 1984 [d]	Oceanic	Jan. & Feb.	2732
0.5	$g\ C \cdot m^{-2} \cdot day^{-1}$	Yoder & Mahood 1983 [d]	West Florida Shelf	April	7588
0.625 [l]	$g\ C \cdot m^{-2} \cdot day^{-1}$	Kondratyeva & Sosa 1966 [c]	Oceanic off Cuba	September	9485
0.19	$g\ C \cdot m^{-2} \cdot day^{-1}$	Kondratyeva & Sosa 1966 [c]	Oceanic off Cuba	November	2884
Spatial patterns					
0.8	$g\ C \cdot m^{-2} \cdot day^{-1}$	Yoder & Mahood 1983 [d]	W. Florida shelf; 100 to 200 m	Summer	12141
0.4	$g\ C \cdot m^{-2} \cdot day^{-1}$	Yoder & Mahood 1983 [d]	W. Florida shelf; inshore 100 m	Summer	6071

Notes: Values in bold are those chosen to represent the West Florida Shelf; [a] in Dawes 1998; [b]Florida Fish and Wildlife Conservation Commission, unpublished data; [c]in Vargo and Hopkins 1991; [d]in Vargo and Hopkins 1990; [e]in El Sayed et al. 1972; [f]median of given range 0.1 – 0.5; [g]grand mean of data from three years and four stations; [h]median of given range 0.04 – 0.14; [i]median of given range 336 - 300; [j]grand mean of provided data; [k]median of given range 14 – 16; [l]median of given range 0.5 – 0.75.

The values of phytoplankton biomass and production chosen to represent the West Florida Shelf are Thomas's (1995) production value equivalent to 4,553 t·km^{-2}·year^{-1} for the West Florida Shelf and loop current and Steidinger's (1973) biomass estimate equivalent to 25 t·km^{-2} for inshore Gulf of Mexico waters. The P/B value corresponding to these estimates is 182.13 ·year^{-1}, which is close to the P/B values corresponding to SUSFIO's (1977) assimilation value estimates for the West Florida Shelf shown in Table 4.3. Representative biomass and production values were chosen *a priori* to comparisons with the P/B values in Table 4.3. A comparison of Vargo's (1995) production and biomass values (see Tables 4.1 and 4.2) renders a P/B estimate of 175 ·year^{-1}, also comparable to these values.

Table 4.3. Derivation of Production/Biomass values from assimilation value estimates.

Assimilation value (mg C·mg chl a^{-1}·hr^{-1})	**Source**	**Region**	**P/B (·year^{-1})**
6.35	Platt and Subba Rao 1975	Caribbean, <22 um fractions	516
3.88	Platt and Subba Rao 1975	Caribbean, >22 um fractions	315
5.20	Cahoon and Cooke 1992	Onslow Bay, North Carolina	423
1.60	SUSFIO 1977	Florida shelf, summer	130
1.33	SUSFIO 1977	Florida shelf, fall	108
1.65	SUSFIO 1977	Florida shelf, winter	134

The phytoplankton production rate per given area is very high in the region's estuaries relative to the West Florida Shelf as a whole. Livingston (1984) found that phytoplankton productivity of the Apalachicola Bay estuary system during the 1970s and 1980s ranged from 63-1,694 mgC·m^{-2}·day^{-1}. Eastbrook (1973 *in* Livingston 1984) estimated the annual phytoplankton production of the Apalachicola estuary to be 371 gC·m^{-2}, which is equivalent to 15,426 t·km^{-2}·year^{-1}. This is over three times the production value chosen here for the West Florida Shelf. Furthermore, this comparison includes phytoplankton only. Comparison of benthic production would undoubtedly show estuaries to have far greater production relative to the shelf as a whole.

In the mid 1970s, SUSFIO (1977) observed the biomass of phytoplankton on the West Florida Shelf to increase considerably near the sediment-water interface during summer (Figure 4.3), repeating the pattern revealed by Saunders and Glenn (1969) a decade previously (Figure 4.1). Sutton et al. (2001) has observed similar near-bottom phytoplankton concentrations using higher resolution sampling near the sea floor. Light penetration is greatest in the summer, but the phenomenon could also be caused by impingement of nutrient rich waters or re-suspension at the sediment-water interface during that time. This seasonal shift in the vertical distribution of phytoplankton production likely reflects similar shifts in the ratio of benthic to planktonic production and cycles of secondary production. Shallow microphytobenthos has been shown to triple in abundance during the fall (Figure 5.1) when phytoplankton is least abundant.

Such seasonal and spatial patterns of production might have changed since the early 1970s as surface plankton blooms increasingly blocked light to deeper primary producers. Estimates of coastal phytoplankton production in the region surrounding the

West Florida Shelf have indeed consistently increased since the early 1970s. It is possible that this trend simply reflects an evolution of detectability, or a chance sequence of differences in study areas. Alternatively, it could portend widespread ecological changes on the West Florida Shelf that goes un-noticed.

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4.2 Microphytobenthos

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Microphytobenthos are microscopic primary producers that live within the top few millimeters of sea floor sediment and hard substrate. It has recently come to light that these microscopic photosynthesizers can contribute a significant portion of the primary production in nearshore marine ecosystems (Colijn and de Jonge 1984, Cahoon and Cooke 1992, MacIntyre et al. 1996), though high rates of benthic primary production has been recognized for more than 30 years (e.g., Bunt et al. 1972, Sournia 1976, Hartwig 1978). The benthic diatoms, dynoflagellates, euglenoid flagellates, unicellular eukaryotic algae, and cyanobacteria that make up these microphytobenthis are adapted to very low light conditions, and they are present throughout the West Florida Shelf, and probably beyond the 200 m depth contour.

The production of benthic microalgae increases when and where the biomass of overshading plankton decreases (Cahoon and Clarke 1992), thus probably evening out primary production across horizontal space on the shelf as a whole. Nevertheless, both horizontal and vertical distributions of micro-photosynthesizers within sub-systems undoubtedly mediate the character of secondary and higher level production in the West Florida Shelf food web. Light penetration into marine systems like the West Florida Shelf is a critical determinant of microphytobenthic production, biomass, and distribution (MacIntyre et al. 1996, Miller et al. 1996), though it can persist at low light levels (Cahoon and Cooke 1992). The photosynthetic dinoflagellates that live symbiotically in the tissues of corals and anemones, zoozanthellae, are also included in the microphytobenthos category.

The realization of high production of microphytobenthos begs for the reorganization of quantitative, and conceptual, energy flow models of most nearshore systems. For example, many species traditionally categorized as detritivores can now be thought of as more like herbivores. A large proportion of the energy and nutrient requirements of these organisms can be met by microphytobenthos, a high quality and fast growing food, rather than by dead organic detritus, a lower quality and less biologically available food (Miller et al. 1996). Most benthic detritus feeders and deposit feeders eat microphytobenthos, from microfauna (ciliated protozoans), to the suite of meiofaunal and macrofaunal species (and phyla) like amphipods and polychaetes (fish food), to megafaunal invertebrates like holothurians, large, gastropods, asteroids, crabs, and shrimps. But furthermore, suspension feeders and zooplankton consume microphytobenthos re-suspended by wave surge or by bioturbation. Biotic facilitation of this production also occurs through localized nutrient enrichment, such as around worm tubes (Miller et al. 1996).

The rate of primary production by microphytobenthos, as well as its biomass, is strongly influenced, and limited, by the amount of light reaching the sediment (Hartwig 1978, MacIntyre et al. 1996, Miller et al. 1996). On the West Florida Shelf, microphytobenthic production on the West Florida Shelf declines with depth, but it also varies among seasons. Higher microphytobenthic production in October appears counterintuitive since more light should penetrate the water column during summer when solar radiation is more direct. However, this pattern can be explained by summertime phytoplankton blooms, which may inhibit microphytobenthic production, as observed by Hartwig (1978). Declining microphytobenthic production with increasing depth has also been observed off Madagascar, though various studies indicate intrinsic minimum values for biomass and production of microphytobenthos (Hartwig 1978, Cahoon and Cooke 1992).

Representative values of biomass (29.778 $t \cdot km^{-2}$) and productivity (706.496 $t \cdot km^{-2} \cdot year^{-1}$) for the West Florida Shelf were chosen from a variety of estimates resulting from studies of marine sands on continental shelves. Considering the depth attenuation of microphytobenthic production on the West Florida Shelf and on other continental shelves, normalized estimates were corrected with a coverage factor of 0.25 (except for estimate from Cahoon et al. 1990, which integrated deeper depths). The biomass estimate of 29.778 $t \cdot km^{-2}$ and the productivity estimate of 706.496 $t \cdot km^{-2} \cdot year^{-1}$ are the respective means of the normalized and corrected values shown in bold in Table 4.4 and Table 4.5. The resulting P/B value for microphytobenthos is 23.725. However, Cahoon and Cooke 1992 derived an assimilation value for benthic microalgae in the shallow sands of Onslow Bay, North Carolina of 0.8 mg $C \cdot mg\ chl\ a^{-1} \cdot hr^{-1}$, which corresponds to a P/B value of 65 using conversions specified in Appendix 6. Although these are different locations, this discrepancy begs the question of whether the representative production value was biased downward by exclusion of higher end values (see Table 4.5).

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Table 4.4. Estimates of microphytobenthos biomass in marine sands of the West Floirda Shelf.

Chlorophyll *a* concentration (mg·m^{-2})	Source	Location	Depths (m)	Sediment	Biomass within habitat (t·km^{-2})	Biomass on shelf (t·km^{-2})
293.5	Sournia 1976	Takapoto Atoll lagoon	0 - 17	calcereous sands	548	137
101 [a]	Bunt et al. 1972	Key Biscayne, Florida	3 – 60	calcereous sands	189	**47**
70.8	Colijn & de Jonge 1984	EMS Dollard estuary, Netherlands	intertidal	sandy / muddy	132	33
58 [b]	Plante-Cuny 1978 [e]	Madagascar	5 – 60	marine sands	108	**27**
44 [c]	Colocoloff 1972 [e]	Mediterranean coast, France,	to 12	marine sands	82	**21**
36.4	Cahoon and Cooke 1992	Onslow Bay, North Carolina	14.6 – 41	marine sands	68	**17**
19.9	Cahoon et al. 1990	Onslow Bay, North Carolina	11 – 285	marine sands	37	**37**
14.4 [d]	Hartwig 1978	La Jolla bight, California	9 - 24	marine sands	27	7

Notes: Values in bold are those chosen for averaging to derive a representative value. [a]mean of June and July transects; [b]mean of provided values 38 and 78; [c]median of provided range 24 – 64; [d]median of range values 5.3 – 23.5 estimated from a figure by MacIntyre et al. 1996 (high uncertainty); [e]in Colijn and de Jonge 1984.

Table 4.5. Estimates of microphytobenthic production on the West Floirda Shelf.

Value	Provided unit	Source	Location	Depths (m)	Sediment	Production in habitat (t·km^{-2}·year^{-1})	Production on shelf (t·km^{-2}·year^{-1})
146.5 [a]	mg C·m^{-2}·hr^{-1}	Sournia 1976	Takapoto Atoll lagoon	0 - 17	calcereous sands	26681	6670
1.1 [b]	kg C·m^{-2}·year^{-1}	Valiela 1984	general			21175	5294
97.5	mg C·m^{-2}·hr^{-1}	Sournia 1976	Takapoto Atoll lagoon	0 - 17	calcereous sands	17757	4439
37	mg C·m^{-2}·hr^{-1}	Colijn & de Jonge 1984	EMS Dollard estuary, Netherlands	intertidal	sandy / muddy	6738	1685
24.9	mg C·m^{-2}·hr^{-1}	Cahoon and Cooke 1992	Onslow Bay, North Carolina	14.6 – 41	marine sands	3779	**945**
66	g C·m^{-2}·year^{-1}	Plante-Cuny 1978 [f]	Madagascar	5 – 60	marine sands	2744	**686**
158 [c]	mg C·m^{-2}·day^{-1}	Hartwig 1978	La Jolla bight, California	9 - 24	marine sands	2398	**599**
157 [d]	mg C·m^{-2}·day^{-1}	Colocoloff 1972 [f]	Mediterranean coast, France,	to 12	marine sands	2383	**596**
8.1 [e]	mg C·m^{-2}·hr^{-1}	Bunt et al. 1972	Key Biscayne, Florida	3 – 60	calcereous sands	1475	369

Notes: Values in bold are those chosen for averaging to derive a representative value. [a]median of provided range 72 – 221 converted from oxygen data by Cahoon and Cooke 1992; [b]median of provided range 0.2 – 2 in Dawes 1998; [c]mean of provided data in Table 1 of Hartwig 1978; [d]median of provided range 120 – 194; [e]probably an underestimate (see Bunt et al. 1972); [f]in Colijn and de Jonge 1984

4.3 Macroalgae

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The contribution of macroalgae to marine organic production is known to be significant along the West Florida Shelf, and in other continental shelf ecosystems (El-Sayed 1972). Earle (1972) described 357 species of marine plants on the West Florida Shelf, 90% of which were macroalgae (Table 4.6 also see El-Sayed et al. 1972; Plate 6). Few studies of benthic macroalgae had been conducted on this shelf prior to Earle's (1972) investigation, leading to her conclusion that macroalgal assemblages beyond 10 miles on the western Florida shelf "remains unexplored" (Earle 1972). Since that time, oil development studies have treated the West Florida Shelf macroalgae descriptively (see review by Phillips and Thompson 1990). Explicit quantitative or detailed studies of this diverse flora are still lacking.

Table 4.6. Numbers of species in the 5 divisions of plants on the West Florida Shelf.

Division	Species
Rhotophyta (red algal macrophytes)	171
Chlorophyta (green algal macrophytes)	97
Phaeophyta (brown algal macrophytes)	52
Cyanophyta (blue-green algae, or cyanobacteria)	30
Tracheophyta (seagrasses)	6
Xanthophyta	1
Total	357

Note: From Earle (1972).

The biomass estimate for attached macroalgae over the whole of the West Florida Shelf (36 t·km^{-2}) was derived by combining estimates of live macroalgae occurring on 'live bottoms,' in seagrass habitats, and in algal nodule habitats. These estimates are shown in Table 4.7. The approaches to deriving all of these estimates are described in the following sections

Table 4.7. Estimates of macroalgae biomass on the West Florida Shelf.

Macroalgae category	Biomass (t·km^{-2})
Macroalgae on 'live bottom' reefs	25.7
Macroalgae in seagrass habitats	6.00
Algal nodules	6.00
Floating *Sargassum*	0.35
Total	36.05

The biomass of macroalgae associated with 'live bottom' reefs (25.7 t·km^{-2}) was roughly estimated using the following information. Phillips and Thompson (1990) found that forty percent of live-bottom organisms on the West Florida Shelf was allocated among macroalgae, hard corals, octocorals, and bivalves. Assuming that macroalgae comprises 10% of the total live bottom biomass (i.e., 700 t·km^{-2} ; see 'sessile epibenthos' section), macroalgae would equal approximately 73.5 t·km^{-2}. The estimate of 25.7 t·km^{-2} was derived by correcting this value with an areal correction factor of 0.35 (hard bottom is ~35% of the total shelf area; Parker et al. 1983, Phillips et al. 1990 *in* Phillips and Thompson 1990). This estimate represents the lower end of the range for the estimate of 'live-bottom organisms,' the average value of which was 1,500, which would likewise lead to a macroalgae estimate of 52 t·km^{-2}. The arbitrary assumption that macroalgae makes up 10% of the biomass of 'live-bottom organisms' indicates that reasonable confidence bounds for macroalgae biomass would surround these estimates by at least a factor of three.

The biomass estimate for live macroalgae in seagrass habitats (6 t·km^{-2}) was derived using the following approach. Zieman et al. (1989) found 15.3 g dwt·m^{-2} in the seagrass habitats of Florida Bay, which is equivalent to 117.81 t·km^{-2} when adjusted with a dry weight to wet weight conversion factor of 7.7. This value was further adjusted with an areal conversion factor of 0.05, representing the proportion of the West Florida Shelf covered with *Thalassia* seagrass beds (see Section 4.4). However, using the macroalgae estimate by Zieman et al. (1989) for Florida Bay may underestimate the seagrass-associated macroalgae biomass for the West Florida Shelf as a whole because their estimate represents 18% of the total macrophyte standing crop, whereas Dawes et al. (1979, 1985 in Dawes 1998) estimated that macroalgae comprised up to 40% of the total standing crop of Florida's seagrass beds.

A large band of algal nodules can be found between 70 and 100 m depths on the outer reaches of the West Florida Shelf. Estimates of the biomass of algal nodules in these habitats are not currently available. In order to include this macrophyte component in the model, however, place-holder values equivalent to the values used for macroalgae in seagrass beds are used for algal nodules. An areal conversion factor of five percent is approximately correct for algal nodules after Phillips and Thompson (1990).

Drifting mats of *Sargassum*, which are entirely pelagic, are present across large areas of the Gulf of Mexico. Parr (1939 in Earle 1972) estimated the density of *Sargassum* in the Gulf of Mexico to be one short ton per square mile. This is equivalent to 0.35 t·km^{-2}. Howard and Menzes (1969) estimated their production at to be approximately 0.32 gC·m^{-2}·day^{-1}, which is equivalent to 2,248 t·km^{-2}·year^{-1}, but these values are not compatible for calculating a P/B ratio, as they are from different places and times.

The P/B ratio used for West Florida Shelf macroalgae is 4 year^{-1}, from Luning (1990).

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4.4 Seagrasses

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Production of seagrasses makes up a considerable portion of the total primary production on the West Florida Shelf. The sea grasses in this unique region are comprised mainly of *Thalassia testudinum*, which occurs between 1 and 10 m depths, and *Halophila* spp., occurring between 8 and 40 m depths. *Syringodium* spp. is found at the outer edge of *Thalassia* beds, or intermixed with *Thalassia*. *Halodule* spp. is found at the shoreward margins of these seagrass beds (Iverson and Bittaker 1986, Josselyn et al. 1986, Phillips and Thompson 1990). A variety of types of species use seagrasses as food or habitat on the West Florida Shelf.

The overall biomass estimate of 175.617 $t \cdot km^{-2}$ and the overall production estimate of 1583 $t \cdot km^{-2} \cdot year^{-1}$ were made based on the estimates shown in Tables 4.8 and 4.9. These estimates lead to a P/B ratio of 9.014 $\cdot year^{-1}$, which is close to the P/B estimate of 7.3 $\cdot year^{-1}$ that corresponds to 2%$\cdot day^{-1}$, independently suggested by P. Carlson for Thallassia seagrasses on the West Florida Shelf (Florida Marine Resources Institute, personal communication, 3 March 2000).

The P/B for Thallassia is approximately 2% per day in the productive parts of the seagrass beds, though production rates might be lower in the deeper parts of seagrass beds. This is equivalent to a P/B estimate of 7.3 $\cdot year^{-1}$ for such grasses on the West Florida Shelf.

The gross primary production value of a bed of seagrasses and algae was measured at 4,650 $gC \cdot m^{-2} \cdot year^{-1}$ (dry weight) at long key in the Florida keys (Odum 1957 *in* Earle 1972). However, Livingston (1984) estimated net annual seagrass production in Apalachicola Bay to be 500 $gC \cdot m^{-2} \cdot year^{-1}$ for *Thalassia* and from 320-350 $gC \cdot m^{-2} \cdot year^{-1}$ for *Vallisneria*. Even with these lower figures; Livingston estimated the total production of seagrasses in the 210 km^{-2} Apalachicola Bay system as 27,213 $tC \cdot year^{-1}$.

Hallophillia seagrass beds are far more extensive than the narrow bands of *Thallassia* along shorelines because of their adaptation to low light, and because of their opportunistic nature. They are far less dense than *Thallassia*, but their P/B ratio is also subsequently much higher. Josselyn et al. (1986) found that the biomass of Halophila beds ranged from 5 to 12 $g \cdot m^{-2}$, and their production ranged from 100 to 500 $mgC \cdot m^{-2} \cdot day^{-1}$, for a median P/B ratio of 31$\cdot year^{-1}$.

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Table 4.8. Estimates of seagrass production relevant to the west Florida Shelf.

Species	**Provided value**	**Central measure**	**Provided unit**	**Source**	**Region**	**Production in habitat ($t \cdot km^{-2} \cdot year^{-1}$)**	**Production on shelf [e] ($t \cdot km^{-2} \cdot year^{-1}$)**
Seagrasses	0.5 - 16	8.25	$g\ C \cdot m^{-2} \cdot day^{-1}$	Zieman 1987	South Florida	57967	2898
Seagrasses	0.4 - 1.5	0.95	$kg\ C \cdot m^{-2} \cdot year^{-1}$	Valiela 1984 in Dawes 1998	general	18288	914
Seagrasses	900	900	$g\ C \cdot m^{-2} \cdot year^{-1}$	Jones 1968	Miami area	17325	866
Thalassia bed[a]	0.9 - 16	8.45	$g\ C \cdot m^{-2} \cdot day^{-1}$	Odum 1953[a]	Texas	59372	2969
Thalassia testudinum	0.6 - 7.2	3.9	$g\ C \cdot m^{-2} \cdot day^{-1}$	Buesa 1972, 1974	Cuba	27402	1370
Thalassia testudinum	0.051[c]	0.051	$g\ dwt \cdot g\ dw^{-1} \cdot day^{-1}$	Zieman et al. 1989	Florida Bay	9589	**479**
Thalassia testudinum	330	330	$g\ C \cdot m^{-2} \cdot year^{-1}$	Dawes 1998	Florida area	6353	318
Thalassia testudinum	0.97[d]	0.97	$g\ dwt \cdot m^{-2} \cdot day^{-1}$	Zieman et al. 1989	Florida Bay	2726	136
Syringodium filiforme	0.8 - 3.0	1.9	$g\ C \cdot m^{-2} \cdot day^{-1}$	Zieman 1987	South Florida	13350	667
Syringodium filiforme	0.052[c]	0.052	$g\ dwt \cdot g\ dw^{-1} \cdot day^{-1}$	Zieman et al. 1989	Florida Bay	5364	**268**
Halophila decipiens	100 – 500	300	$mg\ C \cdot m^{-2} \cdot day^{-1}$	Josselyn et al. 1986	Salt River canyon	2108	**827**
Halodule wrightii	0.072[c]	0.072	$g\ dwt \cdot g\ dw^{-1} \cdot day^{-1}$	Zieman et al. 1989	Florida Bay	1599	**8**
Total production							**1583**

Notes: Values in bold are those chosen to represent each species on the West Florida Shelf. [a]Total of seagrass, epiphytes, and benthic algae in a *Thalassia* bed; [b]and Odum 1963; Jones 1968; Zieman 1975; [b]Buesa 1972 in Zieman 1987; [c]Determined using C14 uptake technique; [d]Determined using leaf-mark technique; [e]Calculated by multiplying habitat-specific production by species-specific areal coverage factors on the West Florida Shelf; 0.05 was applied to general seagrasses, *Thalassia testudinium,* and *Syringodium filiforme* corresponding to the ratio of Iverson and Bittaker's (1986) areal estimates and the overall West Florida Shelf areal estimate of 170,000 km^{-2} (Houhoulis, this volume); 0.005 was applied to *Halodule wrightii* corresponding to 1/10 of the area covered by *Thalassia* and *Syringodium* beds; and 0.392 was applied to *Halophilia decipiens* corresponding to half of the proportion of area between 9 and 37 m (Houhoulis, this volume).

Table 4.9. Estimates of seagrass biomass relevant to the west Florida Shelf.

Species	**Provided value**	**Central measure**	**Provided unit**	**Source**	**Region**	**Biomass in habitat (t·km^{-2})**	**Biomass on shelf [d] (t·km^{-2})**
Seagrass Meadow	100 - 1200	650	g dwt·m^{-2}	Dawes 1998	general (Florida area)	5005	250
Thalassia testudinum bed	500-3100	1800	g dwt·m^{-2}	Bauersffeld et al 1959[a]	Florida, West Coast	13860	693
Thalassia testudinum bed	66.9[b]	66.9	g dwt sc·m^{-2}	Zieman et al. 1989	Florida Bay	2944	147
Thalassia testudinum bed	126 - 215	170.5	g dwt·m^{-2}	Hall et al. 1999	Florida Bay, pre-decline	1313	**66**
Thalassia testudinum	123.26	123.26	g dwt·m^{-2}	Hall et al. 1999	Florida Bay, post decline	949	47
Thalassia testudinum bed	63 - 137	100	g leaf afdwt·m^{-2}	Iverson and Bittaker 1986	NW and S. Florida	770	39
Syringodium filiforme	100-300[c]	200	g dwt·m^{-2}	Zieman 1987	Florida	1540	**77**
Syringodium filiforme	36.7	36.7	g dwt sc·m^{-2}	Zieman et al. 1989	Florida Bay	514	26
Halodule wrightii	50-250	150	g dwt·m^{-2}	Zieman 1987	Florida	1155	**6**
Halodule wrightii	7.9[c]	7.9	g dwt sc·m^{-2}	Zieman et al. 1989	Florida Bay	111	1
Halophila decipiens	5 to 12	9	g dwt·m^{-2}	Josselyn et al. 1986	Salt River canyon	69	**27**
Seagrass drift	0.309	0.309	g·m^{-2}	Zieman et al. 1989	Florida Bay	2.4	2
Total biomass							**176**

Notes: Values in bold are those chosen to represent each species on the West Florida Shelf. [a]and Phillips 1960, Taylor et al. 1973 *in* Zieman 1987; [b]Estimate is for 'standing crop'; value was divide by 0.175 for biomass estimate corresponding to the specified ratio of standing crop to biomass for *Thalassia testudinium*; [c]Estimate is for 'standing crop'; value was divide by 0.55 for biomass estimate corresponding to the specified ratio of standing crop to biomass for *Syringodium filiforme* and *Halodule wrightii*; [d]Calculated by multiplying habitat-specific production by species-specific areal coverage factors on the West Florida Shelf; see Table 4.1 for these coverage factors.

5. DETRITUS

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Four detritus groups are included in the West Florida Shelf model: water column detritus, benthic detritus, drifting macrophytes, and dead carcasses. Approaches for estimating biomass for each of these groups are included in the following sections.

5.1 Water column detritus

Water column detritus exists as particulate organic carbon (POC) and dissolved organic carbon (DOC), the latter being approximately an order of magnitude greater in mass than the former on the West Florida Shelf. These two components exhibit converse seasonal fluctuations when plotted on comparable scales.

Values chosen to represent POC and DOC masses are the means of values converted those given by Fredericks and Sackett (1970 in Fredricks 1972) and SUSFIO (1977). The sum of these values 313 t·km^{-2}, which is multiplied by the assumed biologically useable proportion of water column organic carbon (0.4) leading to a water column detritus estimate of 125 t·km^{-2}. Conversion factors for carbon mass to dry mass was 2.5 and dry to wet weight was 5 (Parsons et al. 1977 in Browder 1993). Volume data were integrated to 70 m depth, and an areal adjustment factor of 0.25 was applied to account for the fact that OC decreases rapidly below the surface (Fredricks 1972), but probably increases again near the benthic boundary layer. A summary of the biomass estimates is shown in Table 5.1.

Table 5.1. Derivation of water column detritus for the West Florida Shelf.

Carbon mass (mg C·l^{-1})	**Source**	**Detritus wet mass (t·km^{-2})**
Particulate organic carbon		
0.214	Fredericks and Sackett 1970 [b]	47
0.128 [a]	SUSFIO 1977	28
Mean		37
Dissolved organic carbon		
1.080	Fredericks and Sackett 1970 [b]	236
1.440 [a]	SUSFIO 1977	315
Mean		276
Total organic carbon in water column		313
Estimated water column detritus		125

[a] presented values are the grand means from two transects and three seasons over the West Florida Shelf (Tables 59 and 60 in SUSFIO 1977);
[b] in Fredericks 1972.

The rate of import of detritus into the pool of water column detritus is another important aspect of water column detritus, and this flow was calculated as follows. Based on information from Moody (1967) and Brooks et al. (1971) in Fredericks (1972), the runoff of DOM to the West Florida Shelf equals 15,938 t·year^{-1}, assuming that the shelf receives 5.313% of the total DOM input to the Gulf of Mexico, which is half of the shelf's areal proportion (to account for a disproportionately higher contribution of DOM to the area adjacent to the mouth of the Mississippi River). Moreover, the net export (annual output minus input) of the Apalachicola-Chattahoochee-Flint drainage basin is 213,800 tonnes of Carbon, 21,480 tonnes of Nitrogen, and 1,652 tonnes of Phosphorus (Mattraw and Elder 1982 *in* Livingston 1984). The latter figures represent all forms of carbon imports into the West Florida Shelf system. Several other (smaller) drainage basins boarder the West Florida Shelf system, so the sum of these two figures (229,738 t·year^{-1}) expressed on a shelf-wide basis equals (1.351 t·km^{-2}·year^{-1}) should be considered an underestimate of the organic carbon inputs to the system.

5.2 Benthic detritus

The wet mass of sediment detritus on the West Florida Shelf is estimated to be 390 t·km^{-2}. Degradable organic carbon on continental margins is estimated to range from 450-760 tC·km^{-2}, while on abyssal plains it may range from 53-103 tC·km^{-2} (Emerson et al. 1987). Bunt (1972) found the same percentage organic carbon in Florida and Caribbean calcerious sands as Emerson et al. (1987) found to be the average on the world's abyssal plains (Table 5.2). Therefore, the median of the range given above for mass of OC on abyssal plains (78 tC·km^{-2}) is a reasonable value for the mass of carbon in the sediment of the West Florida Shelf. Cushing (1984) might have used similar reasoning, as he reported the same value for the detritus pool on the West Florida Shelf (78 gC·m^{-2}), though this was prior to the work of Emerson et al. (1987). A wet mass estimate for sediment organic carbon (975 t·km^{-2}) was then derived using a factor of 2.5 to convert carbon mass to dry mass and a factor of 5 to convert dry to wet weight (Parsons et al. 1977 in Browder 1993). Finally, the assumption that only 40% of this organic carbon is biologically useable leads to390 t·km^{-2} as a sediment detritus estimate (useable organic carbon) on the West Florida Shelf.

Table 5.2. Percent organic carbon in sediment relevant to the West Florida Shelf.

Percent	Source	Location
2.29 [a]	ESE et al. 1987	Southwest Florida
0.159	Cahoon et al. 1990	Onslow Bay, North Carolina
4	Josselyn et al. 1986	Salt River canyon
0.34	Bunt et al. 1972	Florida & Caribbean calcareous sand
0.15	Hartwig 1978	La Jolla Bight, California
1.02	Emerson et al. 1987	Earth's continental margins
0.34	Emerson et al. 1987	Earth's abyssal plains

[a] mean of provided data from sampled stations

Rowe and Menzel (1971) found the equivalent of 0.409 t·km^{-2} of sediment organic carbon on the upper slope (180 and 275 m depth) in the Gulf of Mexico. The mass of useable organic carbon (i.e., detritus) in the sediment declines logarithmically with distance from shore in the Gulf of Mexico, and this could explain such low values on the shelf break. These authors also found patches of terrestrial and shallow water plant detritus beyond the shelf break in which organic carbon was considerably higher. These elevated patches were not included in the average value above, but they are implicitly included in Section 5.3.

5.3 Drift macrophytes

Zeiman (1989) estimated the biomass of seagrass drift to be 2.379 t·km^{-2} in Florida Bay, he also estimated the biomass of drift algae to be 0.28 t·km^{-2}. The sum of these estimates (2.659 t·km^{-2}) is taken to represent the biomass of drift macrophytes, though the latter estimate of drift macroalgae is probably an underestimate for the shelf as a whole. Drifting mats of sargassum on the surface are not counted here because drift macrophytes is a category of detritus, not a category of living algae, even though drift macroalgae is often still alive. The main distribution of living Sargasso mats in the Gulf of Mexico rarely intersects with the West Florida Shelf (El Sayed et al. 1972).

5.4 Dead carcasses

There are two components of the 'dead carcasses' group: one is the standing mass of dead carcasses, and the second is the flow of dead carcasses. *Ecopath* models are more sensitive to the second component, as it is the energy (biomass) flows upon which mass balanced models are focused.

We use a standing estimate of 0.001 t·km^{-2} for a standing mass of dead carcasses. Assuming that the average residence time of a dead carcass is 10 days (the assumed average time for a dead nektonic organism to be consumed on the sea floor), the standing biomass of 'dead carcasses' is the flow of nekton input (0.020 t·km^{-2}·year^{-1}) multiplied by the ratio of average residence duration to annual duration (10 days / 365 days), resulting in a standing biomass of 0.0005 t·km^{-2}. Doubling this value to account for natural inputs of dead carcasses (other than fishery inputs) results in a standing dead carcass estimate of 0.001 t·km^{-2}.

The flow of dead discards to the dead carcass group is estimated to be 0.058 t·km^{-2}·year^{-1}, based on the following formulation. Cushing (1984) provided estimates for annual flow of shrimp discards on the West Florida Shelf between 0 and 44 m depths. This zone was taken to be roughly 60% of the 170,000 km^{2} area of the presently defined West Florida Shelf, and his estimates were adjusted accordingly. Using this approach, the flow of shrimp discards to the 'dead carcass' group would be 0.0115 t·km^{-2}·year^{-1}. Cushing (1984) uses a factor of 10 to then estimate fish discards (e.g., fish discards are 0.1152 t·km^{-2}·year^{-1}), but J. Nance (NMFS, pers. com., 18 October 2000) suggests that a factor of four (4) is more realistic (i.e., fish discards are 0.046 t·km^{-2}·year^{-1}). This leads to a summed flow of 0.058 t·km^{-2}·year^{-1}.

In the West Florida Shelf model, dead discards for each group were estimated based on fisheries-dependent information (see Section 13.1), and these dead discards were specified to flow to the 'dead carcass' group using the 'discard fate' interface. The estimate of fishery discards based on Cushing's (1984) shrimp discard estimate and J.

Nance's four-fold shrimp to non-shrimp conversion factor (0.058 $t \cdot km^{-2} \cdot year^{-1}$) was 25% lower than the fisheries-dependent estimate for dead discards (0.077 $t \cdot km^{-2} \cdot year^{-1}$).

Natural deaths are specified to go to the 'dead carcass' group through the 'detritus fate' settings. Because the flow of carcasses from natural death are unknown, a value of 1% was assigned to the 'dead carcass' group from all groups except for primary producer and detritus groups (squid was set at 5% because of high mortality after spawning). The resulting total flow of carcasses to the 'dead carcass' group is 143 $t \cdot km^{-2} \cdot year^{-1}$, and this value might be high.

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6. MICROBIAL HETEROTROPHS

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The microbial community is centrally important in the utilization and flows of energy in marine ecosystems. It is, however, the least known ecosystem component due to its inconspicuous nature. Organisms in this category include bacteria, fungi, and ciliated protozoans. Many of the larger biological components of marine ecosystems rely directly on the energy flow from the microbial community, and they influence all of these components directly or indirectly. In turn, larger components of the ecosystem shape the structure and interactions of the microbial community through foraging activities and patterns defecation, excretion, and mortality.

The biomass estimate for microbial heterotrophs on the West Florida Shelf (60 $t \cdot km^{-2}$) is the sum of bacteria in substrate, bacteria in water column, and forams (Odum and Odum 1955 and Sorokin 1987 in Opitz 1993). This value will be used until estimates more specific to the West Florida Shelf can be made. Dames and Moore (1979) did estimate that living carbon (microbes) accounted for roughly 0.25% of the total organic carbon in the sediment. Livingston (1984) estimated that 0.005% of the sediment dry weight in the Apalachicola is composed of bacterial biomass. This proportion is derived from the sediment relationships only, and should not be applied to the water column, the pool with the bulk of the organic carbon (see Section 5).

The P/B value for microbial heterotrophs of the West Florida Shelf (100 $year^{-1}$) was taken from Sorokin (1987 in Opitz 1993), and the Q/B value (215 $year^{-1}$) is from Opitz (1993). The assimilation efficiency of microbial heterotrophs is low (e.g., 0.60 at the most). Microbial heterotrophs probably consume all four of the identified detritus categories, microphytoplankton, and microphytobenthos, roughly in proportion to their respective abundance. An estimated diet composition is shown in Table 6.1 based on this assumption.

Table 6.1. Estimated diet composition of microbial heterotrophs on the West Florida Shelf.

Prey categories	**Proportion of diet**
Water column detritus	0.87
Sediment detritus	0.05
Phytoplankton	0.03
Microphytobenthos	0.03
Drift macrophytes	0.01

Dead carcasses	0.01

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7. ZOOPLANKTON

7.1 Zooplankton

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The West Florida Shelf (WFS) zooplankton community is comprised of oceanic and neritic forms. Hydrographic conditions exist that can transport oceanic and nearshore fauna onto the shelf (Stepien 1980). Upwelling associated with the Loop Current significantly affects plankton production and standing crop on the WFS (Khromov, 1965; Bogdanov *et al*., 1969; Austin and Jones, 1971). These effects are seasonal, with greatest impact in summer. The nearshore plankton communities are also impacted by seasonal variations in runoff, with greatest runoff occurring in summer. Annual variations in temperature also affect plankton abundance to some extent, mainly along the north Gulf coast (Hopkins, 1966). Overall, evidence for distinct seasonal patterns in WFS zooplankton is weak (Vargo and Hopkins, 1990), with peaks of biomass only 2-3 times the minima. Kelly and Dragovitch (1967) found larger macrozooplankton biovolumes differed by a factor of 10 from summer to winter in a study of Tampa Bay and the adjacent Gulf. Fall and spring values were one-half and one-fourth those of summer, respectively. As this estuary undergoes a dramatic seasonal freshwater input cycle (wet in summer, dry in winter), it is reasonable to assume that WFS zooplankton abundances vary less than this amount.

There are few detailed, quantitative published reports on the zooplankton of the WFS. Most previous studies of zooplankton from the eastern Gulf describe estuarine ecosystems (Hopkins, 1966; Kelly and Dragovitch, 1967; McIlwain, 1968; Gillespie, 1971; Hopkins, 1977). The few studies dealing with the shelf fauna were primarily taxonomic and results were not quantitative (King, 1949; Davis, 1950; Grice, 1953; Fleminger, 1965). Arnold (1958) reported plankton volumes for shelf to be 0.171 ml m^{-3} (0.031 mg WW m^{-3} using the conversion regression of Wiebe *et al*., 1975). The most extensive Gulf shelf zooplankton data are those of the Soviet-Cuban fishery investigations (Bogdanov et al., 1969). They found highest plankton productivity in the northern Gulf, mediated by runoff from the Mississippi River and winter destratification. Highest zooplankton biomass occurs in fall and winter in this region. Loop Current-generated upwelling in summer enhances the southWest Florida Shelf production, which results in a biomass peak during this season. Annual ranges of biovolumes for the northern Florida shelf are 0.3-1 ml m^{-3} (0.06-0.2 mg WW m^{-3}), while the southWest Florida Shelf values are 0.3-0.6 ml m^{-3} (~0.06-0.12 mg WW m^{-3}). Standing crops within these areas can be locally high (e.g. Middle Grounds; Austin and Jones, 1971).

More recently, Sutton *et al*. (2001) conducted a high-resolution survey of zooplankton abundance across the central WFS using a multisensor towed array. These data were collected during the warm season (September 1998) and will be the focus of this chapter. Sampling was conducted using 163 μm mesh nets, chosen to include the smaller copepod forms that dominate this fauna. Most previous studies used larger meshes, excluding the smaller mesozooplankton. Zooplankton samples were processed at the University of South Florida College of Marine Science using standard subsampling techniques. Biomass was determined by applying length/dry weight regressions to size frequency distributions of the subsamples. Dry weights were then converted to wet weight biomass for this model using the empirical relationships of Wiebe *et al*. (1975). Biomass was estimated as mg m^{-3} and then converted to areal estimates (t WW km^{-2}) by integrating depth of water column and distance traveled during each deployment.

The overall zooplankton distributional pattern determined by optical sensors (Optical Plankton Counter, Dual Light Sheet; see Sutton *et al*., 2001) revealed a close correlation between hydrography and zooplankton abundance. Abundance maxima were seen nearshore, associated with a salinity gradient, and along the pycnocline offshore. Increased suspended particulate matter characterized both of these zones. These distribution patterns mirror those found on the northeastern Florida shelf (NEFS). Paffenhöfer (1983) found that the dominant copepods of the NEFS region (*Oncaea, Temora, Eucalanus)* showed a significant positive correlation with the abundance of particulate matter. He also found that on a subtropical vertically stratified shelf multicellular zooplankton is most abundant in cooler upwelled water than warmer surface water (Paffenhöfer,1980). Thus, the patterns seen during our warm season transect are reasonably characteristic of the low latitude shelf regimes of the region.

For this model our data were divided into three groups. Group 1 includes carnivorous zooplankton (mainly chaetognaths). The primary prey of this group is copepods, while this group is preyed on primarily by planktivorous fishes (e.g. clupeids). This group dominates the zooplankton biomass in many areas of the WFS, and so is given separate treatment. Group 2 includes small (< 1.5 mm TL) copepods (Paracalanidae*, Oncaea, Oithona*). This group is primarily herbivorous, but much of its diet intake may consist of detritus, as the distribution of this group's members is highly correlated with suspended particulate matter at hydrographic discontinuities. This group is preyed on largely by larger zooplankton and larval fishes. This group is the numerically dominant component of the WFS zooplankton. Sutton *et al*. (2001) found that the genus *Oncaea* alone contributes 50% of the zooplankton numbers across the WFS and is the dominant grazing component (low specific grazing rates are more than offset by high abundance). Group 3 includes other mesozooplankton (larger copepods, meroplankton, ostracods). These groups are the most herbivorous of the three groups, feeding mostly on phytoplankton (e.g. chain-forming diatoms). This group is also the principal prey of the planktivorous baitfishes of the West Florida Shelf (e.g. clupeids, engraulids, carangids), and is thus given separate treatment. In summary, these groupings represent the biomass dominants (Group 1), the numerical and grazing dominants (Group 2), and the principal diet component of planktivorous fishes (Group 3).

Standing stock values across the WFS as a function of depth zone showed variable contributions by each group (Table 7.1). Chaetognaths alone accounted for three-fourths of zooplankton standing stock in the inshore zone (shore to 20 m isobath), while accounting for ~ 40% offshore (20-100 m). Overall biomass estimates of the two zones were quite similar. It should be noted that these estimates should be considered minimal, as younger life stages of the dominant small copepods are undersampled by traditional net-based methodologies.

Table 7.1. Warm season biomass estimates for WFS zooplankton by depth zone.

Zooplankton component	Inshore biomass[a] (t WW km^{-2})	Offshore biomass[b] (t WW km^{-2})
Carnivorous zooplankton	41.7	22.8
Small copepods	8.2	16.8
Other mesozooplankton	7.1	12.8
Total	57	52.4

[a] shore to 20 m isobath
[b] 20 m to 100 m isobath

Seasonal changes in zooplankton biomass are presently being investigated. As a first order approximation, the values presented in Table 7.1 can be considered the summer peak for the southWest Florida Shelf and the winter peak for the northern Gulf (Bogdanov *et al*., 1969). Minimum values could be estimated as one-third of these values (Vargo and Hopkins, 1990). Annualized values were then calculated for the three WFS zooplankton components based on these parameters (Table 7.2). Offshore vs. inshore biomass estimates (Table 7.1) were prorated by the area of each zone on the WFS to generate the annualized values. The copepod assemblage of the WFS is relatively short-lived due to high temperature, resulting in a high P/B ratio (P=B×no. generations year^{-1}). Generation times of two and four weeks were taken as summer and winter values, respectively, for small copepods and other mesozooplankton (Raymont, 1983). Generation times of one and two months were taken as summer and winter values, respectively, for carnivorous zooplankton (Reeve *et al*., 1970). Consumption values (Q) were calculated by applying a 30% gross growth efficiency to the yearly production values. Thus, Q/B = P/B×3.33. Lacking a way to measure ecotrophic efficiency, we assigned a value of >0.90.

Assigning diet composition for various zooplankton groups is problematic, especially in low latitude coastal regimes. The concept of herbivory is rarely applicable. Most “herbivorous” forms are omnivorous, taking phytoplankton, detritus, and microzooplankton in varying amounts. The best understood group is the chaetognaths, who show a marked selectivity for copepods (Reeve *et al*., 1970). The small copepods are known to take phytoplankton and detritus, with the latter component unquantified. A first order approximation would be to assign 50% herbivory and 50% detritivory to this group. Larger mesozooplankton take phytoplankton, other crustacean zooplankton (mainly nauplii and early copepodites), and protozoan microplankton. A first order approximation would be to assign 75% herbivory and 25% carnivory to this group. Knowledge of the feeding of some potentially important zooplankton components (e.g. ostracods) is totally lacking.

Table 7.2. Annualized *Ecopath* parameters for zooplankton of the West Florida Shelf.

Zooplankton component	Biomass (t km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE

Carnivorous zooplankton	21.6	8.7	29.0	> 0.90
Small copepods	8.3	17.3	57.7	> 0.90
Other Mesozooplankton	6.7	17.3	57.7	> 0.90
Total	36.5	13	43.3	> 0.90

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7.2 Ichthyoplankton

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The early life stages of many fishes are planktonic. Ichthyoplankton are the planktonic eggs and larvae of these fishes. The importance of ichthyoplankton is self-evident by their potential fate as fish (those that escape predation), but their potentially profound ecological importance in their own right on the West Florida Shelf is indicated by the high estimates for consumption rates (P/B = 50.448 $\cdot$year^{-1}) and production rates (Q/B = 132.13 $\cdot$year^{-1}). Ichthyoplankton influence the structure of the plankton community through their voracious feeding, and they may be important food for a spectrum of animals on the West Florida Shelf.

Thomas (1995) found dramatic spatial concentrations and patterning of ichthyoplankton on the West Florida Shelf that varied according to season. He suggested that high ichthyoplankton concentrations were associated with nutrient inputs and chlorophyll plumes, and his results also show the Florida middle grounds to support elevated biomass. This could be due to nutrient impingement (upwelling) over this area, or high occurrences of fish spawning related to the pinnacles there. Distinct concentrations of fish larvae in particular areas of the shelf may also be related to elevated nutrients in cold core cells associated with the loop current, or physical entrainment in them, or both. He also found that low salinity stress associated with rivers could have a detrimental effect on ichthyoplankton during years of high precipitation.

In general, ichthyoplankton were most abundant in the northern and eastern areas of the West Florida Shelf, as well as nearshore between Tampa and Sanibel during the late summer. Larval densities in some areas north of Tampa Bay and in the Big Bend area reached 200 larvae$\cdot$10m^{-3}. These highly concentrated cells at the middle coast area during summer moved offshore during fall. See Thomas (1995) for figures of spatial distributions.

Although both fish eggs and fish larvae were always more abundant than zooplankton in these samples, fish larvae increased from a relatively low abundance and even distribution during February to an increasingly higher abundance and patchy distribution during April and then August (Figure 7.1). Higher standard error bars depict less even spatial distributions, since samples were distributed throughout the West Florida Shelf. During August, highly concentrated cells of ichthyoplankton accounted for most of the fish larvae over the whole shelf. Fish eggs, however, were more even in both time and space.

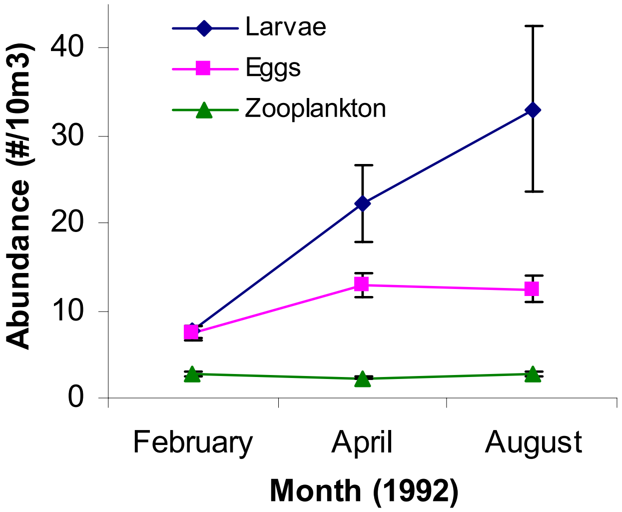

Figure 7.1. Changes in the abundance and spatial distributions of ichthyoplankton on the West Florida Shelf relative to zooplankton captured concurrently. Error bars are standard error; large error bars represent uneven spatial distributions. Sample sizes (number of stations) ranged from 45 to 71.

The estimated biomass of ichthyoplankton on the West Florida Shelf (0.04754 t·km^{-2}) was derived by multiplying the grand mean densities for larvae and eggs (2.092 individuals·m^{-3} and 1.084 individuals·m^{-3}) by 70 m, and by the wet weight of a larval fish individual (0.0002858 g ww; converted using 7.5 from mean dry weight from Theilacker 1987) and the assumed wet weight of a fish egg (0.000075 g ww) respectively. The above grand mean estimates of density were calculated from unpublished data from Carmelo Tomas and the Florida Marine Research Institute (also see Tomas 1995)

The P/B (50.448 ·year^{-1}) and Q/B (132.13 ·year^{-1}) estimates used for ichthyoplankton on the West Florida Shelf were derived from consumption and growth data in Theilacker (1987) from a laboratory experiment in which larval northern anchovies (*Engraulis mordax*) were placed in a solution of 2 rotifers·ml^{-1} (2 million·m^{-3}). These values might overestimate rates of growth and consumption in the real ocean even though the data used were from the lower experimental food concentration. This concentration of rotifers is, however, not comparable to C. Tomas' zooplankton data since his sampling was not designed to assess rotifers. De-La Cruz-Aguero (1993) used P/B and Q/B values of 15 ·year^{-1} and 110 ·year^{-1} respectively and these lower values should be considered if the Theilacker (1987) values cause thermodynamic problems in the model.

The assimilation efficiency of ichthyoplankton used in the West Florida Shelf model (0.40) is slightly higher than the mean of values derived by Theilacker (1987) for anchovy larvae in the laboratory (0.374). Erring on the high side of this value assumes that the assimilation efficiency of wild fish larvae would be at least slightly higher than those fed relatively high densities of food in the laboratory.

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7.3 Carnivorous jellyfish

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The jellyfish or ‘jellies’ group is comprised of gelatinous zooplankters such scyphomedusae, hydromedusae, siphonophores and ctenophores. These organisms are all omivorous or carnivorous, consuming other zooplankton including copepods and ostrocods, and ichthyoplankton including fish eggs and larvae. Some direct consumption of phytoplankton occurs, but not in quantity. Characterizing the gelatinous zooplankton of the West Florida Shelf is a challenging task, as the distinctly different regimes in its northern and southern zones further complicate the problems presented by limited information. Nevertheless, there is some basis for making estimations of parameters for a model of the West Florida Shelf.

The biomass estimate for jellies on the West Florida Shelf (0.221 t ww·km^{-2}) was derived by multiplying the volumetric estimate (0.00067 g dw·m^{-3}) by the average depth of the West Florida Shelf (60 m), and then by a factor of 10 to convert from dry to wet weight. The volumetric estimate is the average of two estimates from the north (my own data), collected during August 1999 in the vicinity of the DeSoto Canyon. These are 0.52 and 0.82 mg dw·m^{-3} from a 20 m representation of the middle water column (of a 80 m total water column). The resulting value of 0.402 t ww·km^{-2} is then corrected for seasonal and areal variability as explained in the following two paragraphs.

The region is divided into two halves. The northern represents a temperate fauna and the southern, a sub-tropical fauna (Phillips 1971). The northern region likely supports maximum biomass and production during the spring and summer, while the southern sub-tropical region likely supports highest production and biomass during the 'wet' season (Winter and Spring).

My best estimate from numerical comparisons primarily is that the southern half's peak biomass likely approximates the northern half's peak biomass even if these maxima are offset temporally (Larson 1982). Therefore a good start would be to use simply the peak areal biomass of 0.402 t ww·km^{-2} for 6 months and cut this number to 10% or 0.0402 tonnes for the remaining low productivity period. Thus the average volumetric biomass estimate throughout the year and throughout the region would be 0.221 t ww·km^{-3}.

No data for daily P/B of jellies exists for the eastern Gulf. However, a reasonable number to use would probably be 0.20 day^{-1}. I chose this number as the maximum daily turnover since it reflects maximum daily growth rates of young jellies. Assuming that bioenergetic efficiencies remain constant as animals grow, production would go into maintenance. This value is higher than the 10% day^{-1} value used in the model of the Prince William Sound ecosystem (Okey et al. 1999), but the warmer waters warrant increased turnover rates.

P/B estimate of 40.15 year^{-1} was derived using a similar approach to that discussed above. The mean of the estimated maximum daily growth rate (0.2 day^{-1}) and 10% of that value (0.02 day^{-1}), which represents the minimum daily growth rate during the less-productive season, results in the estimated daily growth rate (0.11 day^{-1}), which was multiplied by 365 days.

The ratio of consumption to biomass (Q/B) for jellies of the West Florida Shelf is estimated to be approximately 80 year^{-1} assuming a maximum turnover of once every 5 days and an assimilation efficiency of 0.9 (see Purcell 1983) This is probably a reasonable number given the warmer water and higher metabolic costs.

The diet composition used for the jellies of the West Florida Shelf based on our own composition information from the scyphomedusa *Aurelia aurita* (Graham and Kroutil, submitted): 67% omnivorous meso-zooplankton, 23% small herbivorous copepods, and 10% fish eggs and larvae is modified from the diet used for jellies in Prince William Sound (Okey et al. 1999). Dietary proportions for omnivorous meso-zooplankton and small herbivorous copepods were switched based on my personal observations of cut contents from the region. As a final note, I think eggs and larvae are important in the diets of jellies; but 10% used here may ultimately be high and could accordingly be adjusted in the future.

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8. BENTHIC INVERTEBRATES

8.1 Meiobenthos

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Meiobenthos are benthic invertebrates smaller than 0.5 mm in length, most of which live interstitially (between sediment grains) in soft sediment. The lower size limit of meiobenthos is thought of as 65 microns (0.065 mm) as most organisms smaller than this threshold are microbes. Meiobenthos have close trophic relationships with microbes (as predators) and macrofauna (as prey). Many meiobenthos live on the sediment surface as 'micro-epifauna'.

Nematodes (round worms) are the most abundant meiobenthic group on the West Florida Shelf followed by harpacticoid copepods (a type of benthic copepod). These are, in turn, followed by turbellarians and gastrotrichs, and others including priapulid larvae, crustacean larvae, polychaete larvae, kinorynchs, tartigrades, coelenterates, and halacarid mites (SUSFIO 1977). Meiobenthos undergo extreme seasonal fluctuations and they are extremely patchy on the West Florida Shelf, relative to macroinfauna and macroepifauna which are far more stable in time and space (Dames and Moore 1979). Nevertheses, the sampling design used by SUSFIO (1977) integrates this heterogeneity in space and time, resulting in representative density estimates for these organisms.

The biomass estimate of meiobenthos on the West Florida Shelf (2.051 $t{\cdot}km^{-2}$) was derived from MAFLA surveys (SUSFIO 1977) and information on individual sizes of meiobenthos. Nematodes averaged 330,775 $individuals{\cdot}m^{-2}$, and copepods had an overall average of 58,333 $individuals{\cdot}m^{-2}$ in the MAFLA study area (Mississippi, Alabama, Florida, outer continental shelf baseline environmental survey), which overlaps considerably with the West Florida Shelf area defined herein. These density estimates lead to biomass estimates of 1.45 $t{\cdot}km^{-2}$ and 0.415 $t{\cdot}km^{-2}$ respectively after mean individual nematode and meiofaunal copepod weights were applied (0.00000438 g $ww{\cdot}individual^{-1}$ and 0.00000712, the respective averages of a suite of estimates (see Donovario et al. 1999, Warwick et al. 1977, and Schwinghammer et al. 1986) These average individual sizes also compares favorably with meiofaunal estimates adapted from Drgas et al. (1998) by converting from carbon to wet weight. The sum of these values (1.865 $t{\cdot}km^{-2}$) is increased by an additional 10% to account for meiobenthos other than nematodes and harpactictoid copepods.

The P/B for meiobenthos was set at 12.5 $year^{-1}$ based on estimates by Schwinghamer et al. (1986). It is worth noting here that Elmgren (1984 in Pauly and Christensen 1993) used 5.33 $year^{-1}$ as P/B for meiobenthos, but Warwick et al. (1979 in Pauly and Christensen 1993) used a P/B of 8.38 $year^{-1}$ for nematodes.

The Q/B was set at the reasonable minimum value of 25 $year^{-1}$—twice the P/B value. This is very close to the Q/B value 22.5 $year^{-1}$ provided by Tom Shirley for an *Ecopath* model of Prince William Sound, Alaska (pers. com., UAF Institute of Marine Sciences; see Okey 1999), but Shirley's value for Prince William Sound is likely to underestimate the Q/B of meiobenthos for a sub-tropical setting like the West Florida Shelf where the higher temperature would mean higher metabolic costs. Vidal (2000) has uses a meiobenthic Q/B of 42.15 for her overall Gulf of Mexico model, and this may be closer to the actual value.

The diet used for meiobenthos on the West Florida Shelf is 10% other meiobenthos, 25% microbial heterotrophs, 25% microphytobenthos, and 40% sediment detritus.

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8.2 Small infauna

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The ‘small infauna’ group consists of sea floor invertebrates that do not wash through a 500 micron screen (0.5 mm), but are generally smaller than 20 mm. The term ‘small infauna’ is being used here in place of, and sometimes interchangeably with the more conventional term ‘macrofauna.’ This group does not include the interstitial ‘meiofauna,’ which are smaller than (0.5 mm). Small infauna live in the top layers of sediment (infauna) or on the sediment surface (epifauna), and they include polychaetes, small crustaceans, small molluscs, and small echinoderms. The species in this aggregated group exhibit a variety of life habits and niches, but in general, they consume microphytobenthos, microbial heterotrophs, meiobenthos, each other, mobile epifauna, and detritus, whether suspended or deposited. Small infauna are important prey for larger fish and invertebrate predators on the West Florida Shelf (Dames and Moore 1979). For the purposes of this model, small infauna is distinguished from swarming macro-epifauna, which is a separate group (see Section 8.3). This distinction is made because the general goal of this modeling effort is to examine the trophic forces relating to the production of forage fishes on the West Florida Shelf. This distinction is also based on recent work showing the functional differences between these two groups to be profound (Okey, in press).

The amount of carbon present as living biomass in the benthos of the slopes and the deep basins of the Gulf of Mexico is relatively small because of the low surface productivity (Rowe and Menzel 1971 *in* Collard and D’Asaro 1973), but also probably because of efficient utilization of available carbon within shelf ecosystems, effectively minimizing carbon transport across shelves. The logarithmic decline in the amount of carbon in live organisms with increasing distance from coasts (Rowe and Menzel 1971) probably also holds for useable organic carbon (i.e., detritus) in the sediment (see Section 5).

In general, the small infaunal community of the shelf has been characterized as considerably more even in time and space than the more ephemeral and patchy shelf meiobenthos (Dames and Moore 1979). Nevertheless, macrofaunal assemblages do exhibit some seasonal fluctuations (Figure 8.1).

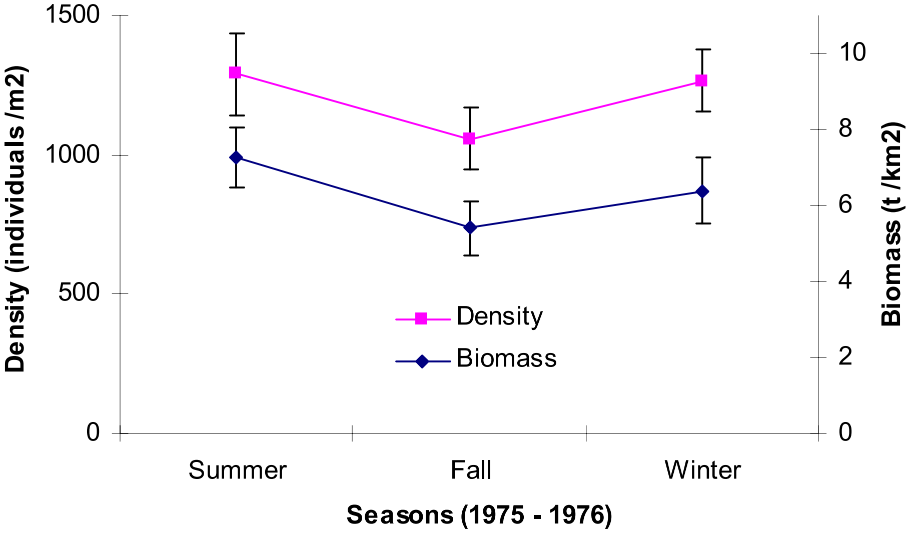

Figure 8.1. Seasonal change of polychaete abundance and biomass on the West Florida Shelf in 1975 and 1976 (data from SUSFIO 1977). Polychaetes make up approximately 64% of 'small infauna' individuals on the SouthWest Florida Shelf (ESE et al. 1987). Error bars are standard error.

The Mississippi, Alabama, Florida, Outer Continental Shelf Baseline Environmental Survey (MAFLA) included the only sampling programs that appeared capable of characterizing the small infaunal assemblage for the whole West Florida Shelf (e.g., SUSFIO 1977). The estimate of small infaunal biomass on the West Florida Shelf (9.923 t·km^{-2}) chosen from this program nevertheless contains uncertainty because the value was extrapolated from polychaete biomass to overall small infauna biomass with a ratio developed from abundance information from the southWest Florida Shelf (ESE et al. 1987). Estimates from other studies were used for verification, but the SUSFIO (1977) estimates contained the least uncertainty of the studies identified (see Table 8.1), for the purposes of this modeling exercise.

Table 8.1. Biomass estimates of small infauna biomass on the West Florida Shelf.

Value	Provided unit	Source	Region	Biomass in habitat (t ww /km^2)	Coverage ratio	Biomass on shelf (t ww /km^2)
<20	g·m^{-2}	ESE et al. 1987	Southwest Florida Shelf	<20.000 [g]	1	<20.000
1,970	# · 0.59 m^{-2}	Dames and Moore 1979	West Florida Shelf	19.032 [h]	1	19.032
7,062 [a]	mg·m^{-2}	Rowe and Menzel 1971	Compeche shelf break, GoA	7.062	1.5 [i]	10.593
6.349 [b]	g·m^{-2}	SUSFIO 1977	West Florida Shelf (MAFLA)	6.349	1.563 [j]	**9.923**
9.05 [c]	g·m^{-2}	Continental Shelf Associates 1986 [f]	20-25 m off Tampa Bay	9.050	1	9.050
25.533 [d]	g·m^{-2}	Sheridan 1997	Rookery Bay	25.533	0.333 [k]	8.502
20.9 [e]	g·m^{-2}	Estevez 1986	Charlotte Harbor	20.900	0.333 [k]	6.960

Notes: Bolded value is the one chosen to represent the defined shelf area. [a]mean of values 6800 and 7320 taken from 185 and 282 m depth respectively; [b]grand mean of polychaete biomasses from three seasons and six transects in the MAFLA area; [c]median of range 2 – 16.1 in 20 to 25 m off Tampa Bay; [d]mean of median

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biomasses from different habitats; [e]25 stations and two different seasons in Charlotte Harbor; [f]in ESE et al. 1987; [g]but Vittor (1979 in ESE 1987) might contain data to calculate accurate values; [h]the product of # · m^{-2} and the mean weight of a sandflat polychaete (0.0057 g) from Okey (1997); [i]Assuming that infaunal biomass is 50% greater on the shelf as a whole than at the shelf break; [j]Conversion from polychaetes, which make up approximately 64% of macrofaunal individuals on the southWest Florida Shelf (ESE et al. 1987); [k]the present author's best judgment for converting from estuaries to the West Florida Shelf, assuming that small infauna are less abundant on the more distant portions the West Florida Shelf, as observed by SUSFIO (1977), Dames and Moore (1979), and ESE et al. (1987) (also see Rowe and Menzel 1971).

Average sizes of polychaetes were derived from density and biomass data from three Rookery Bay, Florida habitats (Sheridan 1997) in order to estimate biomass from macrofaunal abundance information on other studies (see Table 8.2).

Table 8.2. Representative abundances and biomasses from Rookery Bay and Charlotte Harbor.

Habitat	Abundance (individuals·m^{-2})	Overall abundance	Biomass (g·m^{-2})	Overall biomass	Individual biomass (g)
Red mangrove[a]	22,591 – 52,914	37,752	3.6 – 8.2	5.9	0.000156
Mixed seagrasses[a]	6,347 – 23,545	14,946	15.7 – 87.4	51.6	0.003452
Non-vegetated mud[a]	3,611 – 22,465	13,038	11.9 – 26.2	19.1	0.001464
Overall Rookery Bay		21,912		25.5	0.001163
Charlotte (May-June)[b]		17,165		19.0	
Charlotte (September)[b]		19,584		22.8	
Overall Charlotte Har.[b]		18,375		20.9	
West Florida Shelf[c]	3,339	3,339		19.0	

[a]Abundance and biomass ranges from Sheridan (1997); average individual biomasses were calculated using median values of abundance and overall biomass; [b]Mean abundance values calculated from 25 stations monitored by Estevez (1986). Overall Charlotte Harbor biomasses were calculated by applying the overall individual biomass from the [c]Rookery Bay habitats (0.001163 g; Sheridan 1997); From Dames and Moore (1979); 1,970 individuals · 0.59 m^{-2} converted to m^{-2} and multiplied with the overall individual biomass for a sandflat polychaete (0.0057 g) from Okey (1997).

Rowe and Menzel (1971) found a high correlation between wet weight and carbon (0.96), numbers and carbon (0.86), and wet weight and dry weight (0.85), and a moderate correlation between dry weight and carbon (0.73). They also found the wet weight of these infauna to be 5 to 10 times the dry weight, and dry weight was 5 to 15 times organic carbon weight.

The P/B and Q/B estimates for small infauna on the West Florida Shelf (4.6 ·year^{-1} and 15.9 year^{-1} respectively) were developed for Yucatan shelf annelids by Arreguín-Sánchez et al. (1993). These values were developed as independently estimated inputs, not outputs of their model.

The diet composition estimation for the West Florida Shelf is shown in Table 8.3. However, these diet compositions are based on studies by Feder and Jewitt 1988 and Feder et al. 1989 in subpolar environments. The assimilation efficiency of small infauna is probably low since they consume low quality, or difficult to digest, food items. Assimilation efficiency should be set at 0.06 at best.

Table 8.3. Estimated diet composition of

‘small infauna’ on the West Florida Shelf

Prey categories	Proportion of diet [a]
Phytoplankton	0.22
Microphytobenthos	0.22
Sediment detritus	0.15
Microbial heterotrophs	0.15
Meiobenthos	0.10
Water column detritus	0.05
Drift macrophytes	0.05
Macrofauna	0.05
Sm. mobile epifauna	0.01

Notes: Diets expanded and modified from Feder and Jewitt (1988) and Feder et al. (1989 in Jewett 1999). [a]Jewett’s (1999) 61% value for detritus was equally apportioned among detritus, two microbe categories, and meiobenthos.

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8.3 Small mobile epifauna

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Small mobile epifauna are highly mobile, epifaunal macro-invertebrates (0.5 mm to approximately 20 mm in size) that live associated with the sea floor, but which swim above it in search of food or refuge. Small mobile epifauna are found over hard and soft bottoms, often in association with drift macrophytes. They mainly consist of swarming amphipod crustaceans and mysids. Ostrocods, some other crustaceans, and a few polychaetes can emerge demersally from the sediment to become mobile epifauna. In this model, juvenile shrimp and small crabs are included in ‘small mobile epifauna.’ Swarming amphipods live mainly by cropping microbial flora from the surfaces of decomposing macrophytes, by directly grazing micro and macroalgae, by scavenging animal carcasses, and by eating zooplankton and small infauna. Mysids mainly consume phytoplankton. Small mobile epifauna are an important, though underemphasized and understudied, link of secondary production in marine food webs of continental shelves and the deep sea. They are also probably an underemphasized component of the diet of fishes and other larger organisms.

Quantitative density or biomass information on small mobile epifauna was not found for the West Florida Shelf ecosystem, although good evidence exists of a diverse and abundant small epifauna (e.g., Myers 1981, Menzies and Kruczynski 1983, Oritz 1991). A large proportion of this group is comprised of organisms that are highly mobile, and which actively seek out food resources and refuges that can have extremely patchy distributions in time and space (e.g., swarming benthic amphipods and mysids; Okey 1997; Okey, in press.). These characteristics make reliable estimates of density and biomass difficult to develop without sampling programs that explicitly account for relative distributions in the context of their patchy resources (e.g., drift algae, carcass falls). The biomass for this group was left to be estimated by the *Ecopath* model, as P/B, Q/B, and EE values were entered as inputs.

The P/B and Q/B estimates for small mobile epifauna on the West Florida Shelf (7.01 ·year^{-1} and 27.14 year^{-1} respectively) were developed for Yucitan shelf microcrustaceans by Arreguín-Sánchez et al. (1993). These values were developed as independently estimated inputs, not outputs of their model.

The estimated diet composition shown in Table 8.4 is based roughly on estimates by Dean (1999), considering that his small epibenthos group was defined differently than the current ‘small mobile epifauna’ group, and that the present model contains more possible prey groups.

Table 8.4. Estimates of the diet composition of small mobile epifauna on the West Florida Shelf

Prey categories	Proportion of diet
Microbial heterotrophs	0.15
Drift macrophytes	0.15

Macroalgae	0.12
Microphytobenthos	0.11
Phytoplankton	0.10
Sediment detritus	0.07
Water column detritus	0.07
Meiobenthos	0.07
Dead carcasses	0.05
Small infauna	0.05
Seagasses	0.05
Sm. mobile epifauna	0.01

Note: Based on estimates by Dean (1999).

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8.4 Bivalves

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Marine bivalves are a diverse and energetically important component of Florida's nearshore and shallow shelf communities. Unfortunately, basic population parameters for non-commercial species do not exist in these habitats. Understandably, the only research of this nature has been conducted in estuarine or very near shore environments and mainly focusing on species that are targets of fisheries. The other 250 plus species of bivalves that occur along the Florida Gulf coast, which are not fisheries species, are often small, abundant, and important in marine food webs. Obtaining more than qualitative information on these bivalves is difficult, and we have had to generalize and make estimates based on experience and information gleaned from the literature. Clearly for these numbers to be meaningful, an extensive survey of the habitats in question is required. Both deposit-feeding and suspension-feeding modes are represented within the Bivalvia. Suspension-feeding bivalves generally dominate in hard-bottom and sandy substrates. These are usually replaced by deposit-feeding species in muddy substrates. Although they are treated as one group in this model of the West Florida Shelf, we have separated the approaches of estimating the parameters for scallops and infaunal clams, as source data are separate for these groups. For similar reasons, oysters and attached sessile bivalves are included in another group of this model (i.e., sessile epibenthos).

Table 8.5. Parameter estimates for bivalves on the WFS including infaunal bivalves and scallops.

Bivalve group	**Biomass ($t \cdot km^{-2}$)**	**P/B ($year^{-1}$)**	**Q/B ($year^{-1}$)**
Infaunal bivalves	16.75 [a]	1.35 [c]	--
Scallops	31.848 [b]	1.15 [d]	--
Overall	48.598	1.219 [e]	23 [f]

[a] This rough approximation of infaunal bivalve biomass is simply the mean of the two median values from the estimated ranges of small and large infaunal bivalves, assuming that small and large bivalves have equal biomasses. Ranges are provided in the text;
[b] Sum of the estimates of Calico and Bay scallops (see text);
[c] Mean of given estimates for small and large infaunal bivalves;
[d] Sum of 1.0 for replacement and Barber and Blake's (1980) estimate for cost of reproduction (0.15);
[e] Average of P/B estimates for infaunal bivalves and scallops weighted by biomass of those two groups;
[f] From Guénette (1996).

Infaunal bivalves

The vast majority of bivalves in soft-bottom communities are small (D. Marelli, personal knowledge) and have high production to biomass ratios (Dame 1996). Biomass estimates for these bivalves do not exist for the West Florida Shelf, but for the purposes of this modeling exercise, I (D. Marelli) estimate that the biomass of small infaunal bivalves in the defined West Florida Shelf area ranges from 5 to 50 t·km^{-2}, and the biomass of larger infaunal bivalves ranges from 2 to 10 t·km^{-2}. Dame (1996) suggests that bivalve production to biomass ratios average 1.2. Thus, an estimate between 1 and 1.2 is probably a good value for larger infaunal bivalves. Smaller bivalves have greater ratios of P/B, with values probably exceeding 1.5. Many of these smaller bivalves have short generation times and multiple generations annually. Considerable uncertainty still exists for infaunal bivalves, and more precise estimates would require an increased investment of scientific resources in the region.

Scallops

Scallops are a specialized group of mobile epifaunal bivalves found on soft bottoms. Their visual abilities and their ability to swim to escape predation and otherwise move about sets them apart from all other bivalved molluscs. Scallops are suspension feeders like many other clams and sessile epibenthos. On the West Florida Shelf, scallops include calico scallops (*Argopecten gibbus*) and bay scallops (*Argopecten irridians*).

The biomass of scallops on the West Florida Shelf (31.848 t·km^{-2}) is equal to the sum of the biomasses of Calico and Bay scallops. Cummins (1971) found Calico scallop densities equal to 43 scallops·m^{-2} in commercially fished areas. The average wet weight of the soft tissue of a calico scallop is 7.4 grams (B. Arnold, unpublished data), which is equal to 318.2 t·km^{-2}. If we assume that 10% of the total area of the shelf supports scallops, the biomass of scallops on the West Florida Shelf would be 31.82 t·km^{-2}. Given the paucity of quantitative information for scallops outside of the fishery zones, we will take this as a working biomass estimate for Calico scallops on the West Florida Shelf. The biomass estimate for Bay scallops in their preferred habitat (0.555 t·km^{-2}) is based on FMRI surveys (B. Arnold; published and unpublished data) and the same individual weight estimates as for Calico scallops above. The bay scallop biomass estimate for the whole shelf area would be 0.028 t·km^{-2} assuming that Bay scallop habitat covers 5% of the West Florida Shelf.

We take the ratio of production to biomass (P/B) for bay scallops to be 1.0 plus the cost of reproduction, which Barber and Blake (1980) estimated to be approximately 0.15 for this species. This leads to a P/B of 1.15 year^{-1} for bay scallops. This is very close to the P/B ratios suggested by Dame (1996), discussed above (1.2 year^{-1}). We use 1.2 as the P/B for the bivalve group in the model of the West Florida Shelf.

The value used for bivalve Q/B in this model (23 year^{-1}) is from estimates given by Guénette (1996) for an *Ecopath* model of the North Pacific. The estimated diet composition of bivalves on the West Florida Shelf is shown in Table 8.6. The assimilation efficiency of bivalves is probably low because of the low quality of their food (e.g., 0.50).

Table 8.6. Estimated diet composition of bivalves on the West Florida Shelf.

Prey categories	Proportion of diet
Sediment detritus	0.25
Phytoplankton	0.23
Microphytobenthos	0.22
Water column detritus	0.19
Microbial heterotrophs	0.10
Meiobenthos	0.01

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8.5 Sessile epibenthos

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Sessile epibenthos are non-mobile, suspension or filter feeding invertebrates, usually attached to hard substrate. The West Florida Shelf contains extensive areas of low-lying carbonate reef platforms that provide substrate for most sessile epibenthos. Organisms include sponges, corals, tunicates, gorgonians, hydroids, bryozoans, attached bivalves, crinoids, and ophioroids. These assemblages comprise what local fisheries scientists refer to as “live bottoms,” with which mean communities that develop on exposed hard bottoms. The organisms in these low reef habitats are adapted to varying degrees of sand scour and inundation; exposed hard bottoms are characterized by a dynamic veneer of carbonate sand (Phillips and Thompson 1990). The algal nodule community is another type of live bottom that is relatively extensive on the West Florida Shelf. These beds of rhotoliths (branching, non-attached, non-geniculate, calcified, red algae) harbor a unique suite of epifauna and interstitial macroinfauna.

The biomass estimate for sessile benthic epifauna on the West Florida Shelf is 472.5 t·km^{-2}, based on the following derivation. The biomass of sessile epibenthos (and macroalgae) on ‘live bottom’ in the shallow portion of the West Florida Shelf was estimated to be 2,000 t·km^{-2} by Continental Shelf Associates, Inc. (1987), though deeper portions of the shelf had less cover and biomass. Assuming the deeper biomass is 1,000 t·km^{-2}, the mean biomass on hard bottom for the overall shelf would be 1,500 t·km^{-2}. Sponges comprised fully 58% of the biomass of sessile epibenthic fauna (Phillips and Thompson 1990; and a 1984 estimate by Darcey and Gutherez was 54%), with the bulk of the remaining portion split between hard corals, octocorals, bivalves, and macroalgae. Thus, subtracting 10% of this ‘live bottom’ (the rough percentage of macroalgae) leads to a sessile epibenthos estimate of 1,350 t·km^{-2}. Correcting this with an areal correction factor of 0.35 (hard bottom is ~35% of the total shelf area; Parker et al. 1983, Phillips et al. 1990 *in* Phillips and Thompson 1990) leads to an estimate of 472.5 t·km^{-2} for epifauna over the West Florida Shelf.

This estimate of very high for any group in any *Ecopath* model, and this aggregated group would have the potential to dominate energetic processes in the model system. The lower limit of the confidence range presented by Phillips and Thompson 1990 results in a sessile epifauna biomass estimate of 219 t·km^{-2}. Use of this lower estimate might be preferable for this model, especially if problems are encountered related to its size.

The P/B value of sessile epibenthos on the West Florida Shelf (0.8 ·year^{-1}) is from Odum and Odum (1955) and Sorokin (1987) in Opitz (1993). The Q/B value (9 ·year^{-1}) is the mean of sponges (based on Wilkinson 1987) and corals (based on Sorokin 1987) also in Opitz (1993). The assimilation efficiency of sessile epibenthos should be relatively low (e.g., 0.60). Table 8.7 shows the estimated diet compositions of sessile epibenthos on the West Florida Shelf.

Table 8.7. Estimated diet compositions for sessile epibenthos on the West Florida Shelf.

Prey categories	Proportion of diet
Water column detritus	0.27
Microbial heterotrophs	0.25
Phytoplankton	0.20
Sm. mobile epifauna	0.07
Zooplankton	0.05
Sediment detritus	0.05
Microphytobenthos	0.05
Meiobenthos	0.02
Sessile epibenthos	0.01
Dead carcasses	0.01
Demersal reef fishes	0.01
Small infauna	0.01

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8.6 Echinoderms and large gastropods

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The Echinoderms and large gastropods group for the West Florida Shelf model consists of a suite of mobile invertebrates larger than 20 mm (except for crabs, shrimps, and lobsters, which have their own groups). Echinoderms and large gastropods are comprised of asteroids (sea stars), holothurians (sea cucumbers), echinoids (urchins and sand dollars), and large gastropods, both with and without shells. This aggregated group includes predators, scavengers, detritus feeders, and filter feeders. They are grouped together because the focus of the present model is forage fishes and directly associated sub-webs, and because information on some of these groups is limited for the West Florida Shelf.

Information from the Hourglass Cruises (e.g., Serafy 1979, Miller and Pawson 1984) was used to estimate composite biomass and diet compositions for this group. Thirteen stations were sampled at five depth intervals across the West Florida Shelf during this exploratory monitoring program. Distinct depth partitioning among species was revealed within several of the classes of organisms aggregated into Echinoderms and large gastropods. Even after aggregation, Echinoderms and large gastropods were generally concentrated near shore because of the effect of highly concentrated and abundant sand dollars.

The biomass estimate of Echinoderms and large gastropods on the West Florida Shelf is 19.246 $t{\cdot}km^{-2}$—the sum of biomass estimates for echinoids, holothurians, asteroids, and gastropods. The derivation of this biomass estimate is described in the following subsections and in Table 8.8. However, the estimates herein are likely to underestimate actual biomass because of the cryptic nature of urchins and the expectation of undersampling these organisms on reefs.

Opitz (1993) estimated echinoderms to be two orders of magnitude higher in a Caribbean coral reef ecosystem than our current estimates for the West Florida Shelf. However, echinoderms would be expected to be considerably more abundant on coral reefs than on the West Florida Shelf. Browder's (1993) estimate for total benthos on the West Florida Shelf was 5 $t{\cdot}km^{-2}$, which is considerably less than the total benthos biomass estimates in the present model.

The P/B value of 'echinoderms and large gastropods' on the West Florida Shelf (1.2 $year^{-1}$) is a mean of values from Lewis (1981) and Schwinghamer et al. (1986) in Opitz (1993). The Q/B value (3.7 $year^{-1}$) is the mean of the echinoids and holothurians from Pauly et al. (1993). The assimilation efficiency of echinoderms and large gastropods should be low (i.e., 0.60 maximum). See Table 8.9 for diet compositions.

Echinoids

Echinoids exhibit depth partitioning, but overall they are profoundly more abundant at the most shallow depths because of dense sand dollar (*Mellita quinquiesperforata*) beds in a narrow band beyond the surf zone. The various urchin species have preferred depth ranges, but they are relatively evenly distributed across the West Florida Shelf when considered overall (Serafy 1979).

The biomass of echinoids was estimated to be 18.789 t·km^{-2} on the West Florida Shelf based on samples collected during the hourglass cruises (Table 8.8). During these 1965 to 1967 cruises, a 0.91 m - wide box dredge was towed along the sea floor for 30 minutes at a speed of 2 knots, covering 1,685 m^2 area (0.001685 km^2) at each of 10 stations distributed across the West Florida Shelf (two east-west transects, each with five sampling stations, were located approximately adjacent to Tampa Bay and Fort Meyers, and were sampled monthly for 28 months).

Densities of echinoids (individuals ·km^{-2}) at each of five southern stations were calculated by dividing reported abundances by 0.04718 km^2 (28 months x 0.001685 km^2)(Table 1). Biomass estimates were then calculated by multiplying estimated abundances by mean individual weights for sand dollars (0.0000995 t·individual^{-1}; Lane and Lawrence 1980; converted from dry weights of the sand dollar) in the shallowest depth zone (6 m depth) and for urchins (0.000125 t·individual^{-1}; adapted from Lawrence and Byrne 1994) in the rest of the zones, where more spherical echinoids (i.e., urchins) predominated. The overall echinoid value should be considered a minimum biomass estimates since box dredge samples were not independent in time, and since sampling efficiency for this species was likely less than 1. However, it should be noted that these values include the tests and spines.

Table 8.8. Biomass estimates of echinoderms and large gastropods on the West Florida Shelf.

Depth (m)	Total individuals	Individuals (·km^{-2})	Biomass (t·km^{-2})
Echinoidea [a]			
6	39,870	845,061	84.084
18	1,201	25,456	3.182
37	536	11,361	1.420
55	1,094	23,188	2.898
73	892	18,906	2.363
Overall	43,593	184,794	18.789
Holothuriodea [b]			
6	34	360	0.118
18	69	731	0.240
37	92	975	0.320
55	5	53	0.017
73	13	138	0.045
Overall	213	226	0.148
Asteroidea [c]			0.258
Gastropoda [c]			0.050
Total			**19.246**

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[a] To calculate densities, total holothurian individuals were divided by 0.04718, corresponding to the area sampled at each station. Overall echinoid densities were divided by five since abundance data came from one station at each of five depths (Serafy 1979);
[b] Total holothurian individuals were divided by 0.09436, rather than 0.04718, to calculate densities, and overall holothurian densities were divided by ten, rather than five, since abundance [c] data came from two stations for each of five depths (Miller and Pawson 1984);
See appropriate subsection for estimation method used.

Bluhm et al. (1998) found the urchin *Strongylocentrotus pallidus* to have an average biomass of about 1 g afdw·m^{-2} in the northern Barents Sea, which is approximately equivalent to a wet weight biomass 5 to 7.5 t·km^{-2} (using conversions listed in Appendix 6). This range represents a relatively high biomass (see Bluhm et al. 1998), yet it is only a small portion of the estimate derived above for the West Florida Shelf. Ebert (1982) estimated Z (total mortality) to be as low as 0.58 for *Echinometra mathaei*. In equilibrium conditions, Z is equal to P/B. The P/B ratio suggested by Bluhm et al. (1998) for the North Barents Sea population of urchins was estimated to be 0.07 year^{-1}, a value that is far lower than the P/B estimate used herein. This very low P/B value in the northern Barents Sea may reflect a relatively slow-growth population structure in very cold waters of high latitudes, but these lower values should be kept in mind during model balancing.

Sea urchins are famous for eating macrophytes. For example, the consumption of seagrasses by urchin populations can rival or surpass the seagrass production (Moore and McPherson 1965, Camp et al. 1973). However, urchins consume a variety of other prey, such as bryozoans, forams, gastropods, worms, sponges, octocorals, coral polyps, mussels, sand dollars, crustaceans, and strips of fish (see Serafy 1979). Sand dollars eat detritus, diatoms, dynoflagellates, sponges, fine sand, and forams. Heart urchins consume detritus and other items. In one individual heart urchin (Meoma ventricosa ventricosa), 3,000 mollusks from 167 species were found (see Serafy 1979).

Holothurians

Taxonomically related to asteriods (sea stars) and echinoids (urchins), the 16 species of holothurians (sea cucumbers) on the West Florida Shelf exhibit depth partitioning, but overall they are more abundant in shallow to mid depths. These are deposit feeders, which ingest large quantities of sediment relative to their body size in order to absorb nutrition from small animals, microbes, and other organic material.

The estimate of holothurian biomass on the West Florida Shelf (0.148 t·km^{-2}) was made using abundance information from Hourglass Surveys (Miller and Pawson 1984), as in the echinoid example above. Density estimates were multiplied by 0.000328 t, assuming that the average weight of a West Florida Shelf holothurian is 328 g, twice the size of the holothurians that reside on Phillippines coral reefs (Pinto 1982 *in* Pauly et al. 1993). Table 8.8 also shows this derivation.

The dietary habits of holothurians are diverse. Many species are strictly deposit feeders, consuming sediment to extract microflora, meiobenthos, and some macrofauna (i.e., ‘small infauna’), but others are suspension feeders and plankton feeders. Still others can apparently be more selective with live prey (see Miller and Pawson 1984).

Asteriods

Little is known of the population dynamics of sea stars on the West Florida Shelf. The biomass estimate of asteroids (0.258 t·km^{-2}) was estimated by extrapolating from commercial bycatch (437.7 t·year^{-1}) based on the assumption of a 1% year^{-1} exploitation rate. This leads to a standing biomass estimate of 43775 t, which is equivalent to 0.258 t·km^{-2}. Catch data were provided by Bob Muller (Florida Fish and Wildlife Commission, April 2000). Although the FMRI landings data are reliable, the assumed exploitation rate used here is little more than a guess. The resulting biomass estimate for asteroids should be considered a placeholder.

Large gastropods

Biomass estimates for large gastropods on the West Florida Shelf are also unavailable to my knowledge. The biomass estimate of large gastropods (0.050 t·km^{-2}) was estimated by extrapolating from commercial bycatch (84.6 t·year^{-1}) based on the assumption of a 1%·year^{-1} exploitation rate. This gives a standing biomass estimate of 8460 t, which is equivalent to 0.050 t·km^{-2}. Catch data were provided by Bob Muller (Florida Fish and Wildlife Commission, April 2000). As for asteroids, the assumed exploitation rate used here is little more than a guess. As such, the resulting biomass estimate for large gastropods is a place holder.

The estimated diet composition for echinoderms and large gastropods (Table 8.9) is based on the qualitative diet composition information available for echinoids and holothurians, discussed in the previous sections and estimations for asteroids and gastropods.

Table 8.9. Estimated diet composition of echinoderms and large gastropods on the West Florida Shelf.

Prey categories	**Proportion of diet**				
	Echinoids [a]	Holothurians [a]	Asteroids [b]	Gastropods [b]	Overall [c]
Drift macrophytes	0.19	0.05	0.02	0.30	0.181
Macroalgae	0.13	0.02	0.00	0.10	0.122
Sessile epibenthos	0.10	0.03	0.18	0.10	0.102
Microbial heterotrophs	0.10	0.19	0.10	0.05	0.101
Sediment detritus	0.10	0.20	0.05	0.10	0.100
Microphytobenthos	0.10	0.18	0.05	0.10	0.099
Water column detritus	0.07	0.01	0.03	0.00	0.067
Small infauna	0.04	0.10	0.20	0.10	0.049
Seagasses	0.05	0.02	0.00	0.05	0.047
Meiobenthos	0.03	0.10	0.03	0.03	0.031
Phytoplankton	0.03	0.03	0.00	0.00	0.028
Echino. / lg. gastro.	0.02	0.00	0.10	0.02	0.023
Sm. mobile epifauna	0.02	0.05	0.02	0.01	0.020
Dead carcasses	0.02	0.02	0.02	0.01	0.020
Bivalves	0.00	0.00	0.20	0.03	0.009

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[a] Roughly adapted from Serafy 1979 and Miller and Pawson 1984;

[b] These are currently placeholder guesses;

[c] Overall echinoderms and large gastropods diets are averages weighted by the relative biomass estimates for each predator group.

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8.7 Adult shrimp

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The West Florida Shelf contains at least 17 known species of shrimp and 5 other shrimp genera (Darnell et al. 1987). Pink shrimp, *Farfantepenaeus duorarum*, are the most abundant of the three commercially important penaeid shrimps on the shelf (i.e., white, pink, and brown shrimp). Most of the pink shrimp catch is concentrated in the southern region of the West Florida Shelf, though an important portion of the fishery occurs in the big bend area (Figure 8.2). This group is called 'adult shrimp' because most of the information available for shrimp pertain to commercial sizes, or to individuals near commercial sizes. Smaller shrimp are included in the 'small mobile epibenthos' group, and this younger portion of the shrimp populations probably comprise most of the overall shrimp biomass on the West Florida Shelf.

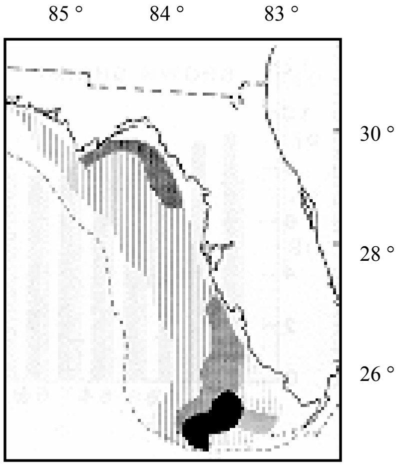

Figure 8.2. Distribution of pink shrimp catches in the Gulf of Mexico. Areas of higher catches are darker (from Klima 1989).

Adult shrimp are a very important component of the Gulf of Mexico from the standpoint of commercial fisheries. Virtually all the individuals caught are either newly recruited into the fishery (through growth) or they are smaller than legal size. Effort studies show that average fishing days per trip doubled in central and southern regions (Fort Myers, St. Petersburg, and Key west ports)(Nance 1993), yet relatively consistent annual catches over long time periods (Nance 1997, Nance and Harper 1999) indicates that shrimp as a group have withstood these intensive recruitment fisheries. This enigma has been the subject of some debate in the past (e.g. Cushing 1984), and the answer may lie in the competitive advantages afforded to shrimp given the exotic stresses imposed on the system as a whole (e.g., trawling, coastal eutrophcation)—explanations that are beyond simple population-exploitation analyses.

The considerable uncertainty of adult shrimp biomass estimates for the West Florida Shelf does little to alleviate this conundrum. Several approaches to estimate the biomass of shrimp on the West Florida Shelf are presented in the following paragraphs to provide a range of choice of biomass estimates, as well as confidence bounds. Most of these methods, including the one ultimately chosen to estimate shrimp biomass, are based on two sources of landings data: the National Marine Fisheries Service (NMFS) and the Florida Marine Research Institute (FMRI).

The 1998 NMFS landings estimate for the West Florida Shelf including the Florida Keys (i.e., statistical zones 1-9) was 8,324 tonnes (1,8346,160 pounds) of pink, brown, and white shrimp (Nance, unpublished data). These data covered data collection from all the port agents in the Gulf of Mexico. The FMRI total shrimp landings estimate for the West Florida Shelf was 5,339 tonnes for all the areas *except* the Florida Keys (except Monroe County landings) (R. Muller, FMRI, unpublished data). These landings data are from the Florida state trip ticket information program. The estimates from these two independent programs are only 8% different when FMRI's 1998 Florida Keys landings data (2,330 tonnes) are added to their estimate for the West Florida Shelf area (the resulting inclusive landings value is 7,669 tonnes). This verification of accuracy of the two approaches is apparent despite different delineations of the annual shrimping season (NMFS data corresponds to the calender year, while FMRI data corresponds to the July 97-June 98 season). The FMRI value was chosen for the purposes of the present model because the defined area does not include the Florida keys, and to keep the model consistent with respect to other biotic compartments whose parameters are based on the same 1998 FMRI landings database.

The total catch of all shrimps on the West Florida Shelf in 1998 is estimated to be 7,297 tonnes. This catch estimate is the sum of the total shrimp landings reported for that year (5,339 tonnes; R. Muller, FMRI, unpublished data) and the estimated the annual shrimp discards on the West Florida Shelf (1,958 tonnes; adapted from Cushing 1984). The discards of organisms other than shrimp from the shrimp trawl fishery is taken as four times the amount of shrimp discard (*see* Section 5 for explanation of shrimp discard derivation). To put these estimates in regional perspective, the total penaeid shrimp catch for the western central Atlantic region (the Caribbean, the Central American states, and the Gulf of Mexico) has fluctuated around 170,000 tonnes (373,850,000 lbs.) for the last two decades. Most of this catch comes from the Gulf of Mexico (FAO 1997). Vidal (2000) estimated the annual GoM shrimp catch to be 144,000 $t{\cdot}year^{-1}$ (317,520,000 lbs.) by adding Mexican and US reported landings (SEMARNAP 1987, NMFS 1987). If these estimates are accurate, the catch of shrimp on the West Florida Shelf comprises only 4.4% of the total shrimp catch in the Gulf of Mexico.

An estimate of the overall adult shrimp biomass on the West Florida Shelf, 0.0859 $t{\cdot}km^{-2}$, or 14,595 tonnes overall was calculated by dividing the 1998 West Florida Shelf shrimp catch (~7,297 tonnes or 16,090,767 lbs.) by a 50% exploitation rate corresponding to the findings of a recent VPA assessment of Gulf of Mexico shrimp (J. Nance, unpublished estimate). The estimate derived above is taken as the biomass of adult shrimp on the West Florida Shelf for the purposes of initial parameterization of the

Ecopath model. This estimate falls in the center of the range of other estimates derived during this exercise (Table 8.10). The next higher estimate in that range (0.2635 t·km^{-2}) is a back-calculation from Walsh's (in Cushing 1984) estimate of total shrimp production on the West Florida Shelf (1.0752 t·km^{-2}·year^{-1}; 70% area-adjusted). This production estimate was divided by the adult shrimp P/B estimate (4.08 year^{-1}).

Population parameter estimates for Florida adult shrimp do vary considerably, sometimes leading to profoundly divergent estimates of abundance and biomass (Table 8.10). For example, a biomass estimate of 0.4293 t·km^{-2}, or 72,974 tonnes can be derived in the same manner using an exploitation rate of 10%, which is based on the shrimp catchability coefficient from another study (Steele 1997). Application of Ehrhardt and Legault's (1999) assumed fishing mortality rate of 1.4 for pink shrimp in Florida Bay to the same west Florida catch data leads to a West Florida Shelf standing biomass estimate of 0.0307 t·km^{-2}, or 5,212 tonnes. Note that this example is more than an order of magnitude smaller than the first.

Table 8.10. Estimates of adult shrimp biomass on the West Florida Shelf.

Approach [a]	**Sources**	**Biomass**		
		t·km^{-2}	**Tonnes**	**Pounds**
F_{MSY}	SAFMC 1999	0.0201	3,421	7,542,431
F = 1.4	Ehrhardt & Legault 1999	0.0307	5,212	11,493,405
50% exploitation	J. Nance (unpub. estimate)	**0.0859**	14,595	32,181,534
Production estimate	Walsh (in Cushing 1984)	0.2635	44,800	98,784,000
10% exploitation	Steele 1997	0.4293	72,974	160,907,670
Combined fishery-independent estimates	Coleman & Koenig 1998, Darnell et al. 1987	0.6273	107,307	236,613,412
Unknown method, minus 30%	Browder 1993	8.708	1,480,360	3,264,193,800

[a] Fishery-dependent approaches combined the 1998 reported shrimp landings (5,339 tonnes, or 11,772,495 lbs.) and estimated discards (1,958 tonnes) with different scenarios of exploitation rate to estimate standing biomass on the 170,000 km^2 West Florida Shelf. See text for a detailed explanation of each approach; fishery-independent approaches are explained in the accompanying text.

An even smaller biomass estimate for the West Florida Shelf, 0.0201 t·km^{-2} or 3,421 tonnes can be derived by back-calculating from MSY and the annual catch estimate used above. Considering that the mean total landings of shrimps in the south Atlantic region of US is currently used as a proxy for MSY (South Atlantic Fisheries Management Council, 1999), the rationale is that at B_{MSY} (biomass that produces the maximum sustainable yield) the exploitation rate (F/Z) should be in the order of 0.4. With a natural mortality rate of 3.6 year^{-1}, F_{MSY} is estimated at 2.13 year^{-1}, and B_{MSY} at 1,806.25 tonnes. There are, however, many sources of uncertainty in such a calculation.

Such an extreme variability in estimates calls for a comparison to other estimates and approaches. Both of these estimates appear very low when compared to other estimates for shrimp biomass in other Gulf of Mexico habitats, as summarized by Vidal

(2000). These habitats include GoM soft bottoms 12.44 t·km^{-2} (Browder 1993), estuaries 13.11 t·km^{-2}, and other non-estuarine areas 11.59 t·km^{-2}. Applying Browder's soft-bottom estimate to the West Florida Shelf area (and subtracting 30% for hard bottoms) leads to an estimate of (1,480,360 tonnes, or 3,264,193,800 lbs.)—an enormous biomass that seems very unlikely given more recent information.

An alternate, fishery independent, approach for estimating adult shrimp biomass on the West Florida Shelf resulting in an estimate of 0.6273 t·km^{-2}. This was derived by combining a recent estimate of pink shrimp abundance in big bend area seagrass beds with an older estimate of shrimp abundance on the broader West Florida Shelf (documented in the following paragraphs). The overall estimate used here was the area-weighted average of these two estimates. The resulting estimate is equivalent to a biomass of 107,307 tonnes (236,613,412 lbs.) over the whole of the West Florida Shelf. Dividing the 1998 total Florida shrimp catch (7,297 tonnes) by the total biomass estimate leads to an annual shrimp catch rate of 0.07, which seems low considering that the area swept for shrimp on the West Florida Shelf is quite high (B. Mahmoudi, FMRI, pers. com., 17 July 2000). This low back-calculated estimate for shrimp catch rate indicates that the biomass value resulting from this composite approach, detailed in the following paragraphs, is an overestimate.

The rough biomass estimate for pink shrimp in big bend area sea grass beds (used above) was calculated from a reported of 500 and 20,000 individuals per hectare (Coleman and Koenig 1998). These values lead to a median estimate of 6.15 t·km^{-2} based on a mean adult shrimp weight of 6g (Pauly and Christensen 1993). My assumption that seagrass beds containing such densities cover 10% of the West Florida Shelf leads to a biomass estimate of 0.615 t·km^{-2}, if spread over the 170,000 km^2 area of the West Florida Shelf.

A rough estimate of the biomass of adult shrimp on the other areas of the West Florida Shelf, 0.0137 t·km^{-2}, was calculated using abundance estimates from Table 3 in Darnell et al. (1987), which shows abundance of shrimp by species captured in 433 trawl samples that were distributed throughout the West Florida Shelf area (Table 8.11). The sampled area corresponding to the adult shrimp abundance data (28.148 km^2) was calculated by multiplying the distance of each trawl tow (5.556 km) with the standardized effective width of the trawl net opening (0.0117 km) resulting in a single tow swept area of (0.0644 km^2; corresponding to a net headrope length of 0.0137 km (45 feet) based on the empirical equations presented by Darnell et al. (1987)). The swept area of one tow was then multiplied by the number of tows in the sampling regime (433 tows) resulting in an overall swept area of 28.148 km^2. The density of adult shrimp on the West Florida Shelf (2,282 individual shrimp ·km^{-2}) was then calculated by dividing the number of captured shrimp (64,235 individuals) by the sampled area (28.148 km^2). Adult shrimp biomass (0.0137 t·km^{-2}) was then calculated by applying an average biomass for an individual shrimp (0.000006 t) from Pauly and Christensen (1993). The density estimates from each of the studies described in this and the previous paragraph were multiplied by the proportion of area that they inhabit on the shelf. The two adjusted values were subsequently added.

Table 8.11. Number of WFS shrimp caught in 433 trawl samples in a swept area of about 28 km^2.

Scientific name	Common name	Number	Percent
Solenocera atlantidis		18,169	28.29
Farfantepenaeus duorarum	Pink shrimp	10,408	16.20
Trachypeneus sp.		6,624	10.31
Sicyonia brevirostris	Rock shrimp	6,484	10.09
Trachypeneus similis		4,489	6.99
Metapenaeopsis goodei		4,452	6.93
Sicyonia dorsalis	Rock shrimp	2,862	4.46
Farfantepenaeus aztecus	Brown shrimp	2,417	3.76
Mesopenaeus tropicalis		2,310	3.60
Solenocera sp.		1,608	2.50
Parapenaeus sp.		1,416	2.20
Sicyonia sp.		1,119	1.74
Trachypeneus constrictus		665	1.04
Sicyonia typica	Rock shrimp	444	0.69
Litopenaeus setiferus	White shrimp	368	0.57
Parapenaeus longirostris		187	0.29
Penaeus sp.		66	0.10
Solenocera vioscai		54	0.08
Sicyonia stimpsoni	Rock shrimp	33	0.05
Sicyonia burkenroadi	Rock shrimp	28	0.04
Sicyonia laevigata	Rock shrimp	27	0.04
Solenocera necopina		5	0.01
Total		64,235	100.00

Notes: Sampling is reasonably representative of the West Florida Shelf as a whole, and it indicates the relative abundance distribution of both commercial and non-commercial shrimp species (values directly from Darnell et al. 1987, but scientific names are updated here).

The ratio of production to biomass (P/B = 4.08 year^{-1}) for West Florida Shelf adult shrimp was calculated using the following approach. Ehrhardt and Legault (1999) assumed the natural mortality (M) of pink shrimp to be 3.6; the fishing mortality (F) is 1.4. Likewise, Parrack (1981) found M to equal 2.8 and F to be 0.36 for brown shrimp, which was within 5% of the average annual catch of pink shrimp in 1998. Since P/B, under equilibrium, equals total mortality (Allen 1971), and Z = M + F, the P/B ratios can be roughly estimated as 3.6 + 1.4 = 5 year^{-1} for pink shrimp and 2.8 + 0.36 = 3.16 year^{-1} for brown shrimp, resulting in a mean shrimp equation of 3.2 + 0.88 = 4.08 year^{-1}. The P/B estimate by Arreguín-Sánchez et al. (1993) for the north continental shelf ecosystem of the Yucatan provides some verification for this rough estimate, as it is close (5.38 year^{-1}).

The ratio of consumption to biomass for adult shrimp of the West Florida Shelf (19.2 year^{-1}) was taken from an independent estimate for the adult shrimp of the Yucatan continental shelf (Arreguín-Sánchez et al. 1993).

The diet of adult penaeid shrimp includes sediment, detritus, algae, and benthic organisms nematodes, annelids, molluscs, crustaceans, higher plants, algae, and diatoms. These have been found in the stomachs of white shrimp, which are considered selective particulate feeders (Steele 1997). Brown shrimp ingest detritus and algae throughout their lives, but they actively seek out polychaetes, nematodes, and chironomid larvae as adults (Broad 1965 *in* Jones 1973). Eldred et al. (1961) found the following groups in the stomachs of pink shrimp: sand, debris, diatoms, seagrass particles, dinoflagellates, foraminiferans, nematodes, polychaetes, ostracods, copepods, mysids, isopods, carridean shrimp, caridean eggs, molluscs, and fish scales. The ontogenetic shift in the diet of shrimp is important to note. Juvenile shrimp consume detritus and a small amount of fishery discards, while adults primarily consume meiobenthos, macrobenthos, and fishery discards (Cushing 1984). Shrimp are important prey for other species; they are eaten by virtually any animal big enough and inclined to catch them (Steele 1997; also see Costello and Allen 1970). Huff and Cobb (1979) presented quantitative diet information for seven species of shrimp on the West Florida Shelf and this was adapted here (Table 8.12). The assimilation efficiencies of adult shrimp are low when the algae mat is the main source of food or when the diet is largely carbonate (Cushing 1984). But, the AE can be surprisingly high when the food consists of detritus (Qasim and Easterson 1974).

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8.8 Large crabs

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The three most conspicuous crabs on the West Florida Shelf are the blue crab (*Callinectes sapidus*), the stone crab (*Menippe mercenaria*), and the western Gulf stone crab (*M. adina*). Others include various species of hermit crabs (e.g., *Pylopagurus operculatus* and *Clibanaris vittatus*), arrow crabs (e.g., *Stenorynchus seticornis* and *Metoporhaphis calcarata*), and spider crabs (e.g., *Stenocionops furcatus*). Each crab species exploits a unique niche, but for the purposes of the present trophic model, all crab species are aggregated into one functional group. In addition, horseshoe crabs (*Limulus polyphemus*) are included in the crab group, even though they are phylogenetically distant from true crabs. This crab group includes only individuals larger than 5 cm; crabs smaller than 5 cm are included in the ‘small mobile epifauna’ group. The derivation of generalized parameters for West Florida Shelf large crabs are shown in Table 8.13.

Table 8.13. Summary of *Ecopath* parameters for large crabs on the West Florida Shelf.

Type of crab	1998 landings [a] (t)	Biomass (t·km^{-2})	Biomass (t)	Biomass (1000s of lbs.)	P/B (year^{-1})
Blue crab	4,012.45	0.0381 [b]	6,482	14,293	1.12 [f]
Stone crab	1,127.00	0.0323 [c]	5,497	12,122	1.69 [g]
Hermit crab	3.46	0.0020 [d]	346	762	
Arrow crab	0.82	0.0005 [d]	82	181	
Spider crab	0.33	0.0002 [d]	33	73	
Horseshoe crab	131.25	0.0154 [e]	2,618	5,773	
Generalized crab	5,275.31	0.0886	15,058	33,203	1.3816 [h]

[a] Landings from FMRI landings database combining federal and state fishery landings data; [b] Derived by applying a mean fishing mortality to mean catches; [c] Derived from landings and exploitation assumptions (see text); [d] Derived by applying assumed exploitation rates of 0.01 to 1998 catches; [e] Derived by applying assumed exploitation rates of 0.05 to 1998 catches; [f] P/B value equivalent to total mortality from GSFMC, in press; [g] P/B value equivalent to total mortality from Ehrhardt and Restrepo 1989; [h] Biomass-weighted average of the two crab groups with P/B estimates.

The biomass estimate used for large crabs of the West Florida Shelf (0.0886 t·m^{-2}) is the sum of the independently-estimated biomasses of blue, stone, hermit, arrow, spider, and horseshoe crabs. The ratio of production to biomass (P/B) used for large crabs in this model (1.3816 year^{-1}) is a biomass weighted average of empirically-based P/B estimates for blue and stone crabs (Table 8.13). The derivation of these parameters can be found in the following sub-sections on individual crab species. The estimate of Q/B (consumption/biomass) used for this composite group (8.5 year^{-1}) is an independently-estimated parameter used in an *Ecopath* model of the nearby Yucatan continental shelf (Arreguín-Sánchez et al. 1993). The estimated diet composition for large crabs on the West Florida Shelf is a biomass weighted average of the estimated diets of the seven crab groups in this composite crab group (Table 8.14). Specific information on diets can be found in the sub-sections that follow. There is considerable uncertainty in the parameters for this group, and continuing research will lead to more representative estimates.

Table 8.14. Estimated diet composition for large crabs on the West Florida Shelf.

Prey category	Proportion of diet in six categories of large crabs						Overall diet
	Blue [a]	Stone [b]	Hermit [c]	Arrow [c]	Spider [c]	Horseshoe [d]	
Bivalves	0.25	0.25				0.930	0.364
Sessile epibenthos	0.14	0.25		0.16	0.20		0.153
Small infauna	0.03	0.03	0.09	0.30	0.30	0.020	0.032
Large crabs	0.20	0.10			0.02		0.120
Sediment detritus	0.05	0.11	0.30	0.15	0.11	0.005	0.070
Microbial heterotrophs	0.05	0.05	0.20	0.15	0.11	0.005	0.045
Fishes	0.14	0.01			0.02		0.061
Microphytobenthos	0.05	0.04	0.10	0.15	0.05	0.005	0.038
Meiofauna	0.02	0.04	0.20	0.03	0.02	0.005	0.029
Echinoderms & lg. gastropods		0.10			0.10	0.015	0.041
Adult shrimp	0.06	0.01			0.02	0.005	0.029
Dead carcasses	0.01	0.01	0.01	0.01	0.01	0.005	0.009
Drift macrophytes	0.01		0.10	0.05	0.04	0.005	0.008

Notes: Diets in Proportion wet weight;
[a] Adapted from quantitative diet composition provided by Laughlin (1982);
[b] Adapted from D. Scholnick, Eckerd College, St. Petersburg, pers comm. July 2000;
[c] Rough estimates of diet compositions;
[d] Adapted from (Botton 1984 and Botton and Ropes 1989).

Blue crab

Blue crabs (*Callinectes sapidus*) are estuarine animals, and so occur in highest densities along west Florida's coastal embayments. The estimate of blue crab biomass on the West Florida Shelf (0.0381 $t \cdot km^{-2}$) was derived by dividing the average landings in the region from 1989 to 1997 (4,012 tonnes; from FMRI landings database combining federal and state fishery landings data) by the mean fishing mortality (0.619; provided by GSMFC, in press.) to roughly estimate the biomass of the whole population (6,482 tonnes, or 14,293,128 lbs.). This overall biomass was then divided by the estimated area of the West Florida Shelf to 200 m depth (170,000 km^{-2}), resulting in a blue crab biomass estimate of 0.0381 $t \cdot km^{-2}$ on the West Florida Shelf. This biomass of blue crabs is overwhelmingly concentrated inshore.

Total mortality of blue crabs has been estimated to be 1.12 ± 0.02 (GSFMC, in press.). This value (1.12) is used as the P/B estimate for blue crabs since P/B equals total mortality when populations are at equilibrium (Allen 1971).

Blue crabs are opportunistic benthic omnivores, feeding on fish, aquatic vegetation, mollusks, crustaceans, and annelid worms (Darnell 1961, Muller 1999). In Apalachicola Bay, Laughlin (1982) found that blue crabs fed on fishes, xanthid crabs, smaller blue crabs, and bivalves such as American oysters, Mercenaria hard clams, coot clams, mussels, rangia, and periwinkles (Millikin and Williams 1984 in Williams et al. 1990). Smaller blue crabs (3 – 7.4 cm) contain equal volumes of crustaceans and molluscs, but larger blue crabs (7.4 – 12.5 cm) contain larger proportions of molluscs (Jaworski 1972 in Steele 2000).

Stone crab

The two stone crab species on the West Florida Shelf (*M. mercenaria* and *M. adina*) feed primarily on bivalves until their claws are pulled off by fishers. The small percentage of stone crabs that survive the initial dismemberment and the associated increases in predation risk (~30%) undergo the dietary stress of switching to detritus feeding while their claws regenerate. The number of stone crab traps in the region attest to the importance of the fishery in Florida: Muller and Bert (1997) estimated that 600,000 traps existed in Florida, but the consensus of participants of the fishery is that the number of traps is closer to 1,000,000 (T. Bert, Florida Marine Research Institute, pers. comm., 11 July 2000).

Florida boasts the only extensive stone crab fishery, and most of it occurs along the gulf coast. Fully 75-80% of the catch is landed in southwest Florida; 10-15% is landed in NW Florida; and 10-15% is landed elsewhere. Overall, approximately 3 - 3.5 million pounds of stone crab claws are landed annually in Florida, but only a portion of these claws come from the West Florida Shelf (when the Florida Keys area are treated separately). Like lobsters, the density of stone crabs is undoubtedly lower in the areas north of the Keys due to physical habitat differences, but also because of thermal stress (*M. mercenaria* prefers a temperature range of 23-26°C, while the water temperature reaches 30°C on some parts of the West Florida Shelf north of the Keys) (T. Bert, Florida Marine Research Institute, Pers. Comm., 11 July 2000).

The estimate of stone crab biomass on the West Florida Shelf, 0.0323 $t{\cdot}km^{-2}$, or 5,497 Tonnes (12,122,000 lbs.) is based on the average annual landings between 1988 and 1999 (provided by J. O'hop, M. Tupper, and S. Brown, Florida Marine Research Institute, 13 July 2000; Florida Fish and Wildlife Conservation Commission Marne Fisheries Information System) and the following assumptions: (1) half of Monroe County's stone crab landings come from within the defined West Florida Shelf (excluding the Keys), (2) an average stone crab's claw makes up 41% of its total weight (D. Scholnick, Eckerd College, St. Petersburg, pers. comm., July 2000), (3) the fishing industry lands claws from crabs that represent half of the standing biomass of stone crabs each season (when all age classes larger than 5 cm are considered). Based on these assumptions, half of the Monroe County landings were subtracted from the average landings over the last ten years to exclude the Keys, claw weight was converted to crab weight by dividing by 0.41, and the resulting biomass was doubled to roughly account for the biomass of the population in individuals that are not represented in landings.

The resulting estimate is close to half of the median of the range of standing biomass suggested by T. Bert (20-30 million pounds; Florida Marine Research Institute, pers.

comm., 11 July 2000). Recent field observations of lower-than-expected occurrences of regenerated claws (C. Meyer, personal observations, July 2000; lower than the 10% of total landings suggested by Savage et al. 1975) indicates either a higher population than estimated above (e.g., closer to T. Bert's suggestion) or a lower de-clawing survival rate. However, landings of stone crabs have reached a plateau, and the managers currently tracking the fishery believe that virtually every adult crab is captured each year, and that de-clawing survival rates that are lower than sometimes believed (8-30% rather than 25-97%)(J. O'hop, M. Tupper, and S. Brown, FMRI, pers. comm.,13 July 2000). This implies that the Florida stone crab fishery has become a recruitment fishery rather than a reusable resource in the sense of Erhardt and Restrepo (1989). The uncertainty of the stone crab biomass estimate for the West Florida Shelf is high irrespective of these considerations, as our third assumption in the previous paragraph is a place-holder estimate.

The estimated total mortality of stone crabs (1.69 year^{-1}) is used as the P/B estimate for the purposes of this model based on the notion that P/B equals the rate of total mortality (Z) as the product of the instantaneous rate of natural mortality (M) and fishing mortality (F) in a population in equilibrium (Allen 1971). This estimate of total mortality was derived from estimates of instantaneous natural mortality rates (1.61 year^{-1}) and fishing mortality (0.08 year^{-1}) the latter of which was based on the specified claw size limit of 70 mm propodus length and estimated declawing survival rates (*see* Ehrhardt and Restrepo 1989).

As mentioned above, the diet of stone crabs consists of bivalves and some large gastropods. More specifically, their diet includes *Mercenaria mercenaria*, Florida fighting conchs, mussels, Atlantic surf clams, tulip shells, and Atlantic bay scallops. The diet of crabs whose claws have been removed shifts to detritus, microbial heterotrophs, and microphytobenthos.

Horseshoe crab

The horseshoe crab, *Limulus polyphemus*, is not a crustacean, but a living fossil related to spiders (arachnids). This species resides in estuarine and continental shelf habitats (Botton and Loveland 1989), and their prolific spawning aggregations can be observed at and above the waterline on low energy beaches during spring tides. They are scavengers and they prey on benthic infauna. Although taxonomically distinct from true crabs, horseshoe crabs have enough convergent morphological and ecological similarities to be grouped with the crab functional group for the purposes of this model.

The biomass estimate of Limulus on the West Florida Shelf (0.0154 t·km^{-2}, or 2,625 tonnes, or 5,788,125 lbs. on the overall shelf) is a rough approximation, based only on reported 1998 landings (131.249 tonnes) divided by an assumed catch rate (0.05).

Horseshoe crabs are dietary generalists and opportunistic foragers (Botton 1984, Botton and Haskin 1984), but they appear to specialize on bivalves, as Botton found *Limulus* guts to contain primarily bivalves and other mollusks. Interestingly, Botton and Ropes (1989) found that gut contents in *Limulus* comprised only 0.23 % of the total body mass of males and a mere 0.097% of the body mass of females (the average weight of a male was 0.947 kg compared with 2.257 kg for a female). The estimated diet composition for Horshoe crabs on the West Florida Shelf is shown in Table 8.15.

Table 8.15. Diet composition of horseshoe crabs on the Atlantic continental shelf.

Prey categories	Proportion of diet
Bivalves	0.932
Gastropods	0.052
Polycheates	0.003
Crustaceans	0.002
Misc.	0.011

Notes: These diets were adapted from Botton and Roper 1989 to West Florida Shelf model groups for integration into the overall 'large crab' diet (Table 8.14).

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8.9 Lobsters

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Two general types of lobsters occur on the West Florida Shelf—spiny lobster (*Panulirus arqus*) and slipper lobsters (Scyllaridae). Spiny lobster range from North Carolina, USA to Rio de Janeiro, Brazil, and the US fishery for spiny lobster is concentrated in South Florida, as the region offers good habitat for juvenile and adult life stages (GoM&SAFMC 1982). Spiny lobsters are truly a transboundary stock as the planktonic larvae of the South Florida population likely originate in the Caribbean (Ingle et al. 1963, Little 1977). Postlarvae and juvenile spiny lobsters recruit abundantly into Florida Bay because the local seagrass, macrophyte, and mangrove habitats are ideal for rearing and growth. Spiny lobsters move out of these nursery areas to deeper water reef habitats as they approach commercial sizes (Lyons et al. 1981). Much of this habitat is in the Florida Keys—outside our defined area—but many other adult lobsters reside on the West Florida Shelf. Spiny lobsters emigrate from this ‘source’ region as adults by walking along the sea floor perhaps to the east around the Florida peninsula, but the details of their migration are not well known (R. Muller, FMR, pers. comm., July 2000; *also see* Kanciruk and Herrnkind 1978).

Approximately 90% of the US spiny lobster catch occurs in the Florida keys, and some evidence suggests that fishing effort has been higher then optimal in the recent past (Muller et al. 1997). There is considerable uncertainty in any attempts to estimate overall biomass of spiny lobsters on the West Florida Shelf because of the limited nature of the available information—especially information about the relationship of catch to stock size (R. Muller and J. O’hop, FMRI, pers. comm., July 2000).

The estimate of lobster biomass on the West Florida Shelf used in this modeling exercise (0.007 $t{\cdot}km^{-2}$, or 1,186 tonnes, or 2,614,367 lbs.) is based on the average annual landings between 1988 and 1999 (provided by J. O’hop, M. Tupper, and S. Brown, Florida Marine Research Institute, 13 July 2000; Florida Fish and Wildlife Conservation Commission Marne Fisheries Information System). I summed the mean landings from all west Florida counties and subtracted half of Monroe County’s landings to estimate the total landings from the defined West Florida Shelf area (excluding the keys). This value was doubled to estimate spiny lobster biomass on the wFs, assuming that half of the overall biomass is taken annually. This spiny lobster biomass estimate was then doubled to account for scyllarid lobsters, assuming scyllarid lobster biomass is equal to that of spiny lobsters.

The P/B and Q/B estimates of 0.9 $year^{-1}$ and 8.2 $year^{-1}$ respectively are taken from independent estimates for lobsters from another *Ecopath* model of the nearby Yucatan continental shelf (Arreguín-Sánchez et al. 1993). The estimates for lobster diet composition specified in Table 8.16 are roughly estimated by the present author, and should be refined based on empirical information from the region.

Table 8.16. Rough estimate of lobster diet

composition on the West Florida Shelf.

Group	**Proportion**
Small infauna	0.20
Adult shrimp	0.10
Sessile epibenthos	0.10
Bivalves	0.10
Sediment detritus	0.10
Lobsters	0.05
Large crabs	0.05
Microbial heterotrophs	0.05
Microphytobenthos	0.05
Dead carcasses	0.05
Benthic fishes	0.05
Demersal fishes	0.05
Ichthyoplankton	0.02
Meiobenthos	0.01
Other mesozooplankton	0.01
Water column detritus	0.01

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8.10 Stomatopods

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Stomatopods, or mantis shrimp, are crustaceans that inhabit burrows and crevices on the shallow sea floor of tropical and sub-tropical regions (Caldwell 1987). Stomatopods are carnivorous predators that use their massive raptorial second thoracopods (Caldwell and Childress 1989) and their excellent vision to surprise shrimps, crabs, mollusks, fishes, and other animals with their powerful strikes. They are divided into two functional groups—smashers (i.e., neogonodatylids) and spearers (i.e., squillids)—based on the function and morphology of the raptorial thoracopod (Caldwell and Childress 1989 in Caldwell and Dingle 1976). The Lysquillina and other small borrowing squillids and lysiosquillids are lie-in-wait predators. *Squilla empusa* and other large *Squilla* will forage actively at night away from their burrow. Neogonodactylus do most of their foraging during frequent trips away from their cavity, often going up to several meters to find a snail or crab and then return with it to their cavity for processing (Caldwell et al. 1989). At least twenty-eight species of stomatopods occur in the Gulf of Mexico. Thirteen species identified on the West Florida Shelf are known to inhabit bathymetric ranges from the littoral zone to depths exceeding 200 m (Camp 1973).

The cryptic nature of stomatopods makes estimation of their biomass challenging, but their behaviorally-dramatic lifestyles and their role as predators in structuring benthic communities makes their study particularly desirable, especially in the context of whole-system trophic models capable of dynamic simulation. Stomatopods might have keystone effects (proportionally large effects) related to their predation on herbivores and detritivores. For this reason, it is important to derive reasonably accurate estimations of their population parameters in order to capture the structure and dynamics of the lower trophic levels in the West Florida Shelf model.

The rough estimate of stomatopod biomass used here for the West Florida Shelf model (0.9944 $t \cdot km^{-2}$) was derived taking the average of estimates from two sources: Wenner (1989), and a West Florida Shelf estimate based on the Panamanian studies of Caldwell et. al. (1989, 1991, unpublished data). Wenner (1989) used trawl surveys to examine the composition and abundance of decapods and stomatopods between 8 and 20 m depths on the east coast of Florida. We estimated the biomass of his collected stomatopods to be 0.0987 $t \cdot km^{-2}$ by dividing the weight of his collected specimens by the total area covered by his surveys (1.61 km^2; i.e., 2.2 hectares x 18 stations x 4 cruises). This estimate only includes the *Squilla empusa*, *S. neglecta*, and *Lysiosquilla scabricauda* found in the coastal area between 8-20 meters depth. The limited comparability of this study to the West Florida Shelf as a whole (to 200 m depth) is underscored by the presence of at least thirteen different species endemic to the latter region (Camp 1973). Despite issues of limited comparability, Wenner's (1989) study is useful to us, as it provides some guideline for stomatopod density in the vicinity of the area delineated for the construction of the West Florida Shelf model.

Density estimates of the Panamanian stomatopods (Caldwell et al. 1989, R. Caldwell, unpublished data) were also used to derive a biomass estimate of the West Florida Shelf stomatopods (1.89 t·km^{-2}). This estimate is derived by applying Panamanian density estimates for *Squilla* and *Neogonodoctyla* groups to the West Florida Shelf stomatopod fauna based on relative areal distributions of similar habitats. The *Neogonodactyla* reside primarily in hard bottom habitats, and the *Squilla* live in soft bottoms. Hard bottoms are estimated to make up ~35% of the total area of the West Florida Shelf (Parker et al. 1983, Phillips et al. 1990 *in* Phillips and Thompson 1990), leaving ~65% of the area covered by soft sediments. In addition, Stomatopods are likely to be most abundant in areas shallower than 60 m, which takes up approximately 67% of the area of the West Florida Shelf, or 114,222 km^{-2} of the ~170,000 km^{-2} shelf (see Houhoulis, this volume). The estimate was derived by taking a habitat-weighted estimate of the two groups (2.5 t·km^{-2} · 0.35) + (3 t·km^{-2} · 0.65) and then multiplying the result by 0.67 to adjust the estimates by a simple assumed depth attenuation gradient with the pivot at 60 m depth. Derivations of group-specific biomass values are shown in below.

The estimate for all neogonodactylids over 16 mm on hard bottom habitats on the east Panama shelf is 5 individuals·m^{-2}, and the areal biomass estimate is 2-3 t·km^{-2} (2-3 g·m^{-2}). Densities of *N. bredini* between 36-45 mm in length have been documented to be 1.5 individuals·10 m^{-2} (Caldwell et al. 1989), but this was only one third the density of similar sized neogonodactylids on other back reef areas. Indeed, a large proportion of the population is smaller and larger than this 36-45 mm size class, and much higher densities of neogonodactylids have been revealed in this region (*see* Table 8.17). The estimate for all neogonodactylids over 16 mm is 5 individuals·m^{-2}, equaling approximately 2-3 t·km^{-2} (Caldwell et al. 1991).

The biomass estimate for all squillids and lysiosquillids in the Bay of Panama is ~3 t·km^{-2}, based on 200 (1 m^{2}) quadrats (Caldwell, unpublished data). Four species of squillid inhabited the soft bottoms of the bay, with the largest getting up to 18 cm. The median size was about 40 mm and densities were around 5-6 m^{-2}. The 40 mm animals weighed about 0.7 g, but squillids in the 10 cm range weighed approximately 10 g and the largest 16 cm animals would have weighed over 20 g.

Table 8.17. Estimated biomass of neogonodactylids in hard bottom habitats of the east Panama shelf.

Neogonodactylid size class (mm)	**Density (individuals·m^{-2})**	**Individual weight (g)**	**Biomass (t·km^{-2})**
16	4	0.075	0.288
35		0.5	
40	1	1.0	2.0
50		2.0	
60		3.0	
Overall	5		~2-3

Note: Adapted from Caldwell (1991)

The lack of quantitative density information about stomatopods on the West Florida Shelf compelled us to rely on density information from these similar settings. The studies used for the biomass estimate focused on relatively shallow areas rarely exceeding 20 m (Wenner 1989). No substantial information is available for stomatopods living in deeper waters, although Camp (1973) noted the occurrence of squillids to a depth of 346m in the Gulf of Mexico. The biomass estimate we chose for initial parameterization of the *Ecopath* model of the West Florida Shelf (0.9944 $t \cdot km^{-2}$) was the average of the two methods presented here. In the survey by Wenner (1989) the average weight for the Squilla sp. was 14.5 g. This was considerably higher than the average weight of 2.5 g estimated by the studies in Panama (Caldwell et al 1989), and weight differences may be one source of the discrepancy observed here. The trawl nets utilized by Wenner (1989) may have skewed his samples towards larger specimens, but the trawling approach may have underestimated stomatopod biomass overall.

The production/biomass ratio of stomatopods on the West Florida Shelf was calculated based on the estimated life spans of *Squilla sp* (3-4 years) and *Neogonodatyla sp* (5-6 years) (R. Caldwell, unpublished data). As in Alagajara (1984), the species life span was considered to be the age at which 99% of a cohort had died of natural mortality. That means, under the assumption of constant exponential rate of decline of numbers in a cohort, that

$$M = - \ln (0.01)/T$$

where M is the natural mortality rate ($year^{-1}$) and T is the life span (or longevity) of the species (years). The average of the resulting mortality estimates for the two genera (0.89 $year^{-1}$) is taken as the mean natural mortality rate for the group, and this would equal P/B if no fishing mortality exists. Assuming, however, that fishing mortality (F) of West Florida Shelf stomatopods equals half of the natural mortality, the P/B would then equal the sum of M and F (i.e. 1.335 $year^{-1}$).

The consumption rate (Q/B) of stomatopods (7.432 $year^{-1}$) was estimated based on studies of neogonodactylids, which make frequent foraging trips in search of prey (Caldwell et al. 1989, Caldwell and Childress 1989). It was observed that each stomatopod took an average of 12.1 small gastropods, 1.5 medium gastropods and 5.3 small crustaceans per day. The wet weight of the prey items was 1 mg for the small gastropods and small crustaceans, and 5-8 mg for medium gastropods (6.5 mg was used as an average for medium gastropods). This estimated 27.15 mg of food for each stomatopod each day was divided by 1.2 g—the average weight of a stomatopod in the study—yielding a daily consumption rate of 22.623 ($mg \cdot g^{-1} \cdot day^{-1}$). This was multiplied by 365 days and 1000 mg/g to derive the annual consumption rate (Q/B) 8.258 $year^{-1}$. Stomatopods do not appear to feed during molting, which is approximately 10% of the year (R. Caldwell, personal observations). The consumption rate estimate was weighted for this correction; we thus estimate a Q/B of 7.432 $year^{-1}$.

Stomatopods are carnivorous predators. During the Hourglass surveys (Camp 1973) the gut contents of 105 specimens of stomatopods of 8 different species were analyzed. Stomatopods selected for gut content analysis were the largest adults of the species. These species include *Neogonodactylus bredini* along with several Squillids and Meiosquillids. Occurrence information in the gut content analysis were converted to biomass proportions qualitatively—based on my best judgment. Unidentified animal tissue was apportioned to squid and bivalve groups. Camp (1973) found large crustaceans as the predominant food item; this is apportioned to the adult shrimp, and large crab prey categories, and his is the primary source used in the development of Table 8.18. However, gut content analyses by R. Caldwell (unpublished data) show the unidentified material in the Neogonodactylus gut to be mollusc, particularly gastropod. Although it mainly represents the squillids, these latter findings may be general for stomatopods. Specific diets of the Neogonodactylids and Lysiosquillids are not well represented anywhere. Diets of adult Neogonodactylus consisting mainly of crabs and gastropods (Caldwell, unpublished data) is somewhat reflected in the following estimates. The diet of the Lysioquillids, which is composed mainly of fish (Caldwell, unpublished data), is not accounted for here.

Table 8.18. Estimated diet composition of stomatopods on the West Florida Shelf.

Prey category	Proportion of diet
Shrimp	0.20
Microbial heterotrophs	0.20
Microphytobenthos	0.12
Bivalves	0.11
Squid	0.10
Crabs	0.09
Small infauna	0.09
Small mobile epibenth	0.06
Echinoderms	0.01
Small demersals	0.01
Macroalgae	0.01

Note: Diet extrapolated and modified from occurrence information in Camp (1973).

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8.11 Octopods

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Octopods are intelligent and voracious predators, which share the molluscan class cephalopoda with squids, cuttlefishes, and argonauts. Most octopoods of the West Florida Shelf live and hunt on the sea floor, while squids mostly live and feed above the sea floor. The most important octopod on the West Florida Shelf is probably *Octopus vulgaris*, which is common throughout the Atlantic and the Mediterranean (Grubert et al. 1999), and *Octopus maya*, which is common along the east coast of Mexico (Arreguín-Sánchez et al. 1993). Squids are treated Section 8.12 as an invertebrate segue to forage fishes, because of ecological similarities of squids and forage fishes (e.g., Pauly 1999).

The biomass of octopods on the West Florida Shelf is unknown from independent studies. However, the biomass value of 0.074 t·km^{-2} was calculated by the *Ecopath* software by setting the ecotrophic efficiency at 0.95 in the context of the empirically derived P/B and Q/B estimates, the input diet composition, and the energy flows among the surrounding compartments. This estimate for octopods on the West Florida Shelf is equal to less than 1% of the estimate for the Compeche Bank (17.62 t·km^{-2}), which was also estimated by the *Ecopath* software. In the case of octopods, the estimated biomass parameters for both of these systems are considered equally uncertain. As a potentially important predator in this system, investments in octopod research should be seriously considered.

The P/B value of octopods on the West Florida Shelf (3.1 year^{-1}) is the mean of empirically derived P/Bs from females and males of South African *Octopus vulgaris* from Buchan and Smale (1981; in Opitz 1993).

The Q/B value (7.3 year^{-1}) is from Guerra (1979 in Pauly 1993) from studies in the Mediterranean Sea (near Barcelona) and off Northwest Africa—systems similar to the West Florida Shelf. The estimate for octopod assimilation efficiency (0.97) is the gross conversion efficiency (K; from Pauly et al. 1993) plus 0.15 for respiration.

It should be noted that Arreguín-Sánchez et al. (1993) used a P/B value of 1.10 year^{-1} and a Q/B value of 3.5 year^{-1} for octopods of the nearby Compeche bank off the northern Yucatan. These values appear to be conservative, and can be considered a lower range during mass balancing.

The diet composition used for octopods on the West Florida Shelf are adapted from Whitaker et al. (1991; presented in Grubert et al. 1999), and is shown in Table 8.19.

Table 8.19. Estimated diet composition of octopods on the West Florida Shelf.

Prey categories [a]	Proportion of diet		
	Yucatan [b]	S. Carolina [c]	Florida [d]

Octopods			0.033
Large crabs	0.60		0.200
Benthic fishes			0.200
Lobsters	0.15		0.099
Adult shrimp	0.05		0.099
Demersal fishes			0.081
Mobile macrofauna			0.036
Dead carcasses			0.026
Echino. / lg. gastro.			0.016
Bivalves	0.20	0.099	0.100
Sessile epibenthos			0.100
Meiobenthos			0.010
Crustaceans		0.377	
Fishes		0.325	
Other		0.199	

[a]Prey categories in *italics* are general categories from source documents that were adapted to the more specific categories of this model; [b]*Octoopus maya* diet from Solís (1962, 1967; in Arreguín-Sánchez et al. 1993); [c]*Octopus vulgaris* diet roughly adapted from %occurrence results from Whitaker et al. (1991; presented in Grubert et al. 1999); [d]Adapted mostly from Whittaker et al. (1999) for the West Florida Shelf model.

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8.12 Squids

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Squid are cephalopod molluscs that are recognized as an important food for a variety of medium and large predators throughout the world's oceans. Less emphasized, but just as important, is their role as voracious predators of highly productive benthos and zooplankton. A trophically-unbiased view of squid reveals their role in linking the "furnaces" of primary and secondary production to the organisms at upper levels of the trophic pyramid—a mediating role also played by forage fishes. It has been suggested that squid might be "better understood by pretending they are [fish]", based on criteria relating to their size and growth (Pauly 1998) and their life histories—the parallels mostly apply to 'forage fishes.' Common types of squid of the West Florida Shelf include two loliginids, *Loligo pealei* and *L. plei,* and one ommastrephid, *Illex* spp. (Vecchione 1988).

Like on the West Florida Shelf, *L. pealei* and *L.* plei are the main species of squid on the nearby and ecologically similar northeastern Venezuela shelf. For that system, Mendoza (1993) derived estimates for squid biomass (0.267 t·km^{-2}), P/B (1.70), and Q/B (36.5), using growth and mortality estimates from Pauly (1985) and consumption and diet information from Amaratunga (1983).

We will use Mendoza's biomass and Q/B estimates shown above, but his P/B estimate matches estimates for *Sepioteuthis lessoniana* and *Illex illecebrosus* in Pauly et al. (1993), though they present a higher estimate for two *Loligo* species (3.16 year^{-1}). Since the common species on the West Florida Shelf consist of two *Loligo* species and one *Illex* species, the two P/B estimates are averaged by proportion of representation, yielding a P/B estimate of 2.673 year^{-1} for squid on the West Florida Shelf.

To my knowledge, Mendoza's estimates are the best available for the similar West Florida Shelf; I am aware of no evidence other than that stated above indicating that the Venezuela estimates would either overestimate or underestimate corresponding parameters for West Florida Shelf squid. Mendosa's (1993) diets were adapted to the groups used in this model, as shown in Table 8.20.

Table 8.20. Estimated diet composition of squid on the West Florida Shelf.

Prey [a]	**Proportion of diet**		
	Venezuela [b]	**Monterey** [c]	**Florida** [d]
Sm. mobile epifauna		0.008	0.06
Carnivorous zooplank.		0.483	0.22
Mesozooplankton		0.483	0.23
Small copepods		0.015	0.02
Stomatopods		0	0.05 [e]
Ichthyoplankton		0.001	0.01
Small infauna		0.003	0.02
Carnivorous jellyfish		0	0.02
Squid	0.02	0.003	0.01

Small pelagics	0.41	0.004	0.36
Zooplankton	0.46		
Heterotrophic benthos	0.11		

[a] Prey categories in *italics* are general categories from source documents that were adapted to the more specific categories of this model;
[b] Squid diet presented in Mendoza (1993) from Amaratunga (1983);
[c] *Loligo opalescens* diet from Karpov and Cailliet (1978);
[d] Adapted squid diet used for the West Florida Shelf model;
[e] See Meyer and Caldwell (this volume).

Exactly 38 tonnes of squid were landed in Florida in 1999. Mendoza's (1993) biomass value of 0.267 is equivalent to a standing stock of 45,390 tonnes of squid on the 170,000 km^2 West Florida Shelf area. Application of Mendoza's biomass estimate to the West Florida Shelf means that the instantaneous rate of fishing mortality (F; year^{-1}) would be very low 0.00084, assuming that all squid caught on the West Florida Shelf are landed in Florida.

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9. FISHES

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Input parameters for the majority of West Florida Shelf fish groups were estimated using an integrated approach. Parameters for a few fish groups (i.e., large oceanic piscivores, coastal sharks, and rays and skates) were however estimated separately, as information sources differed from those available for most fish groups.

9.1 Systematic categorization of fish groups

The general goal of our systematic categorization of fish groups was to define functional groups by determining ecological similarity among fish species. This systematic approach consisted of three steps:

(1) Build a catalogue of West Florida Shelf fish species

Reported catches and expert opinion of FMRI scientists were integrated to determine which fish species were present on the West Florida Shelf in at least moderate abundance. A preliminary comprehensive list of over 600 species, taken from the NOAA website, was reduced to about 260 species (or genus or family in some cases).

(2) Sort each species in a database based on 5 criteria:

a. Horizontal distribution (oceanic migrant, coastal resident, estuary migrant)
b. Vertical distribution (surface, mid-water, demersal, benthic)
c. Habitat type (pelagic, coral reef, other structured bottom, soft bottom, sea grass)
d. Trophic habit (planktivore, piscivore, omnivore, herbivore, invertebrate eater, detritivore, coral eater)
e. Approximate size (large, medium, small)

(3) Group species functionally

Species were organized into ecologically functional groups by FMRI scientists using the database classifications. Particular emphasis was given to trophic similarities during grouping because species with dissimilar diets can erode the representativeness of the model. Appendix 7 shows the final list of all functional fish groups.

9.2 Biomasses of fish groups

Four approaches were used to estimate the biomass of fish groups; (i) Fishery independent survey data, (ii) Stock-assessment VPA models, (iii) A basic catch equation, and (iv) Estimates from existing literature.

(i) Fishery independent survey data

Four sets of fishery independent survey data were used to derive abundance estimates for coastal demersal/ structure related species, coastal pelagic species, and oceanic species, though this varied among species.

Average abundance estimates derived from two reports detailing West Florida Shelf surveys in coastal waters (Darcy and Guntherz 1984, Darnell et al. 1987) were used for coastal species for which detailed stock assessment estimates were not available. Average estimates for each species were derived from surveys during which a catch was made. Maximum and minimum estimates from the 2 surveys were used to define confidence limits for model balancing. Demersal trawl-based estimates of non-demersal species were taken as minimum estimates if no other estimates were available for such species. Similarly, estimates using non-trawl methods were emphasized for structure-associated fish species, since trawl estimates in structured habitats were considered unrealiable (Darnell et al. 1987).

A 1978 trawl survey covering the whole West Florida Shelf region (Darcy and Guntherz 1984) was used to derive biomass estimates for various fish groups. These estimates were made by dividing the number of tonnes of each species captured by the defined area of 170,000 km^2 and also applying a trawl efficiency factor of 0.25%, estimated by Gutherz in Klima (1976, also see Darcy and Gutherz 1984). Relative biomasses of each species were calculated based on the total trawl catch of 433,000 tonnes and the proportion of the total catch comprised by each species.

Fish biomass estimates were also calculated based on 12 surveys (433 trawl stations) conducted from late 1960s to early 1980s, covering Lousiana, Alabama and Florida from the shore or barrier Islands to the 120m isobath (Darnell et al. 1987). All data from this study were standardized to a trawl size of 45 feet, a towing speed of 3 knots, and a towing time to 60 minutes. Numbers of fish of each species / family were converted to densities per km^2 using the swept area formulae provided by Darnell et al. (1987). Estimates of relative biomass per km^2 were derived by applying average weights of each species derived from state and Federal catches (Section 13) and from published sources. A trawl efficiency factor of 0.25% (Darcy and Gutherz 1984) was applied here as well. Relative abundance of the top eleven species caught in trawls is shown in Figure 9.1

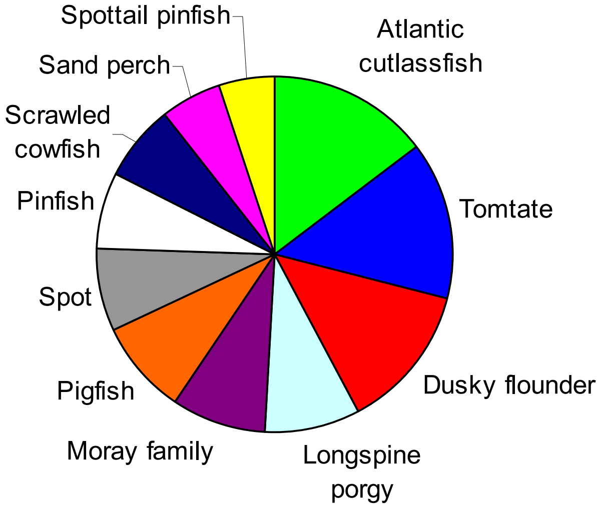

Figure 9.1. Relative abundance of top-eleven species (contributing >2% of total biomass) caught in coastal demersal trawl surveys on the West Florida Shelf (Darcy and Guntherz 1984; Darnell et al. 1987).

Pelagic trawl surveys conducted during 1994 to 1999 by FMRI / FWC's Fishery Independent Monitoring program were used to estimate biomasses of small coastal pelagic species. These surveys cover inshore coastal waters and use a high opening bottom trawl. Estimates of total biomass for each species up to 91m isobath was adjusted to account for a 50% trawl efficiency (Mahmoudi, pers. comm.) and multiplied by the area bounded by 91m isobath (50,915 km^2). These total abundance estimates were then divided by the total area defined for the West Florida Shelf (170,000 km^2) to estimate the average biomass density on the West Florida Shelf.

Offshore survey data collected by the NMFS during 1988, 1990, 1992, 1995 and 1996 were used to biomass estimates of those species with predominantly offshore distributions (oceanic functional groups). NMFS trawl surveys were conducted in shelf-break/offshore waters (around 200m isobath) using high opening bottom trawls directed to sample small pelagics in daytime aggregations near the seabed. This NMFS database included direct estimates of catch rate (relative biomass) per km^2 for each species in each year (for each area covered by the survey). Table 9.1 shows the most common species captured by the high opening bottom trawl. Catch rates were converted to estimates of total biomass per km^2 by applying a 50% trawl efficiency rate (Mahmoudi, pers. comm) and by using species distribution maps (Darnell et al. 1987) to determine the proportion of the defined area occupied by each species.

Table 9.1. Some common shelf region species.

Common name	**Species**	**% of total catch**
Gulf butterfish	*Peprilus burti*	20.710

Round scad	*Decapterus punctatus*	11.297
Rough scad	*Trachurus lathami*	11.186
Spanish sardine	*Sardinella aurita*	10.764
Round herring	*Etrumeus teres*	8.328
Longspine porgy	*Stenotomus caprinus*	5.924
Chub mackerel	*Scomber japonicus*	5.818
Spot	*Leiostomus xanthurus*	5.651
Stingray genus	*Dasyatis spp.*	1.790
Pinfish	*Lagodon rhomboides*	1.580
Silver-rag	*Ariomma bondi*	1.575
Sandbar shark	*Carcharhinus plumbeus*	1.287
Atlantic cutlassfish	*Trichiurus lepturus*	1.240
Tomtate	*Haemulon aurolineatum*	1.234
Bigeye scad	*Selar crumenophthalmus*	0.121
Tilefish	*Malacanthidae*	0.006
Offshore hake	*Merluccius albidus*	0.004
Striated argentine	*Argentina striata*	0.002

Note: From NMFS trawl survey data.

(ii) Stock Assessment models – Virtual Population Analysis (VPA)

Virtual Population Analysis (VPA) estimates were available for king mackerel, Spanish mackerel, sheepshead, spotted seatrout, gag, menhaden, red snapper, red drum, snook, and mullet. VPA abundance estimates for red snapper and menhaden cover the whole Gulf of Mexico, and so only the fishing mortality estimates used in the VPA's were used here to determine abundance on the West Florida Shelf using simple relationship Biomass=Catch/F (see next section). The same procedure was applied to red drum and snook to derive biomass estimates based on 1998 catches from the West Florida Shelf. I include some examples of this approach here.

Biomass of adult Spanish mackerel (age 2+), king mackerel (age 4+) and juvenile mackerel were calculated based on biomass at age estimated from VPA (Legult 1998) (Table 9.2). Summing fishing mortality and natural mortality rates from the VPA provided estimates of total mortality, which also equals P/B (Allen 1971). The mean value (weighted by biomass) for adults was 0.384; for juveniles, 0.434. These values probably underestimate production of juveniles because their mortality rates are probably much higher than those of adults (M=0.2 king mackerel, M=0.3 Spanish mackerel). We opted to assume a juvenile P/B two times that of the adult. The VPA stock assessments produce reasonably reliable estimates of mackerel stocks.

Table 9.2. Stock size estimates for adult and juvenile king and Spanish mackerel.

Species	Stock size (t)	
	Adults	Juvenile
Spanish mackerel	14,195	3,206
King mackerel	16,861	17,939

Note: Based on VPA (Legult 1998).

The West Florida Shelf sheepshead population was estimated to be 14,854,835 individuals using VPA (Murphy and McDonald 2000). Its biomass was estimated as 13,904 tonnes, or 0.082 t/km^2, by dividing by the average weight from west Florida catches (0.936 kg). The current stock size of spotted seatrout in the northwest region (big bend sea grasses) is approximately 15,000,923 individuals (Murphy et al 1999). The biomass is estimated to be 1,818 tonnes (Table 9.3). Biomass of gag was taken as 4,498 tonnes based on a recent NMFS stock assessment (Steve Atran memo to Wayne Swingle).

Table 9.3. Spotted seatrout numbers and weight at age for Northwest Florida.

Age	**Numbers at age**		**Weight at age (kgs)**		**Biomass (t)**
	Male	*Female*	*Male*	*Female*	
0	979665	2010975	0.236364	0.107438	447.6123
1	871312	2482720	0.363636	0.165289	727.2077
2	515085	588145	0.454545	0.206612	355.6471
3	254210	154265	0.531818	0.241736	172.4848
4	80796	72662	0.563636	0.256198	64.15545
5	32750	12354	0.718182	0.326446	27.55337
6	13995	5393	0.954545	0.433884	15.6988
7	6406		1.209091	0.549587	7.745436
				Sum	1818.105
				Biomass t/km^2	0.010695

Note: From 1998 VPA assessment (Murphy et al 1999).

(iii) Estimation using Biomass = Catch/ Fishing mortality

The basic catch equation (Baranov 1918) was used to derive rough estimates of biomass on the West Florida Shelf for several species. This equation assumes that catches are proportional to the biomass present in the area (C=F/B). Our estimates are based on the simplistic assumption that stocks are under the same fishing pressure throughout their WFS distribution. Our calculations may either overestimate or underestimate the biomas of highly migratory fish in the area, considering that fishing effort, stock biomass and catchability are not spatially homogeneous, and fishing mortality ought to vary between fishing areas. Fishing mortality values were derived from various sources. The more reliable ones were taken from species-specific stock assessments covering the whole Gulf of Mexico. Table 9.4 presents derivations and sources.

Table 9.4. Fish biomass estimates based on Catch/F.

Common name	**Species name**	**F**	**Reference**	**Catch (t)**	**Biomass (t)**
Swordfish	*Xiphias gladius*	0.3	ICAAT	141.37	471.23
Blue marlin	*Makaira nigricans*	0.2	Brown et al. 1991	6.6[a]	33 [b]

White marlin and spearfish	*Tetrapturus spp.*	0.2	Brown et al. 1991	2.4[a]	12.2[b]
Sailfish	*Istiophorus platypterus*	0.2	Brown et al. 1991	13.39	66.97
Dolphin fish	*Coryphaena hippurus*	0.4	Brown et al. 1991	4074.38	10185.95
Thresher shark	*Alopias spp.*	0.4	Brown et al. 1991	6.94	17.35
Longfin mako	*Isurus paucus*	0.4	Brown et al. 1991	9.13	22.82
Sixgill shark	*Hexanchus griseus*	0.4	Brown et al. 1991	0.032	0.08
Yellowfin tuna	*Thunnus albacares*	0.5	ICAAT	300.96	601.92
Albacore	*Thunnus alalunga*	0.5	ICAAT	0.10	0.19
Bluefin tuna	*Thunnus thynnus*	0.23	ICAAT	0.38	1.65
Blackfin tuna	*Thunnus atlanticus*	0.3	Brown et al.1991	504.90	1683.00
Bigeye tuna	*Thunnus obesus*	0.35	ICAAT	2.66	7.61
Skipjack tuna	*Katsuwonus pelamis*	0.2	Brown et al. 1991	54.87	274.36
Scalloped hammerhead	*Sphyrna lewini*	0.13	NMFS 1998	9.11	70.11
Great hammerhead	*Sphyrna mokarran*	0.13	NMFS 1998	12.71	97.80
Sandbar shark	*Carcharhinus plumbeus*	0.093	NMFS 1998	473.31	5089.41
Dusky shark	*Carcharhinus obscurus*	0.13	NMFS 1998	19.07	146.73
Blacknose shark[1]	*Carcharhinus acronotus*	0.21	NMFS 1998	19.61	93.38
Spinner shark	*Carcharhinus brevipinna*	0.13	NMFS 1998	0.30	2.29
Silky shark	*Carcharhinus falciformis*	0.13	NMFS 1998	5.03	38.68
Blacktip shark	*Carcharhinus limbatus*	0.166	NMFS 1998	91.30	550.01
Bull shark	*Carcharhinus leucas*	0.13	NMFS 1998	48.49	372.97
Finetooth shark[1]	*Carcharhinus isodon*	0.13	NMFS 1998	3.52	27.06
Atlantic sharpnose shark[1]	*Rhizoprionodon terraenovae*	0.35	NMFS 1998	20.26	57.88
Tiger shark	*Galeocerdo cuvier*	0.13	NMFS 1998	1.11	8.56
Lemon shark	*Negaprion brevirostris*	0.13	NMFS 1998	0.59	4.55
Dogfish[1]	*Squalidae*	0.06	NMFS 1998	0.01	0.12
Sand tiger[1]	*Odontaspis taurus*	0.16	NMFS 1998	0.00	0.00
Wahoo	*Acanthocybium solandri*	0.3	Brown et al. 1991	161.72	539.06
Little tunny	*Euthynnus alletterus*	0.3	Brown et al. 1991	435.99	1453.29
Cobia	*Rachycentron canadum*	0.3	Brown et al. 1991	493.18	1643.95
Crevalle jack	*Caranx hippos*	0.4	?	497.65	1244.13
Greater amberjack	*Seriola dumerili*	0.2	Potts et al. 1998	699.73	3498.66
Red drum	*Sciaenops ocellatus*	0.69	Goodyear 1996 (from VPA)	1623.98	2353.60
Black drum	*Pogonias cromis*	0.4	Brown et al. 1991	133.89	334.72
Red snapper	*Lutjanus campechanus*	0.402	Schirripa and Legult 1999 (from VPA)	891.38	2217.37
Snowy grouper	*Epinephelus niveatus*	0.48	Potts et al. 1998	77.38	161.21
Great barracuda	*Sphyraena barracuda*	0.2	Brown et al. 1991	248.90	1244.49
Jewfish	*Epinephelus itajara*	0.7	Eklund 1994	0.00	0.00
Red grouper	*Epinephelus morio*	0.26	Potts et al. 1998	3522.37	13547.56
Speckled hind	*Epinephelus drummondhayi*	0.43	Potts et al. 1998	32.56	75.73
Scamp	*Mycteroperca phenax*	0.18	Manooch et al. 1997	200.15	1111.97
Yellowtail snapper	*Ocyurus chrysurus*	0.16	Brown et al. 1991	179.56	1122.28
Ladyfish	*Elops saurus*	0.3	Brown et al. 1991	97.19	323.96
Common snook[2]	*Centropomus undecimalis*	0.31	Muller 2000 (from VPA)	150.51	485.51

* Estimates using Catch (Landings+Discards) rather than landings alone.

[1] Fishing mortality rate for small coastal sharks in the period 1986-1991 was estimated to be 89% of

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Fmsy (NMFS, 1998b). Assuming that Fmsy ~ 0.6 M, the current fishing mortality rate of the individual species was considered to be approximately 0.5 M. Natural mortality rates were estimated using Pauly's (1980) empirical equation.

[2] F from 1998, recently F has declined

[a] Using catch data from NMFS (1998), and [b] assuming 1/5th of total biomass is present in study area (see species descriptions section)

(iv) Other estimates

For some species, multiple approaches were used to estimate biomass. For example, an acoustic assessment (Erhardt 1993) led to a Spanish mackerel biomass estimate (28,585 t) that was twice the 1998 VPA estimate.

Another example is that, egg and larvae surveys from plankton collections made in the eastern Gulf of Mexico from 1971-1974 led to alternative abundance estimates of round herring (*Etrumeus teres*) (Houde 1977). Later, Houde and Berkley (1982), provided egg and larvae based estimates for several small pelagic species; Atlantic thread herring (*Opisthonema oglinum*), Spanish sardine (*Sardinella aurita*), round scad (*Decapterus punctatus*), round herring (*Etrumeus teres*), rough scad (*Trachurus lathami*), and Atlantic bumper (*Chloroscombrus chrysurus*). The abundance estimates derived by these methods likely overestimated abundance, as the estimates did not account for batch spawning (Mahmoudi, pers. comm). These estimates serve only as a reference for other abundance estimates.

Menhaden (*Brevoortia sp.*) biomass on the West Florida Shelf (8,003 tonnes) was derived by assuming that the proportion of the overall population occurring in the West Florida Shelf region was equivalent to the proportion of the overall fisheries catch taken there (1.37% of the overall catch). The total menhaden catch in the Gulf of Mexico was 569,600 t in 1989, and the total catch in the WFS area was (7,800 t). The total 1997 estimate of spawning stock biomass (females only) in the Gulf States Alabama, Mississippi, Texas and Florida was 292,100 t (VPA; Vaughan et al. 1999). Assuming a 50:50 male:female ratio (Vaughan pers. comm), the total Gulf stock size of menhaden was estimated to be 584,200 t. This might greatly underestimate the West Florida Shelf population since it is based only on catches taken in the Northeast Panhandle region (Mahmoudi, pers. comm.).

Brown et al (1991) provided Gulf wide biomass estimates for a number of species in the Gulf of Mexico (Table 9.5). These estimates of small pelagics are used here only to provide reference points and alternative estimates.

Table 9.5. Biomass estimates for small pelagics on the West Florida Shelf.

Common name	**Biomass (tonnes)**			**t/km^2**
	Southeast	Northeast	Total	
Thread herring	240,000	50,000(a)	290,000	1.706
Round herring	380,000	10,000	390,000	2.294

Spanish sardines	250,000	100,000	350,000	2.059
Scaled sardine	185,000	20,000	205,000	1.206
Atlantic bumper		20,000(a)	20,000	0.118
Round scad	100,000	100,000(a)	200,000	1.176
Rough scad		20,000	20,000	0.118
Silver driftfish		6,000	6,000	0.035
Anchovies	10,000(a)	20,000(a)	30,000	0.176

Notes: From Brown et al. (1991): "*Coastal pelagic estimates for he Eastern Gulf* (south of 29°N) *were rounded from Houde (1976), which were estimated from larval surveys. Coastal pelagic biomass estimates for the Northeast Gulf* (north of 29°N and east of 88°W) *were obtained from unpublished data by C. Gledhill, NOAA/NMFS/SEFC, Pascagoula, MS. We assumed a trawl catchability coefficient of 0.25 and multiplied Gledhill's cruise data by 4 to use in our estimates. Items indicated with an (a) have been adjusted upward from the original estimates. The upward adjustment was based on (1) landings statistics for the area, (2) stomach content analyses of predators in the area, (3) comments of cruise-data experts.*"

For species with no reliable biomass estimates, approximate biomass estimates were derived using catch data and average fishing mortality estimate from other species in the same functional group. If no substitute values of F were available, the catch was used as a minimum proxy estimate for the biomass. Approximate biomass estimates were preferred over no estimates because groups with no biomass would strongly bias parameters (e.g., production, consumption, and fishing mortality) that were derived with biomass weighting.

Table 9.6 provides a summary of the relative biomass of West Florida Shelf species ranked by abundance estimates derived herein. Total biomass of fish was estimated to be 3.5 million tonnes, with range 0.5 to 6.1 million tonnes. Details of the best estimates for each species are presented with their sources in Appendix 7.

Table 9.6. Relative abundance of fish species on West Florida Shelf.

Common name	**% Total biomass**	**Common name**	**% Total biomass**
	>1%		0.5 to 1%
Gulf butterfish	12.12	Littlehead porgy	0.98
Rough scad	6.55	Silver-rag	0.92
Round herring	5.16	Gray flounder	0.92
Dusky flounder	3.69	Bank sea bass	0.90
Chub mackerel	3.40	Round scad	0.89
Longspine porgy	2.40	Anchovies	0.87
Moray family	2.40	Atlantic croaker	0.81
Pigfish	2.36	Cownose ray	0.76
Pinfish	2.28	Hardhead catfish	0.76
Spot	2.12	Atlantic cutlassfish	0.73
Tomtate	1.97	Spanish sardine	0.67

Scrawled cowfish	1.93	Inshore lizardfish	0.67
Other mullets	1.55	Barbfish	0.62
Sand perch	1.49	White grunt	0.62
Spottail pinfish	1.43	Fringed filefish	0.60
Rock sea bass	1.07	Black sea bass	0.54
Other fish	18.77	Mojarras	0.54
		King mackerel	0.51

Notes: Based on combination of biomass estimation methods. Only those whose relative abundance is greater than 0.5% are listed

9.3 Production (P/B) and Consumption (Q/B) estimates

For each functional group, weighted average production and consumption parameter estimates were calculated from estimates of P/B and Q/B for each group member (species) weighted by their relative biomass in the group. From 264 species listed within the functional groups, individual estimates of P/B and Q/B were made for 229 and 213 of them respectively. Where several alternative estimates existed, local (West Florida Shelf) and species specific values were chosen in preference over more generalized (less robust) estimates for initial model parameterization (see Section 3.3). Minimum and maximum estimates were recorded in all cases for use as balancing limits (Table 9.10). The following sections detail the methods and sources used to derive P/B and Q/B estimates.

Production/ Biomass (P/B)

(i) Determined from total mortality (Z) and natural mortality estimates (M)

Total mortality rate (Z) is equal to production rate (P/B), under the assumption of steady-state (Allen 1971). Estimates of total mortality were derived for a number of species by adding fishing mortality and natural mortality (Z=F+M) from VPA models or other sources (Appendix 6). Independent estimates of Z were gleaned from several species synopses; blue runner, 0.47 (Goodwin & Johnson 1986), round scad, 0.92 (Naughton et al. 1986), lane snapper, 0.68 (Manooch and Mason 1984), vermilion snapper, 0.48 (Manooch & Johnson 1998).

The P/B of small pelagic fish was re-checked by calculating Z from mean length (Beverton and Holt 1956). This calculation relies on the assumption of steady recruitment into the population:

$$Z=K(L_\infty-L_{avg})/(L_\infty-L')$$

L_∞ = asymptotic length (cm);
L_{avg} = average length;
L' = cut-off length;
K of the VonBertallanfy growth equation

Estimates of natural mortality (M) for small pelagics were derived from an empirical formula described by Brey (1999), a modification of Pauly's M formula, as an additional cross-check.

$$\text{Log}(M) = 4.355-0.083\log W_\infty+6.390(W_\infty/L_\infty^3)+0.627\log(K)+1190.43(1/T+273)$$

K of the VonBertallanfy growth equation;
T= temperature in centigrade;
W_∞ = asymptotic weight (g);
L_∞ = asymptotic length (cm).

Total mortality estimates were generally lower than original model estimates, supporting a reduction in P/B to value closer to the published value for round scad on the West Florida Shelf (Saloman and Naughton 1986). However, many P/B estimates were left questionable since empirical estimates of natural mortality were almost double the total mortality estimates (Table 9.7).

Table 9.7. Comparison of P/B (Z) and natural mortality (M) estimates for small pelagics

Group	Initial estimate (P/B)	P/B (Z) from av. Length[1]	M est. (Pauly's M modified by Brey 1999)
Atlantic thread herring	1.60[a]	0.58	1.02
Scaled sardine	1.57[a]	1.04	1.76
Spanish sardine	0.95[a]	1.15	1.58
Menhadens	0.95[a]	0.56	0.93
Round scad	0.92[b]	0.66	1.12

[1] based on assumption that the average length in the population is 2/3rds the asymptotic length and the length of 1st capture (cut-off length) is 2/3rds the average length in the population (assumes knife-edge selection).
[a] average values derived from other GoM models
[b] estimated total mortaility (Naughton & Saloman 1986)

For unfished species (e.g. large oceanic planktivores), however, total mortality is equivalent to natural mortality (M). Values of M taken from Fishbase, were used as minimum proxy value of P/B for 20 species (generally unfished) for which no other estimate could be derived.

(ii) Borrowed from other Gulf of Mexico models

In lieu of local direct estimates, P/B values used in published *Ecopath* models from the Gulf of Mexico were compiled by species and their average values applied as rough estimates for use in the West Florida Shelf model. Where no specific values were available for the species included in the West Florida Shelf model, values from similar functional groups were taken. These cases are shown in Appendix 7.

(iii) Intrinsic rate of increase, r

Under equilibrium assumptions, the intrinsic rate of increase, r, the maximum possible rate of growth given no constraints, may correspond to the total mortality rate (=P/B).

The value of r, was used as an estimate of P/B for sandbar shark *Carcharhinus plumbeus* and blacktip shark *C. limbatus.*

Consumption/ Biomass (Q/B)

Three approaches were used to estimate consumption rates (Q/B) for West Florida Shelf fishes: (1) empirically-based relationships between morphology, physical variables, and consumption rates, (2) species-specific measurements, and (3) estimates from other models. These approaches are described below.

(1) Estimates derived by empirically-based relationships

Palomares et al. (1998) presented the following empirically-based equation describing how consumption rate can be predicted by a combination of size, temperature, tail aspect ratio (i.e., lifestyle / feeding type), and qualitative diet information:

$$\mathrm{Log}(Q/B) = 7.964 - 0.204\log W_{\infty} - 1.965T' + 0.083A + 0.532h + 0.398d$$

W_{∞} = asymptotic weight; from literature or calculated using maximum length and species specific length-weight relationship;

T' = 1000/Kelvin (Kelvin=°C +273.15);

A = aspect ratio of caudal fin, h^2/s, where *h* is the height and *s* is the surface area of the caudal fin, extending to the narrowest part of the caudal peduncle. Calculated for each species from photographs and drawings;

h = Herbivorous feeding (*h=1, d=0*);

d = Detritivorous feeding (*h=0, d=1*); Carnivorous feeding (*h=0, d=0*).

Morphometric information and mean water temperature of fish habitat were compiled from FMRI (1998), NOAA (1997), FishBase (www.fishbase.org), and other individual species reports. Tail aspect ratios were sometimes calculated using the FishBase graphic caudal fin selection tool and applying a applying a water temperature of 22.2 °C to the empirical equation calculator. WFS temperatures are shown in Table 9.8.

Table 9.8. Temperature data for West Florida Shelf

Depth zones	Average water temperature (°C)		
	Winter	Summer	Year round.
Surface	20.0	29.8	24.9
Bottom	17.0	22.0	19.5
Annual average temperature through the water column 22.2°C			

Notes: From Gulf of Mexico data atlas (Berryhill 1977).

(2) Species-specific measurements

Independent estimates of Q/B used in deriving empirical equations are given in Palomares and Pauly (1989, 1998). These values were used as alternative estimates, since many of them were not specific to the Gulf of Mexico.

Other estimates were taken directly from Brown et al. (1991) who published a list of consumption per year as a proportion of body weight (Q/B year^{-1}) from other published sources. They made two general adjustments to original estimates: (1) they multiplied by 2 as an approximate conversion from routine to field (Winberg 1960); (2) they divided by 0.65 to account for losses due to egestion, excretion, and specific dynamic action consumption was estimated were based on oxygen consumption (Kitchell et al. 1978).

Other independent estimates include those for sandbar and lemon sharks. Stillwell and Kohler (1992) estimated the daily ration of sandbar sharks, *C. plumbeus,* to be between 1.43 and 0.86% of mean body weight, leading to annual food consumption (Q/B) estimates of between 5.1 and 3.1 year^{-1}. Daily ration of lemon sharks was estimated to range from 1.5 to 2.1% of body weight (Cortés and Grubber 1990), giving a Q/B of 5.5 to 7.7 year^{-1}.

(3) Estimates from other Gulf of Mexico models

Q/B values used in published Gulf of Mexico *Ecopath* models were compiled by species and their average values used as rough estimates, in cases were Q/B values were not otherwise available. Where no specific values were available for the species included in the west shelf model, values from similar functional groups were taken when species-specific values were not available (Appendix 7).

9.4 Fish diet compositions

Quantitative information on the diet of 171 of the 260 fish species was compiled from detailed stomach content studies and from general feeding habit studies. Composite diets for each functional group were derived by employing 3 steps:

(1) Weighting each species' diet composition by their relative consumption;

For those species with diet information, but no consumption estimate (Q) due to lack of biomass or Q/B estimates, relative consumption =1. For all other species, relative consumption = [1 + Individual consumption ($Q_i = B_i{*}Q/B_i$) divided by total consumption of species within the group ($\Sigma_{i=1 \text{ to } n}Q$)].

(2) Summing the relative proportions of the prey species within their respective functional group;

(3) Normalizing the diet proportions of each predator group to 1 by dividing each relative proportion of prey, by the total proportion of prey consumed.

No quantitative diet information was available for large oceanic planktivores, pelagic oceanic piscivores, Pelagic oceanic jelly eaters, or benthic oceanic piscivores. The diets for these groups were constructed based on qualitative information, expert knowledge, and best judgment.

Diet information from the West Florida Shelf and the Gulf of Mexico before were given priority before extending the search to other similar regions (Table 9.9). Comprehensive local reports included the Hourglass memoirs, diet studies in Tampa bay (Motta et al. 1995, Peebles and Hopkins 1983) and life history summaries for Gulf of Mexico estuarine species (NOAA 1997). When several published diets were available for a single species, the most local diet was used, or diet compositions were averaged.

More generalized diets were derived for swordfish (Nakamura 1985; NMFS 1998), tunas (Dragovich 1969; NMFS 1998), sharks (Cortés 1999; Smale 1991; Dudley and Cliff 1993; Cortés and Grubber 1990; Lowe et al. 1996; Cortés et al. 1996) and rays (Stehmann et al. 1978) due to lack of specific local information. Randall’s (1967) work on stomach contents of West Indies reef fishes (% weight) was the largest source of diet data for the West Florida Shelf model.

Ninety percent of the striped mullet diet was specified as imported food, based on evidence that striped mullet do not generally feed during their residence on the West Florida Shelf (winter months during spawning season). Similarly, demersal coastal piscivores (seatrout) that are restricted to nearshore and seagrass habitat were assumed to obtain 35% of food from outside the system.

Table 9.9. Diet information sources specific to the study region.

Species	Reference
Marlin	Davies and Bortone 1976
Sailfish	Jolley Jr 1977; NMFS 1998
Dolphinfish	Rose and Hassler 1974
King Mackerel (NW Florida)	Saloman and Naughton 1983
Spanish mackerel (NW Florida)	Saloman and Naughton 1983
Juvenile King and Spanish mackerel	Finucane et al. 1990
Crevalle jack	Saloman and Naughton 1984
Gag	Naughton and Saloman 1985
Vermilion snapper	Grimes 1979; Sedberry and Cueller 1993
Silver jenny	Motta et al. 1995
Spotted seatrout	Peebles and Hopkins 1983
Thread herring	Vega-Cendejas et al. 1994
Saddle bass	Bullock and Smith 1991
Black drum	Overstreet and Heard 1982
Red drum	Overstreet and Heard 1978
Lane snapper	Bortone and Williams 1986
Fringed flounder	Topp and Hoff 1972
Blue spotted searobin	Ross 1983
Common snook	NOAA 1997
Dolphin fish	Rose and Hassler 1974
Marlin	Davies and Bortone 1976
Sailfish	Jolley Jr. 1977 and NMFS 1998
Sandbar shark	Stillwell and Kohler 1992
Spanish sardine	Wang and Qui 1986

9.5 Initial fish parameter estimates

Basic input parameter estimates for West Florida Shelf fish groups are shown in Table 9.10 with ranges. Appendix 7 lists sources of parameter estimates for each fish species.

Table 9.10. Best weighted estimates and ranges of parameters for WFS fish groups.

	Group	**Biomass (t/km2)**			**Q/B per year**			**P/B per year**		
		Best	Max	Min	Best	Max	Min	Best	Max	Min
1	Whales and dolphins				40.86	40.86	40.86			
2	Sea birds				80.00	80.00	80.00	3.00	3.00	3.00
3	Turtles				3.50	3.50	3.50	0.15	0.15	0.15
4	Manatees	0.0008			36.50	36.50	36.50	0.10	0.10	0.10
5	Large oceanic piscivores	0.0788	0.0774	0.0788	10.56	12.76	8.54	0.68	1.64	0.66
6	Large ocean planktivores	0.0000	0.0000	0.0000	1.80	1.80	1.80	0.11	0.11	0.11
7	Coastal sharks	0.0381	0.0381	0.0381	3.29	4.10	3.61	0.41	0.42	0.31
8	Rays and skates	0.2387	0.5683	0.0754	7.72	7.72	0.37	0.38	0.38	7.43
9	Pelagic oceanic piscivores	0.1504	0.8448	0.1505	25.54	25.54	25.54	1.06	1.06	1.06
10	Pelagic coastal piscivores	**0.0974**	0.1313	0.0361	11.53	14.02	10.23	0.64	0.67	0.61
11	Mackerels adult	0.1832	0.2673	0.0234	9.49	25.70	8.95	0.38	0.89	0.53
12	Juvenile mackerels	0.1244	0.1244	0.1244	18.97	51.40	17.00	0.77	1.78	1.06
13	Sardine/Herring	0.4570	6.0765	0.0328	12.11	12.58	10.49	1.18	1.18	1.05
14	PelOceJelly/eaters	2.6929	2.6929	0.1855	8.07	23.78	8.08	1.59	1.59	1.56
15	PelOcePlanktivores	3.1387	4.5586	0.0762	11.78	12.97	11.71	0.87	0.87	0.83
16	DemOceInvert/eaters	0.0410	0.0840	0.0409	15.76	15.76	15.76	**2.17**	2.17	2.17
17	DemCoasPisc	0.0671	0.1262	0.0303	6.33	6.75	6.24	0.64	0.64	0.64
18	DemCoasInvert/eaters	2.7134	5.2996	0.2444	8.06	9.15	7.92	0.65	0.65	0.57
19	DemCoasOmniv	1.4289	2.0358	0.2708	15.13	15.04	10.71	1.60	1.60	1.34
20	BentOcePisc	**0.1089**	**0.2175**	**0.0550**	**7.94**	**8.86**	**7.94**	**0.30**	**0.75**	**0.30**
21	BentOceInvert/eaters	0.1210	0.1480	0.0550	15.78	15.78	15.79	**2.24**	2.24	2.44
22	BentCoasPisc	0.2621	0.3684	0.0280	8.39	8.38	8.34	0.30	0.30	0.30
23	BentCoasInvert/eaters	1.6686	2.3294	0.4364	12.21	12.20	10.11	1.16	1.23	0.86
24	SurfacePelagics	**0.0003**	**0.0003**	**0.0003**	11.70	96.73	11.70	2.60	2.60	2.6
25	StrucAssCoasPisc	0.7221	1.0376	0.2243	7.81	8.60	5.40	0.63	0.63	0.55
26	LgGroupers	0.1193	0.1493	0.0306	4.10	4.79	2.59	0.458	0.47	0.40
27	StrucAssCoasInvert/eaters	1.3453	1.9691	0.1925	8.34	8.36	7.33	0.75	0.77	0.54
28	StrucAssCoasOmniv	0.0605	0.0657	0.0350	29.15	29.25	24.37	1.33	1.33	1.32
29	StrucAssCoasPlank	**0.0026**	**0.0026**	**0.0026**	**10.00**	**10.00**	**10.00**	**2.60**	**2.60**	**2.6**
30	NearshAssPisc	0.0048	0.0048	0.0048	7.67	17.25	7.67	1.06	1.06	1.06
31	Mullets	0.3292	0.3292	0.0006	11.03	11.03	10.37	0.70	0.90	0.79
32	NearshPlanktivores	**0.1811**	0.1857	0.0097	15.91	16.42	14.54	0.60	1.32	0.60
33	Other fishes	**3.8768**	**5.8063**	**0.2709**	**7.04**	**7.04**	**7.04**	**0.70**	**0.70**	**0.70**

Notes: Best estimates were used as initial input to the model. Values between minimum and maximum were used in the model during balancing (Table 3.2). Values in bold are highly uncertain.

Input parameter confidence is influenced by several factors. Trawl sampling, for example, under-samples certain species due to inter-specific variability in behavior and preferred habitat. Place-holder values are used for other species due to limited information. The highly uncertain estimates are highlighted in bold in Table 9.10, and these uncertain cases are discussed below.

10. Pelagic coastal piscivores: Large uncertainty in biomass for this group could have a large effect on prey groups in the model. It was assumed during model balancing that this group's biomass must be higher the original estimate because this group comprises many species whose combined biomass is likely to be greater than the biomass of adult mackerel, upon which this estimate was based.
16. Demersal oceanic invert eaters: This group contains only 2 species, goatfish and blackmouth bass, for which there are no good parameter estimates. The initial (borrowed) P/B estimate was likely too high. In the future, these species could be included in another group.
20. Benthic oceanic piscivores (largescale lizardfish, shortjaw lizardfish, offshore lizardfish, duckbill eels): These species might be considerably more abundant on the West Florida Shelf than the trawl estimates suggest. This group has a strong effect on the demersal invertebrate eaters and invertebrate functional groups upon which they feed. Incorrect parameterization of this group thus indirectly influences the thermodynamic 'balance' of these prey groups in the model.
21. Benthic oceanic invert eaters (pancake batfish, spinycheek scorpionfish, slender searobin, shortwing searobin, saddle bass, tilefish family, luminous hake): Very little information is available on any species in this functional group. The best estimate P/B was considered too to high and was considerably reduced during balancing.
24. Surafce pelagics (Halfbeaks and flying fish): These species were not well sampled by any of the gear used to in abundance estimation. However, these species are found in the gut contents of many West Florica shelf fishes, suggesting much higher abundances than estimated. This group's biomass was estimated by *Ecopath* during balancing.
29. Structure associated coastal planktivores (twospot cardinalfish, sponge cardinal fish, purple reeffish, yellowtail reeffish, blue chromis, jawfish): All basic parameters in this group are poorly estimated due to limited information.
32. Nearshore associated planktivores: (bay anchovy, striped anchovy, silverside family, alewife). Anchovies are not well sampled by the methods used in this system, but gut contents of other predators indicate a high biomass for this group. This group's biomass was estimated by *Ecopath* during balancing.
33. Other fishes (all varieties including, flounders, soles, toadfish, spikefishes, boxfishes, cowfish, goosefish, dragonets, stargazers, temperate basses, brotulas, pearlfish, clingfish, codlets, argentines, sculpins, pipefish and seahorse): Biomass of the 'other fishes' group is simply the remainder of the total biomass estimated from trawl surveys after all other species were accounted for. Placeholder P/B and Q/B estimates fall mid-way between piscivores and invertebrate eaters.

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10. SEABIRDS

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One hundred and three seabird species were reported for the Southwest Florida region by Owre (1990). Seabirds of this region feed on a variety of biota ranging from small invertebrates (e.g. Phalaropes) to primarily fishes (e.g. Pelicans, Cormorants, etc.), while others combine fishes and invertebrates in their diets (e.g. Storm-Petrels, Tropicbirds, etc). Here, we have included only the species that primary consume bait fish because detailed abundance and diet information is rare. Birds that consume baitfish include Pelicans, Terns, Gulls, Frigatebirds, Loons, Gannets, and Cormorants. Of these, Brown Pelicans, Northern Gannets, and Double-crested Cormorants are notably abundant (Table 10.1)

Table 10.1. Abundance of bait fish consuming seabirds in the Gulf coast of Florida.

Species	Occurrence	Numbers	Body weight (kg)
Common Loon	Oct- April	4,000	4.00
Brown Pelicans	year round	17,000	3.4
White Pelicans	September - April	4000	7.0
Magnificent Frigatebird	April- October	10,000	1.50
Northern Gannet	November-May	15,000	3.00
Double-crested Cormorant	year round	20,000	1.70
Misc. Terns and gulls	year round	20,000	0.30
Red-breasted merganser, ducks and grebes	October-April	10,000	1.00

Note: From Dunning 1993.

These abundance estimates were used to derive an annual seabird biomass of 0.001 $t{\cdot}km^{-2}$ on the West Florida Shelf. The P/B estimate (0.1 $year^{-1}$) was taken from an *Ecopath* model in the Florida Bay (Acosta *et al.* 1998); these authors based their P/B estimate on an empirically derived value for seabird mortality in Florida waters. A weighted Q/B was calculated using the empirical formula to calculate seabird food consumption per day from Nilsson *et al*. (1976) and the biomass of each species in the group. These parameters are shown in Table 10.2.

Food consumption was estimated with the following formula:

$$\log R = -0.293 + 0.85 * \log W$$

where:
R = food consumption per day, in grams
W = body weight, also in grams

Table 10.2. Seabird parameters for the West Florida Shelf model.

Species	Daily ration (kg)	Annual biomass (t)	Q/B_w
Common Loon	0.147	0.00005	3.0
Brown Pelicans	0.150	0.00034	19.2
White Pelicans	0.135	0.00010	5.1
Magnificent Frigatebird	0.170	0.00005	3.3
Northern Gannet	0.153	0.00015	8.9
Double-crested Cormorant	0.167	0.00020	12.6
Misc. Terns and gulls	0.216	0.00004	2.9
Red-breasted Merganser, ducks and grebes	0.181	0.00003	2.3
Total Seabirds		**0.001**	**57.3**

Brown Pelicans were estimated to have the highest biomass (38%) and total consumption among the bird species scrutinized; and their diet was used as a starting point for estimating the diet composition of birds in the West Florida Shelf model. This diet was refined with the diet information of coastal birds collected by Browder (NMFS, pers. com.) in the South Florida region. Fogarty et al. (1981) characterized the diet of nesting brown pelicans in Florida. They found that the major prey item, by frequency of occurrence were clupeids (30%), sciaenids (21%), Atlantic threadfins (13%), and mullet (12%). Barret *et al*. (1993) showed that seabirds also consumed crustaceans, cephalopods from the upper and mid water column, juvenile demersals, inshore benthic fishes, fish carcasses, and discards. The West Florida Shelf seabird diets were modified based on this additional information.

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11. SEA TURTLES

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Three sea turtle species nest regularly on Florida's beaches: the loggerhead, *Caretta caretta;* the green, *Chelonia mydas;* and the leatherback, *Dermochelys coriacea*. Two other species, the hawksbill, *Eretmochelys imbricate;* and Kemp's ridley, *Lepidochelys kempii*, occur throughout Gulf of Mexico coastal waters, bays, and lagoons. These habitats are used as nursery and development areas by juveniles and subadults. Sea turtles come to Florida's nesting and rearing areas from feeding grounds scattered throughout the Atlantic. Along Florida's Gulf coast, most nesting occurs from Pinellas to Monroe Counties. Sea turtles have not been intentionally harvested in Florida since the 1970s, but they are often caught incidentaly by haul seines, gill nets, shrimp trawls, and pound nets. Most information about west Florida sea turtles in this chapter was taken from Van Meter (1992).

About 14,000 female loggerheads nest in the Southeastern US annually, and this species accounts for ca. 97.9% of the total sea turtle nesting activity in Florida state (Plotkin, 1995). Florida's west coast is also a major feeding area for non-nesting loggerheads. Habitat on the shelf is limited by the turtle diving ability to feed on bottom-dwelling organisms (loggerheads can dive as deep as 50 to 70 m); in southeast Florida, loggerheads are more abundant inside the 50 m isobath (Fritts et al., 1983). Loggerheads forage along the inshore and coastal waters of the Gulf of Mexico, the Florida Keys and north all the way to New England. Nesting females remain in shallow areas near beaches during the nesting season. They then disperse to feeding grounds throughout the Bahamas, Cuba, Dominican Replubic, north along the eastern US coast and south through the Florida Keys and Gulf of Mexico (late April to September). Florida bay is a developmental habitat for loggerheads originating from Southeast US beaches (Schroeder et al. 1998).

Green turtles nest in Florida from June to late September. Between 60 and 800 green turtles nests are reported each year on Florida's east coast (Plotkin, 1995). Immature green turtles have been reported along the west coast, in Florida Bay and in the Cedar Key / Crystal river area, indicating the importance of these areas as developmental habitat (Schroeder et al., 1998). Green turtles prefer shallow, sandy flats covered with seagrasses or seaweeds.

The leatherback is the largest sea turtle species, weighing 700 to 2,000 pounds and measuring 4 to 8 feet in length as adults. This species inhabitats shallow waters along the northern Gulf of Mexico, the east and west coasts of Florida, and north through coastal New England. Global abundance estimates of breeding female leatherbacks range from 70,000 to 115,000, and the number of nests reported in Florida ranges from 39 to 188 since 1979 (Plotkin, 1995). Leatherbacks nest in Florida from April through July, but they are observed along Florida's west coast during all months except February and April (Fritts et al., 1983). Sightings in southwest Florida have been concentrated between 27 and 166 km from shore (Fritts et al., 1983).

The hawksbill is a small to medium sized turtle observed regularly in the Florida Keys. Posthatchlings occupy the pelagic environment, taking shelter in weedlines that accumulate at convergence points. They re-enter coastal waters when they reach 20-25 cm carapace length. Coral reefs are the main foraging habitat of juveniles and adults, which feed primarily on sponges on these reefs. Hawksbills are also known to inhabit mangrove-fringed bays and estuaries where coral reefs are absent.

The Kemp's Ridley is the rarest and most endangered sea turtle. Adults are found in productive coastal and estuarine waters of the Gulf of Mexico, particularly near the Mississippi River mouth. Juvenile and subadults are widely distributed through US coastal waters from Texas to Maine, but the west Florida coast is the area of 'maximum abundance' of Kemp's Ridley in the U.S. Stranding and capture records indicate that Kemp Ridley's were most often encountered in west Florida in the late spring and summer. This temporal pattern is likely due to migration or winter dormancy.

Biomass and Production / Biomass

Sea turtles are monitored by their nesting activity along the beaches of Florida. However, the number of nesting females is not an appropriate index of turtle numbers feeding on the shelf because females probably do not eat during the reproductive season, and because feeding areas are usually distinct from nesting areas (A. Meylan, *pers. comm.*). I used three sources of information to estimate number of foraging individuals on the West Florida Shelf: 1) NMFS stranding data; 2) turtle counts made by aerial surveys by the Mineral Management Survey; 3) turtle bycatch by shrimp trawlers.

Stranding reports of dead or injured turtles represent a minimum mortality estimate. Strandings provide an indication of the characteristics of populations in the area, such as species composition and relative abundance, size and seasonal changes (most stranded turtles have boat related injuries). Table 11.1 shows the number of strandings by species along the west Florida coastline. Loggerheads are most commonly stranded (ca. 54% of total), followed by Kemp's Ridley (ca. 22%) and Green (16%). Leatherback and Hawksbill turtles account for less than 2% of strandings. Henwood and Stuntz (1987) also found a low frequency of occurrence of leatherbacks and hawksbill turtles in shrimp trawlers bycatch. They calculated the turtle catch per unit of effort (CPUE) for the three dominant species from 1973 to 1984 (Table 11.2) (# of turtles per 30.5 m net headrope length per hour fishing). I used CPUE to roughly estimate turtle densities by calculating number of turtles per given swept area. The swept area of a trawl *net hour* was calculated assuming a trawling speed of ca. 2.5 knots. Based on the information available, I estimated the density of loggerheads, the most abundant species over the Gulf shelf, to be 0.0326 turtles·km^2.

Table 11.1. Sea turtle strandings reported in West Florida counties between 1990 and 1999.

Species	*Caretta caretta*	*Chelonia mydas*	*Lepidochelys kempii*	*Eretmochelys imbricata*	*Dermochelys coriacea*	*Unindentified to species*	Total
West coast	1094	337	446	28	33	102	2040
Percentage	53.65	16.51	21.86	1.37	1.61	5.00	100

Note: Data from Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, Sea Turtle Stranding and Salvage Network Database.

Table 11.2. CPUE and density of sea turtles estimated from shrimp bycatch data in the Gulf shelf.

Species/area	CPUE (turtles/net hour)	Density [a] (turtles/km^2)
Loggerhead, Eastern Gulf	0.0046	0.0326
Loggerhead, overall Gulf	0.0025	0.0177
Kemp's ridley, overall Gulf	0.0004	0.0028
Green, overall Gulf	0.0001	0.0007
All turtles, Gulf shelf from Florida to Texas	0.0031	0.0220

Notes: From Henwood and Stuntz, 1987; [a] swept area estimates: one trawl net hour is equivalent to 0.1412 km^2.

Fritts et al. (1983) reported that densities of loggerheads in this area ranged from 0.031 to 0.33 turtles/km^2. Their data were obtained during bimonthly surveys over the southwestern Florida shelf (total area 24,642 km^2) between May 1980 and April 1981. Density estimates were possible for loggeheads only, since the other two species most frequently sighted, green and Kemp's, were observed only a few times. Similarly, Mullin and Hoggard (2000) estimated loggerhead densities to be 0.0407 turtles/km^2 in the Florida panhandle region (waters <100m) and in eastern Gulf shelf slope waters (100 – 2000 m) based on aerial surveys from 1996 to 1998. Estimates of densities of leatherback and Kemp's ridley turtles were 0.00194 and 0.00097 turtles/km^2, respectively. Leatherbacks and loggerheads were the only turtle species sighted in the shelf slope area. The overall density of leatherbacks and loggerheads in slope waters was 0.00238 and 0.002 turtles/km^2, respectivelly.

Given the three independent estimates above, I estimate the density of loggerheads on the West Florida Shelf to be about 0.03 to 0.04 turtles/km^2. The total density of sea turtles in the study area was calculated by extrapolating the loggerhead density to the other species using the stranding data as a measure of the relative abundance (Table 11.1). The sea turtle biomass estimate (0.0069 tonnes/km2) was then calculated by multiplying species densities by mean body weight. A loggerhead production to biomass ratio was estimated as 0.22 year^{-1}, assuming an adult annual survivorship of 80% (Henry et al. 1998). P/B ratios for the other species were assumed to be 0.15 year^{-1} (Polovina, 1984). The P/B ratio for the group was calculated as the average P/B of individual species, weighted by species biomass.

Diet and Consumption / Biomass

Loggerheads are omnivorous, but prefer a carnivorous diet of shellfish and mollusks, especially clams, oysters, and crabs, as well as encrusting animals attached to rocks and reefs. Green turtle hatchlings are carnivorous, but juvenile and subadults are more omnivorous, eating jellies as well as marine plants. When green turtles are 20 to 25 cm long they begin feeding on algae and seagrasses on shallow flats (Mendonça, 1983).

Jellies (*Physalia* spp. and Scyphozoans) are the primary food of leatherbacks. Hawksbills consume a variety of invertebrates, but their predominant prey is sponges. Kemp's ridley is carnivorous, feeding on swimming crabs and other crustaceans, clams, mussels, fish and jellies. Blue crabs are their preferred food in many places (Creech and Allman, 1998). Diet for the group was calculated by the weighted average diet of the individual species, using species total consumption as weighting factor. A sea turtle Consumption / Biomass (Q/B) of 3.5 year^{-1} was taken from Polovina (1984).

Table 11.3. Sea turtle parameter estimates.

Species	**Density turtles/km^2**	**Adult mean weight (Kg)**	**Biomass tons/km^2**	**P/B year^{-1}**	**Q/B year^{-1}**
Loggerhead, Caretta caretta	0.0350	120	0.0042	0.22	3.5
Kemp's Ridley, Lepidochelys kempii	0.0140	42	0.0006	0.15	3.5
Green, Chelonia mydas	0.0110	136	0.0015	0.15	3.5
Hawksbill, Eretmochelys imbricata	0.0009	80	0.000072	0.15	3.5
Leatherback, Dermochelys coriacea	0.0011	500	0.0006	0.15	3.5
Total	0.0620				

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12. MARINE MAMMALS

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12.1 Odontecetes

A variety of marine mammals inhabit the waters over the West Florida Shelf and continental slope. The two dominant species are the bottlenose dolphin, *Tursiops truncates,* and the Atlantic spotted dolphin, *Stenella frontalis* (Mills and Rademacher, 1996). Several other species are commonly observed in the study area, including the Risso's dolphin, *Grampus griseus*, the short-finned pilot whale, *Globicephala macrorhynchus*, the false killer whale, *Pseudorca crassidens*, spinner dolphins, *S.clymene* and *S. longiristris*, the striped dolphin, *S. coeruleoalba*, Gervai's beaked whale, *Mesoplodon europaeus*, and Cuvier's beaked whale, *Ziphius cavirostris* (Odell, 1990).

Biomass and Production / Biomass

Results from Gulf shelf shipboard surveys (Mills and Rademacher, 1996) indicated that about 86% of spotted dolphin sightings occurred in waters shallower than 100 m, and particulalrly between 15 and 100 m isobaths. More sightings recorded east of the Mississippi River mouth (0.4752 sightings per hour) than west of it (0.2489 sights per hour). Survey data also indicated that spotted dolphins migrate inshore and offshore seasonally, and possibly alongshore to the south during winter. Swartz et al. (1999) estimated that at least 12,896 bottlenose dolphins and at least 33 individual stocks inhabit the bays, sounds, and estuaries of the eastern Gulf of Mexico coastal area.

Bottlenose dolphins of the Gulf can also be organized onto different stocks region (Leatherwood and Reeves, 1990): 1) one inhabiting outer shelf waters from the U.S./ Mexican border to the Florida Keys (from about 9 km seaward of the 18 m isobath); 2) an eastern Gulf coastal stock from shore to about 9 km seaward of the 18 m isobath and from 84ºW longitude to Key West, Florida; and 3) several small stocks inhabiting bays, sound, and estuaries. The coastal stock (completely inside the study area) has at least 8,963 individuals; the the outer shelf stock (only part of it in the study area) contains at least 43,233 individuals, and the estuarine, sound, and bay stocks contain at least 1,911 individuals (Leatherwood and Reeves, 1990). I estimate there to be 23,844 bottlenose dolphins in the study area, assuming that 30% of the outer shelf stock occurs within the study area. The estimated dolphin density is thus 0.146 individuals per km^2. This latter estimate is consistent with results of independent aerial surveys between 1996 and 1998 (Mullin and Hoggard 2000).

Mullin and Hoggard (2000) report the results of visual surveys of cetaceans in the continental shelf in the northeastern Gulf of Mexico (both ship and aerial). Surveyed areas were south of the western Florida Panhandle in continental shelf waters from 12.5 km offshore to 100 m deep (12,326 km^2), and also in the continental slope waters (100-2000 m) within the US EEZ (70,470 km^2). Table 12.1 shows the estimated abundance of cetaceans from aerial surveys (aerial survey estimates were generally higher than ship survey estimates). The continental shelf region is inhabited almost exclusively by bottlenose dolphins and Atlantic spotted dolphins (one dwarf/pygmy whale was sighted in the shelf area). In contrast, sixteen cetacean species were sighted in continental slope waters (Table 12.1). Pantropical spotted dolphins and spinner dolphins were the most abundant species there in the slope area.

Biomasses of individual species were estimated by multiplying densities and mean body weights (Trites and Pauly, 1998). The mean biomass of cetaceans in the study area was calculated by weighting species biomasses by the approximate areas of shelf (0 – 100 m = 139,679 km^2) and slope regions (100 – 183 m = 22,848 km^2) of the study area inhabited by each species. I estimated the total biomass of marine mammals in the area to be 0.038 tonnes·km^{-2}. The P/B ratio West Florida Shelf odontoceates was taken to be 0.1 year^{-1} (Browder 1993, Matkin and Hobbs 1999).

Table 12.1. Mean body weight, density and biomass of cetacean species.

Species	**Mean body weight, Kg**	**Shelf indiv./km^2**	**Slope indiv./km^2**	**Biomass t/km^2**
Bottlenose dolphin, *Tursiops truncatus*	187.5	0.14798	0.05617	0.025326
Atlantic spotted dolphin, *S. frontalis*	66.4	0.08890	0.02555	0.005312
Dwarf/pygmy sperm whale	139.0	0.00081	0.00267	0.000149
Bryde's whale	16,143.0	—	0.00035	0.000794
Sperm whale	18,518.5	—	0.00052	0.001354
Cuvier's beaked whale	828.5	—	0.00031	3.61E-05
Beaked whale, *Mesoplodon* spp	444.5[b]	—	0.00084	5.25E-05
Pygmy killer whale	97.5	—	0.00309	4.24E-05
False killer whale	578.0	—	0.00213	0.000173
Short-finned pilot whale	643.0	—	0.00227	0.000205
Rough-toothed dolphin	92.0	—	0.00234	3.03E-05
Risso's dolphin	447.2	—	0.01869	0.001175
Pantropical spotted dolphin	66.4[c]	—	0.19369	0.001808
Striped dolphin	116.0	—	0.03253	0.00053
Spinner dolphin	41.3	—	0.12302	0.000714
Clymene dolphin	46.8	—	0.03253	0.000214

Notes: Density data from aerial surveys in the continental shelf of western Florida Panhandle and slope areas during 1996-1998 (Mullin and Hoggard, 2000); [a] mean weight of males and females (Trites and Pauly, 1998). [b] assuming the same mean weight as the True's beaked whale; [c] assuming the same weight as Atlantic spotted dolphin.

Diets and Consumption: Biomass ratio

The diet of whales and dolphins was based on the Pauly et al. (1998) standardized citation diet. The proportion of fish groups in the diet of dolphins was calculated based on Barros and Odell (1990), Barros and Wells (1998), and Perrin et al (1989). I estimated Q/B ratios for piscivorous and planktivorous marine mammals as 41.07 year^{-1} (Browder, 1993) and 10.95 year^{-1} (Matkin and Hobbs, 1999) respectively. Q/B for the group was calculated as the average Q/B of individual species, weighted by species biomass. Diet for the group was calculated as the average diet of individual species, weighted by the species total consumption.

12.2 Manatees

Manatees, *Trichechus manatus latirostris*, occurr in nearshore coastal areas, and they are rarely observed beyond 1 mile from shore. Manatees migrate seasonally to warmer areas during winter; these include southern coastal waters, natural springs, and industrial warm water effluents (counts at these wintering locations are used to estimate population abundance). This species inhabits estuaries and coastal bays during summer (O'Shea et al. 1995). During winter, they are known to make foraging trips to Salt River and Crystal Bay estuaries to feed on *Rupia maritima* beds (O'Shea et al., 1995).

There are about 350 manatees in Florida's western coastal areas during summer and about 200 during winter (B. Ackerman, *pers. comm.*). I estimate that the biomass of manatees in the study area is 0.0008 tonnes/km^2, given a mean individual weight of ca. 500 kg. The annual death and birth rates are approximately equal at 10% (B. Ackerman, *pers. comm.*). The P/B ratio was estimated to be 0.1 year^{-1}. At least 30% of deaths are from human causes. Manatees feed exclusively on seagrasses. The daily ration is about 10% of their body weight (B. Ackerman, *pers. comm.*). The Q/B estimate is thus 36.5 year^{-1}.

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13. FISHERIES

13.1 Landings

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The variety of species available to any gear makes fisheries on the West Florida Shelf complex. Fishers landed 48 000 tonnes from the shelf during the 1997-98 fishing year. The major fisheries on the shelf are: hook-and-line fishing for the reef fish species such as snappers and groupers, trolling and net fisheries for coastal pelagic species such as king or Spanish mackerel or dolphin fish, long-line fisheries for deeper water species such as tilefish or sharks, traps for invertebrate species such as stone crabs, and trawls for Penaeid shrimp and a variety of ornamental species. To illustrate this complexity, when a hook-and-line boat drops fishing lines over hard bottom habitat, fishers can catch snappers, groupers, grunts, amberjacks, or other species with the same setup. It is necessary to capture this diversity when analyzing catch records.

Harvest information on the West Florida Shelf comes from a variety of sources. The Florida Fish and Wildlife Conservation Commission (FWC) tracks commercial harvests through trip tickets. The information collected includes the fisher's identification, the wholesale dealer's identification, the date landed, county landed, gear fished, depth fished, area fished, and, for each species landed on a trip, species code, quantity landed, size category, and price paid. In addition to commercial fisheries operating on these stocks, recreational anglers also pursue these species. The National Marine Fisheries Service (NMFS) has a program, Marine Recreational Fisheries Statistical Survey (MRFSS), that estimates recreational catches, landings, and releases using angler interviews to identify species and sizes harvested and a telephone survey to estimate the number of recreational fishing trips by two-month time period, geographic and fishing mode (shore, private/rental boat, or charterboat). Average weights by were used to convert landings estimates in number to kg. The National Marine Fisheries Service has another program to monitor angler activity on headboats by month and location. In Florida, FWC personnel conduct the interviews for both of NMFS's recreational programs.

Landings were summarized into 15 gears (only 11 of which had landing data) with recreational landings and headboat landings were included as separate gear codes. For the *ECOPATH* analysis, we extracted landings from the three sources for the latest, complete fishing year, July 1997 through June 1998. We used a fishing year because many of the shelf species are seasonal and, for example, it is necessary to include December and January into the same season.

Landings from the shelf were broken down into geographic regions and also by distance from shore. The three regions were: northern – Escambia through Gulf counties, central region – Franklin through Pasco counties, and southern – Pinellas through Collier counties. Commercial landings were assigned to geographical regions using the county where the species were landed, recreational and headboat landings were estimated for the three geographic regions using MRFSS's post-stratification program. Data were available to identify inland and bay waters, state territorial waters (beach to nine miles out) and federal waters (beyond nine miles). Bay and inland waters were not included in this analysis because the focus on the West Florida Shelf and the number of species which only occur inshore. Similarly the Florida Keys were omitted because of the large number of sub-tropical species that are only found in the Keys.

A conversion table was created to link commercial species codes with their equivalent National Ocean Data Center (NODC) species codes. Commercial landings were combined with MRFSS and headboat landings by NODC species codes and then were linked to the functional groups defined in *Ecopath* west Florida Shelf model. Thus, landings in kg were tallied by functional group, gear, geographic region, and area based on distance from shore. Table 13.1 displays fishery catches on the West Florida Shelf during the 1998-1999 season.

Table 13.1. State and Federal fisheries landings (tonnes) from West Florida Shelf, 1998-1999.

Group	Unknown	Trawl	Recreation	Headboats	Gill net	Trammel net	Spear / gig	Hook and line	Purse seine	Haul seine	Long line	Traps	TOTAL
Large oceanic piscivores	0.47	0.00	4520.68	1.41	0.00	0.00	0.00	79.62	0.00	0.00	507.00	0.00	5109.17
Coastal sharks	4.27	0.06	171.26	0.66	0.02	0.00	0.00	21.81	0.00	0.00	508.04	0.00	706.12
Rays and skates	0.00	0.14	44.50	4.93	0.00	0.00	0.00	0.09	0.00	0.03	0.00	0.00	49.69
Pelagic oceanic piscivores	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.00	15.62	0.00	15.92
Pelagic coastal piscivores	8.07	147.60	2044.79	37.31	11.28	0.00	0.24	293.77	61.10	58.23	41.79	2.32	2706.50
Mackerels adult	0.17	0.71	2289.10	7.03	0.63	0.00	0.00	99.48	0.11	0.02	1.01	0.00	2398.27
Sardine-herring-scad complex	155.40	200.29	316.51	0.00	0.00	0.00	0.00	0.00	2830.56	358.44	0.00	0.00	3861.20
Pelagic oceanic jelly eaters	0.01	434.31	0.00	0.00	0.00	0.00	0.00	0.18	183.06	0.07	0.00	0.00	617.63
Pelagic oceanic planktivores	0.00	136.51	0.00	0.00	0.00	0.00	0.00	0.00	332.28	0.00	0.00	0.00	468.79
Demersal oceanic invertebrate feeders	0.00	67.49	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	68.24
Demersal coastal piscivores	0.40	19.63	974.54	0.00	0.24	0.00	0.00	47.03	0.34	0.44	0.00	0.18	1042.79
Demersal coastal invertebrate feeders	4.63	212.17	2343.35	68.38	214.28	0.17	1.97	78.09	5.07	14.46	1.64	51.16	2995.38
Demersal coastal omnivore	0.15	8.96	325.73	0.47	0.00	0.00	0.00	7.34	0.00	0.31	0.00	5.15	348.11
Benthic oceanic piscivores	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Benthic oceanic invertebrate feeders	0.00	4.67	2.80	0.01	0.00	0.00	0.00	13.77	0.00	0.00	274.86	0.00	296.12
Benthic coastal piscivores	1.02	14.46	76.42	0.47	0.03	0.00	49.38	4.45	0.00	0.69	9.68	1.17	157.79
Benthic coastal invertebrate feeders	0.00	2.88	22.93	1.80	0.00	0.00	0.00	1.58	1.50	0.00	8.37	0.00	39.06
Surface pelagics	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Structure associated coastal piscivore	1.32	2.90	1535.93	100.17	0.43	0.00	0.66	109.63	0.02	0.02	127.11	2.83	1881.01
Large groupers	47.26	30.21	1779.13	104.71	0.69	0.00	8.94	1563.47	0.00	0.00	2062.34	821.07	6417.82
Structure associated coastal invertebrate feeders	7.94	38.33	1696.47	191.53	0.37	0.00	3.09	980.73	1.44	3.73	15.88	84.49	3024.00
Structure associated coastal omnivores	0.00	0.65	2.04	0.01	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	2.75
Structure associated coastal planktivores	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21
Nearshore associated piscivores	35.31	32.18	154.62	0.00	0.00	0.00	0.00	6.58	11.38	7.63	0.00	0.00	247.70
Mullets	14.89	2110.47	618.43	0.00	18.23	0.00	0.87	7.98	71.57	369.32	0.00	0.01	3211.77
Nearshore planktivores	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Other fishes	0.00	58.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	58.40
Squid (Loligo opalescence) and cuttlefish	0.06	34.28	0.00	0.00	0.00	0.00	0.00	0.04	3.62	0.00	0.00	0.00	38.00
Shrimps	18.12	5304.36	0.00	0.00	0.00	0.00	0.00	4.90	0.00	0.41	0.00	11.48	5339.27
Lobsters (Spiny - Panulirus argus)	0.27	23.69	0.00	0.00	0.00	0.00	0.00	0.86	0.00	0.00	0.00	25.75	50.57
Crabs (Blue, stone, fiddler & others)	18.01	193.63	0.00	0.00	0.00	0.00	1.94	6.57	14.60	7.09	0.00	4000.88	4242.71

Octopods	0.00	0.70	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	2.12	2.85
Stomatopods	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(other) large mobile epifauna	0.00	874.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	874.23
Sand dollars	0.00	765.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	765.77
Large infauna	0.00	191.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	191.98
Sessile epifauna	6.34	863.42	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.25	870.39
Small infauna	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
Small mobile epifauna	0.00	84.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.61	85.08
Jellies	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.55
Macroalgae	0.00	1.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.46	0.00	0.00	1.50

13.2 Bycatch and discards

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Two sources of discards in West Florida Shelf were included in the model, from longline and shrimp trawl fisheries.

Longline discards are mainly comprised of sharks and billfishes. Cramer and Scott (1998) estimated that about 37% of sharks caught in longline fisheries in the Gulf of Mexico are discarded. To calculate discards of coastal and large oceanic sharks, the reported landings of shark species from longline fisheries were assumed to represent only 63% of the total catches. There are no reported catches of billfishes (white and blue marlin, and sailfish) from longline fisheries in west Florida (State and Federal Landings Database). Farber (1992) estimated that approximately 85 tons of billfishes were discarded in longline fisheries in the Gulf of Mexico. The total discards of billfishes from longline fisheries operating in the Gulf of Mexico in 1996 are estimated by NMFS (1998) as 24.7 tons of blue marlin, 11.6 tons of white marlin, and 42.1 tons of sailfish. To calculate the total catches (discarded) of billfishes by longlines in west Florida it was assumed that ca. 1/5 of Gulf catches occur off west Florida, based on the fact that billfishes spend at least 1/5 of a year, during peak spawning months, in west Florida. Therefore total catches and discards (tonnes) of billfishes in west Florida were estimated as (Table 14.1):

Table 14.1. Landings and discards of large oceanic piscivores

Species	Landings	Long line discards	Catches
Blue marlin		6.60	6.60
White marlin		2.40	2.40
Sail fish	13.4	8.42	21.82
Total	13.4	17.42	30.82

Shrimp trawlers have a significant bycatch of non-target finfish, invertebrates, and other endangered or threatened species such as turtles and manatees. The average finfish: shrimp ratio in shrimp trawling in the Gulf of Mexico is 10 to 1, but varies significantly by area, from 2:1 in the Dry Tortugas to 14:1 off the Mississippi river. On average, the total discards from offshore shrimp trawling in the Gulf of Mexico represent ca. 97% of the total bycatch (Alverson et al., 1994), although the bycatch discarded in inshore shrimp trawl fisheries is gerenerally lower (Maharaj and Recksiek 1991). In this section we consider that all finfish and invertebrates bycatch in shrimp trawlers are discarded.

To calculate bycatch (discards) from shrimp trawlers we followed three steps:

Firstly, we compiled available information on species composition in the bycatch of shrimp trawlers in west Florida. For inshore trawl fisheries (<areas within 9 nautical

miles from the shore) we used data from Steele *et al*., (unpublished, a and b). Two gear types are commonly used in inshore shrimp fisheries of west Florida: ottertrawls and rollerframe trawl. Otter trawls are used in coastal areas and bays (including Tampa Bay) on nonvegetated, sandy bottom areas. Rollerframe trawls are used in seagrass beds to harvest both food shrimp and shrimp used for bait. Bycatch data for offshore trawlers were obtained from the Gulf of Mexico Fishery Management Council (NOAA). In the latter we assumed that the depth of 10 meters approximately corresponds to the 9 nautical miles distance used as limit between inshore and offshore areas in the state of Florida's catch database.

Secondly, we used the total landings of shrimp by area (inshore, offshore) and the average bycatch: shrimp catch ratio to calculate the total expected amount of bycatch originated from trawlers in west Florida. Finfish: shrimp ratios for inshore fisheries were estimated to be 3.31:1 (Steele *et al*., 2002; Steele et al., in review). On average, the catch of inshore trawlers is comprised of 30-70% finfish, 15% shrimps, 15-58% horseshoe crabs and blue crabs, and 25% of miscellaneous invertebrates (Steele, et al., in review). We therefore estimated the crab and invertebrate: shrimp ratios in inshore fisheries to be ca. 2.4 and 1.7, respectively. For offshore fisheries the estimated ratio is 3.16:1 (Gulf of Mexico Fishery Management Council, NOAA).

Finally, the total bycatch estimated above was then splited among species and functional groups according to species proportion in trawlers bycatch. Table 14.2 shows the bycatch discarded by functional group estimated by accounting for differences in landings, bycatch:shrimp ratios and species composition in the catch of shrimp tralwers in inshore and offshore areas. For mackerel we used discards estimates provided by Legault (1998).

Table 14.2. Discards by shrimp trawlers.

Functional group	**Discards (tonnes)**	**Discards (t·km^2)**
Mackerel juveniles	571.390	0.0034
Mackerel adults	194.166	0.0011
Sardine-herring complex	17.101	0.0001
Demersal coastal piscivores	83.453	0.0005
Demersal coastal invertebrate feeders	1873.639	0.0110
Demersal coastal omnivore	1463.698	0.0086
Benthic oceanic invertebrate feeders	169.573	0.0010
Benthic coastal piscivores	13.199	0.0001
Benthic coastal invertebrate feeders	2331.251	0.0137
Structured associated coastal piscivore	0.908	<0.00001
Structured associated coastal invertebrate feeders	288.089	0.0017
Nearshore planktivores	20.863	0.0001
Other fish	154.179	0.0009
Crabs	2479.909	0.0146
Large mobile epifauna	814.518	0.0048
Sessile epifauna	814.518	0.0048

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14. Limitations, cautions, and guidelines for use

14.1 SCALE AND INFERENCE: THE NATURE OF *ECOPATH* MODELS

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Ecosystems are complex. Moreover, the complexity of ecosystems is fractal; increasing complexity occurring at increasingly narrow scales of examination. Ecosystem processes that occur on micro-scales have fundamental importance to broader-scale ecosystem structure and properties.

To undertake an integrated and quantitative analysis of a whole ecosystem, ones building blocks must represent relatively broad components or processes. The input parameters of an *Ecopath* model (e.g., B, P/B, Q/B, and DC of aggregated functional groups) are such building blocks, and their broad and generalized nature, or the inherent de-emphasis of micro-scale processes, can lead to confusion about the usefulness of the approach. The lack of explicit articulation of micro-scale processes does not, however, imply that these processes are excluded from consideration, or even from parameterization. *Ecopath* parameters, and models, implicitly integrate micro-scale processes.

Indeed, each of the *Ecopath* parameters represents the sum, or the result, of all smaller scale processes (that are considered), which lead to the emergence of measurable ecosystem properties. *Ecopath* parameters thus ideally integrate all smaller scale processes into a description of the food web, vis-a-vis all biotic components of the system (throughout all trophic levels). This is accomplished through measurement and empirical information from appropriate scales of examination. In essence, an *Ecopath* model represents a system that results from micro-processes. This approach is, therefore, not subject to the additivity and multiplicativity of errors that are typically encountered when such models are constructed from the 'bottom up.' The inherent complexity of ecosystems virtually prevents analytical endeavors in which attempts are made to reconstruct all the micro-scale processes to support each consecutive level.

The *Ecopath* approach begins by describing ecosystem components at all levels, with a focus on the 'data richness' of each 'integrative' input parameter (Section 2), and then learning and refining from examination of the imbalance resulting from the broader integration of these parameters into a system-wide picture (Section 3). These initial parameters are subsequently adjusted until thermodynamic constraints are met ('model balancing'). The resulting 'balanced' model then represents one possible average state of the flows in the food web. The model balancing process provides an opportunity for learning about ecosystem structure as the model builders attempt to minimize the introduction of bias.

In contrast, 'bottom up' mechanistic models are attempts to reconstruct nature through representations of deterministic processes on a much finer detail. Although the scale of examination of such an approach effectively prevents representation of whole food webs, the information emerging from these detailed efforts can be used to parameterize components of *Ecopath* models.

Notwithstanding this qualitatively important contrast between these two approaches, a clear view of the nature of *Ecopath* models is essential for understanding its limitations. An understanding of its limitations, in turn, leads to an understanding of its usefulness.

Aspects of the *Ecopath* approach have been described in all of the previous sections. The salient point about *Ecopath with Ecosim* in relation to its limitations relates to the scale at which the system is being examined. Biotic components of a food web analyzed with this approach are generally aggregated into 50 aggregated groups or less. This approach gives us a broad view of the system; the premise of *Ecopath with Ecosim* is that the interaction of these broad ecosystem components in dynamic simulations will represent the interaction of real ecosystem components because enough population and energetic information exists on this broad scale of examination to characterize the mechanisms of interest. Most of the uncertainties, simplifications, and assumptions of the approach relate to this aggregation. This issue has bearing on analyses using *Ecopath*, *Ecosim*, and *Ecospace*, and this issue is therefore an organizing focus of the discussions in this section.

Detailed discussion of the capabilities, limitations, and major pitfalls of the *Ecopath with Ecosim* approach are discussed by Christensen and Walters (2000). Their discussion of how the following major pitfalls can be avoided, or accounted for, is particularly useful:

- Incorrect assessment of predation impacts on rare prey;
- Trophic mediation effects (e.g., biogenic habitat effect);
- Underestimates of predation vulnerabilities;
- Non-additivity in predation rates due to shared foraging arenas;
- Temporal variation in species-specific habitat factors.

14.2 PARAMETER UNCERTAINTIES

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Information about ecosystems is generally limited and uncertain, and these constraints limit the usefulness of ecosystem models. However, explicit recognition of the nature of uncertainties can guide users toward appropriate interpretation of model results. In addition to documenting derived ranges for input parameters, data uncertainties were characterized during model construction using the ‘data pedigree’ approach (Section 3).

Constructing an *Ecopath* model can serve to reduce uncertainty, not only through synthesis, integration, and consilience of information, but because such efforts provoke new empirical programmatic efforts to fill gaps of information needed for whole ecosystem analyses.

A key element of our analysis is the iterative toggling between *Ecopath*, *Ecosim*, and *Ecospace* routines. *Ecopath* forms the foundation upon which *Ecosim* and *Ecospace* analyses are constructed, yet results from these analyses can in turn highlight weaknesses in the foundation; thus serving for refinement of the *Ecopath* model. Users must always bear in mind the intimate link between *Ecopath-Ecosim-Ecospace*, and not consider results of dynamic simulations as solely dependent *Ecosim / Ecospace* parameterization. Comparison of the analyses to independently-derived information about the system is an important effective way to refine the model and continue to reduce uncertainty.

14.3 PROBLEMS WITH FUNCTIONAL GROUP AGGREGATION

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Several pathological problems arise as a consequence of aggregating groups in an *Ecopath* model. It is particularly difficult to alleviate such problems when the number of species in the model system is very large. This is true of the West Florida Shelf model, where in many cases more than 10+ species are aggregated into one functional group. It is necessary to take a pragmatic approach to alleviate such problems and thus minimize crazy dynamics during simulations with *Ecosim*. The problems and solutions relating to the West Florida Shelf model are:

(i) Fishing mortality is overestimated in *Ecopath* when functional groups are composed of several species, for which catch data exists for all, but biomass estimates do not. Since *Ecopath* determines F as F=C/B, an underestimated biomass will result in an overestimated F. The solution is to derive a biomass estimate for all the species for which we have catches. To do this we assumed the average F of the other species in the groups and used B=C/F to estimate the biomass.

(ii) Fishing mortality tends to be underestimated for particular species within functional groups that comprise of many species, of which only several might be fished. Essentially, important species that may have a high fishing mortality are lost in the aggregated group. Their fishing mortality is effectively ‘diluted’ within the group. The consequence in *Ecosim* is that the groups will look very as if they can sustain a much higher fishing mortality than they really can. In reality the gear may only catch one or two species, and these may be heavily exploited. The match between the gear types selectivity is not represented well when groups are aggregated. Little sense can be made from examining harvest scenarios on such groups, and an anylitical focus on these species should be avoided. In the West Florida Shelf model, such groups include (18) Demersal coastal invertebrate eaters, (23) Benthic coastal invertebrate eaters, (25) Structure associated piscivores, (27) Structure associated invertebrate eaters. The solution is to pay close attention to model structure during planning. Functional groups should be aggregated so as to capture the ecological linkages and also emphasize particular groups that attention will be directed during model simulation of harvest scenarios. In the model here, mackerel adults, juvenile, small pelagics and large groupers are important groups that have been ‘broken out’ in to separate box. Ideally *Ecopath* models should examine various levels of aggregation and test if the general results of simulations are robust at the different representations of model structure. Similar warnings are provided by Pauly et al. 2000.

(iii) Cannibalism in *Ecopath* models can lead to misleading results of dynamic simulations. The aggregation process results in apparent cannibalism emerging within the group because species within a functional group may prey on each other. It is best to separate predator and prey groups wherever possible when constructing models. Cannibalism was reduced to a small fraction (1-2%) of the diet composition in most groups to avoid misleading dynamics. This was recommended by D. Pauly.

(iv) In *Ecospace*, spatial distributions for each functional group tend to become widely distributed when many species are aggregated in to a single functional group. This has implications for interpreting the spatial dynamics of particular species. In some cases, the apparent wider distributions, makes the groups available to predation that particular species in reality would not be subjected to. The same is true for distribution of predators, and thus overall the spatial overlaps of highly aggregated groups tend to be quite large and mask real, small scale spatial separations.

14.6 GUIDELINES FOR APPROPRIATE USES OF THE MODEL

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The most important guideline for use of the West Florida Shelf model is to carefully consider how the research question compares to the spatio-temporal scales of the model and the degree of aggregation of functional groups. The model is best designed to address questions regarding processes occuring shelf wide and on time scales greater than one year. For example, the model is not well designed to address questions about processes that occur in a very small portion of the West Florida Shelf as a whole.

The West Florida Shelf model is structured specifically for application to fisheries-related questions, such as sardine/herring and mackerel interactions. For an in-depth analysis of the consequences of levels of model aggregation, ideally, multiple models of the West Florida Shelf should be constructed; the aim being to search for generalized ‘robust’ results from various levels of aggregation.

The structure of the model is also considered suitable to explore the effects of other disturbances, whether natural or anthropogenic. These could include any disturbance or source of stress with a known, or presumed, effect on some biotic component(s) of the system. One example is the simulation of nutrient enrichment and subsequent plankton blooms in the waters overlying the shelf in order to explore the interference effects of such blooms on benthic primary producers. Such analyses can point to implications of such changes on the organization of the broader biotic community, and this example is being pursued as a continuing research question. Another research group is interested in using the model to explore questions related to the interactions of grouper and their benthic habitat. Many such ‘ecosystem organization’ can be addressed, although the users should always be aware of how their questions relate to the functional groups defined in the model. In this respect, some investigators might find it helpful to modify the structure (and or content) of the model, to address particular questions of interest. Radical modifications might include using the current model and accompanying documentation as a template and a guide for constructing a model that covers a smaller region within the West Florida Shelf such as the Big Bend area.

In general, we emphasize that the model should be used by the broadest possible array of researchers at least for exploratory gaming. Furthermore, the model should be a ‘living model’ in the sense that investigators feel free to refine the model or modify it for their uses. We emphasize just as strongly, however, that refinements or improvements to the model should be documented and published in some form.

One relatively new line of research emerging from the new capabilities of *Ecosim* is the effort to distinguish biotic forces from physical forces in ecosystems. Traditionally, the capabilities of food web models were limited to explorations of the relative importance of trophic forces, or simulations of the indirect trophic forces assuming constant physical conditions, or assuming no physical forcing. Now, several tools are available in *Ecosim* to begin teasing apart all the variables and factors that may influence particular biotic components of concern. These tools include forcing functions, trophic mediation functions, and the ability to fit simulations and trajectories to real time series data. As an example, the approach can now be used to address seemingly intractable mysteries such as the reasons for declines of Stellar Sea Lions in the Aleutian Islands, or the relative importance of fisheries on marine mammal populations on the West Florida Shelf.

A very recent development soon to be included within the framework of the *Ecopath* approach is a routine for quantifying biomaccumulation of pollutants. The routine requires input of the decay rates of pollutants to trace their fate throughout the ecosytem (contact Villy Christensen for further details).

Although the *Ecopath with Ecosim* approach is designed for fisheries applications, we suggest that the approach be viewed as a complement to current single-species fisheries models, or currently implemented fisheries strategies. The approach is not a replacement of these other time-tested approaches. The *Ecopath* approach is a powerful new tool in the sense that it is a single analytical framework that integrates all biotic components of the ecosystem, and has the capability of integrating physical forces. The main purpose of the approach is the help managers and policy makers prevent themselves from making profoundly bad decisions by giving them a view of the possible surprising and counter-intuitive effects of particular management and policy options.

APPENDICES

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APPENDIX 2. DIET MATRIX OF THE WEST FLORIDA SHELF ECOPATH MODEL

Table A2. Diet Matrix of the West Florida Shelf model (%)

Prey		Predators																							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Dolphins	.02																							
2	Seabirds																								
3	Turtles	.02																							
4	Manatees																								
5	LgOcePisc					1					0.2														
6	LgOcePlank										0.1														
7	Coastalsharks					1		2			0.7														
8	Rays/skates					1.2		15																	
9	PelOcePisc					7				7															
10	PelCoasPisc	1.7	0.2			8.5		2.5			1	1													
11	MackerelAdul					5.7		0.3		1	0.3														
12	MackerelJuv	1.5	0.2			5.7		0.3		2	0.5														
13	Sardine/Herring	5.3	24	0.7		7.3		3.7		10	15	45	41		0.1	1.6		1.7	0.6						
14	PelOceJelly/eaters		0.2			9.2		3		10	7.6				0.1										
15	PelOcePlanktivores	1.6	5			9.6	12	3		11	6.2	11	22		0.1	1									
16	DemOceInvert/eaters										0.6										10				
17	DemCoasPisc		9.9									1.2						1			10				
18	DemCoasInvert/eaters		14			1.5		3			8.1	2.9	15					4	0.4				8.8		
19	DemCoasOmniv	21	9.9			5.2					5.6							2	0.1				5.4		
20	BentOcePisc																				0.1		0.1		
21	BentOceInvert/eaters					0.1		0.3			0.2										20		4.7		
22	BentCoasPisc					1.5		4					2.1						0.1		5		1		
23	BentCoasInvert/eaters	0.1	13			1.6		2.2	4.5		0.3							2.5	0.6		15		2.1		
24	SurfacePelagics	1.5	0.2			9.8					0.9	9.4													
25	StrucAssCoasPisc					1.4		3.1				2.3							0.1						
26	LgGroupers					0.5		2.4																	
27	StrucAssCoasInvert/eaters		1.1			1.1		3.7			6.2	3.4	4.5				2.3		0.1			5.8	10		
28	StrucAssCoasOmniv	1.1				1.3		0.7	2.3		5.4						2	2							
29	StrucAssCoasPlank																								
30	NearshAssPisc	0.2	3.2			0.4		1.1																	
31	Mullets	2.3	12								0.4	1.3													
32	NearshPlanktivores	13	6.2	0.7				2.1	2.3		19	12	10			1		20	5.2				13		12
33	Other fishes	7.7				3.3		9	1.5	10	1	3.4		5.8		3.6		2.2	5.2	1.1	10		7.2	7.1	9.1

34	Squid	40				12	6.5	9.1	10	29	7.4	5.6	5.8			1.4		6	0.1				7		
35	Adult Shrimps					0.5		1	1	0.5	1	1.6		0.1		0.1	1	1	4	1	1	4	1	8	
36	Lobsters	0.1						0.2	0.2																
37	Large Crabs	0.1		23		1.5		3	10		1			0.1			4		3	1	3	3	3	2	
38	Octopods	0.1				1.6		4.9	2									1							
39	Stomatopods								0.5		0.4						2		1.3	0.4		4	1	1	
40	Echinod / Lg gastropods	0.1					4.9	1.8	16								5.5		8.6	4.7		10	6.4	8	
41	Bivalves	0.1		22				4	12										0.3			2	2	8.4	
42	Sessile epibenthos			23					4.2					1.7			4		8.4	30		0.6		7	
43	Small infauna							1.2	15		0.3			1.7			44	0.6	14	7.8	9	27	14	17	5.8
44	Small mobile epifauna							1.5	17		4.3	0.1		5		6.8	35	15	32	15	17	30	13	35	26
45	Meiofauna													3.2					0.3	0					
46	Small Copepods						24							32		12			2.6	0					
47	Other Mesozooplankton						24			5	5			21		27		5	4.6	1.9		2.8			0.8
48	CarnivZooplank	1.1				0.1	23			5	1.7			6	59	30		0.2	4.5	1.1		8.3	0.1	5.7	
49	Ichthyoplankton					0.1				10					1				0.5						
50	CarnivJellyfish			10			4.9								40										
51	Microbial Heterotrophs																								
52	Macroalgae			11	100									2.9				0.1	0.6	13		2.8			
53	Microphytobenthos			11				1.3	1.6					0.2				0.2	0.1	5				0.4	
54	Phytoplankton																								
55	Sea grasses						1.8							9		16									47
56	Dead carcasses	1.5						6.6																	
57	Sediment Detritus													2.6				0.1	2.9	18					
58	Watercolumn Detritus													8.5											
59	Drift Macrophytes																								
60	Import							4										35							

Prey	Predators																									
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
1																											
2																											
3																											
4																											
5																											
6																											
7																											
8	0	1.6																									
9	0.3	0.5																									
10	0.5	0.7				2.5																					
11		0.1																									
12		0.1																									
13	5.8	5.8	0.9			3.8				0.5																	
14										5																	
15	3.8	1.5								0.5																	
16						2.5																					
17																											
18	2	4.2				9.5								8.1	1												
19	0.4	6.6	0.7			1.8																					
20	0.1	2.3	0.1																								
21	0.9	3.1	0.2																								
22	0.8	2.3	0.1																								
23	3.8	2.2	0.5			1.5								20	2												
24	1																										
25	1	2.4										1															
26	0	0.1																									
27	13	8.6	0.1																								
28	7.3	4.7	0.7									1															
29	4.4	6.2										1															
30																											
31		3.6				5.5						1															
32	2.6	2.5	1.3			9.5				5																	
33	1.7	0.4	3.6	0.6	2	26			0.1																		
34	6	6.3	3.1		0	10			1	0.1	0.8				6												
35	3	2	5			1		0.1			0.4		1	0.1	10												
36	0.1	0.2	0.1											0.1													
37	15	15	3			9			0.1			19	0.5	0.5	3												

38	3.3	10	0.7											0.1													
39	1	2	0.9																								
40	2.1	1.5	10	0.1					5		0.6	23	4.1	5.6	1	1											
41			5	0					16		0	18	36	24	11	1											
42		1.5	16	21	1.6				14		8.2	5.7	15	12		10		1									
43	5		17	3	8.2					2	20	3.7	15	16	15	4.9		0.1	1	4							
44	11	2	22	5.6	17	13	0.5	9	30	15	23	2	1.9	10	18	2		2	1	1							
45			0.1					1		2	12		2.9	1		3.1	1	3	10	7	1						
46	1.8		1.5		20			34	4	2								0.1				2	12	12	35	20	
47	2.2		2.6	0.7	36			36	4	33								0.1					1	10	25	47	
48			4	1.9	16	3.9		8.4	19	33														1	4	10	
49			0.2						1	0.1														0.2	1		
50										2								0.1									
51												22	11		20	10	10	30	15	19	35	13	40	64	5	23	
52				54		0.3	5		2		0.3	3.7			1	12				12							
53							1				10		3.8		6	9.9	12	4	9	8	20	4	5		5		0.5
54							0.5	3.1			0					2.8	23	23	22	10		80	37	10	15		0.5
55			0.3	0.7					1		0					4.7				5							
56								1	1.5		3.1		0.9	3.3		2		1		5							0.7
57				12			3		2		21		7		6	11	41	17	32	7	44		1		5		45
58								5								6.7	13	18	5	7	0	1	4	2.8	5		50
59								2.5					0.8			18	0	0	5	15							3.5
60							90																				

APPENDIX 3. DETRITUS FATE OF EACH FUNCTIONAL GROUP

Table A3. Fate of detritus for each functional group.

Source \ Fate	Dead carcasses	Sediment Detritus	Watercolumn Detritus	Drift Macrophytes	Export	Sum
Dolphins	0.01	0.29	0.7	0	0	1
Seabirds	0.01	0	0.5	0	0.49	1
Turtles	0.01	0.29	0.7	0	0	1
Manatees	0.01	0.29	0.7	0	0	1
LgOcePisc	0.01	0.29	0.7	0	0	1
LgOcePlank	0.01	0.29	0.7	0	0	1
Coastalsharks	0.01	0.29	0.7	0	0	1
Rays/skates	0.01	0.7	0.29	0	0	1
PelOcePisc	0.01	0.29	0.7	0	0	1
PelCoasPisc	0.01	0.29	0.7	0	0	1
MackerelAdul	0.01	0.29	0.7	0	0	1
MackerelJuv	0.01	0.29	0.7	0	0	1
Sardine/Herring	0.01	0.29	0.7	0	0	1
PelOceJelly/eaters	0.01	0.29	0.7	0	0	1
PelOcePlanktivores	0.01	0.29	0.7	0	0	1
DemOceInvert/eaters	0.01	0.8	0.19	0	0	1
DemCoasPisc	0.01	0.8	0.19	0	0	1
DemCoasInvert/eaters	0.01	0.8	0.19	0	0	1
DemCoasOmniv	0.01	0.8	0.19	0	0	1
BentOcePisc	0.01	0.9	0.09	0	0	1
BentOceInvert/eaters	0.01	0.9	0.09	0	0	1
BentCoasPisc	0.01	0.9	0.09	0	0	1
BentCoasInvert/eaters	0.01	0.9	0.09	0	0	1
SurfacePelagics	0.01	0.29	0.7	0	0	1
StrucAssCoasPisc	0.01	0.8	0.19	0	0	1
LgGroupers	0.01	0.8	0.19	0	0	1
StrucAssCoasInvert/eaters	0.01	0.8	0.19	0	0	1
StrucAssCoasOmniv	0.01	0.8	0.19	0	0	1
StrucAssCoasPlank	0.01	0.8	0.19	0	0	1
NearshAssPisc	0.01	0.29	0.7	0	0	1
Mullets	0.01	0.29	0.7	0	0	1
NearshPlanktivores	0.01	0.29	0.7	0	0	1
Other fishes	0.01	0.29	0.7	0	0	1
Squid	0.5	0.25	0.25	0	0	1
Shrimps	0.01	0.89	0.1	0	0	1
Lobsters	0.01	0.89	0.1	0	0	1
Crabs	0.01	0.89	0.1	0	0	1
Octopods	0.01	0.94	0.05	0	0	1
Stomatopods	0.01	0.99	0	0	0	1
Echinoderms/Lg. gastropods	0.01	0.99	0	0	0	1
Bivalves	0.01	0.79	0.2	0	0	1
Sessile epibenthos	0.01	0.89	0.1	0	0	1
Small infauna	0.01	0.99	0	0	0	1
Small mobile epifauna	0.01	0.79	0.2	0	0	1
Meiofauna	0.01	0.89	0.1	0	0	1

Small Copepods	0.01	0.09	0.9	0	0	1
Other Mesozooplankton	0.01	0.09	0.9	0	0	1
CarnivZooplank	0.01	0.09	0.9	0	0	1
Ichthyoplankton	0.01	0.09	0.9	0	0	1
CarnivJellyfish	0.01	0.09	0.9	0	0	1
Microbial Heterotrophs	0.01	0.49	0.5	0	0	1
Macroalgae	0	0	0	1	0	1
Microphytobenthos	0	0.9	0.1	0	0	1
Phytoplankton	0.01	0.04	0.95	0	0	1
Sea grasses	0	0	0	1	0	1
Dead carcasses	0	0.9	0.1	0	0	1
Sediment Detritus	0	0	0	0	1	1
Watercolumn Detritus	0	1	0	0	0	1
Drift Macrophytes	0	0.9	0.1	0	0	1

Note: The specific proportions are assumed based on a subjective judgment relating to the habitat and niche of the various organisms.

APPENDIX 4. MARKET VALUES OF UTILIZED GROUPS

The table below lists the price per unit of landed weight (pounds) of the harvested groups in West Florida shelf. The market value of catches was calculated as the weighted average price of landings of individual species in the group. Price information is from the 1999 Annual Landings Summary of the Marine Fisheries Information System, Florida Fish and Wildlife Conservation Commission.

Table A4. Market values of functional groups

Group Name	$/pound
LgOcePisc	1.55
Coastalsharks	0.40
Rays/skates	0.19
PelOcePisc	0.89
PelCoasPisc	1.01
MackerelAdul	1.12
Sardine/Herring	0.23
PelOceJelly/eaters	0.89
PelOcePlanktivores	1.12
DemOceInvert/eaters	0.50
DemCoasPisc	1.66
DemCoasInvert/eaters	1.25
DemCoasOmniv	3.60
BentOceInvert/eaters	1.39
BentCoasPisc	1.96
BentCoasInvert/eaters	1.13
StrucAssCoasPisc	1.87
LgGroupers	2.04
StrucAssCoasInvert/eaters	1.12
StrucAssCoasOmniv	0.89
StrucAssCoasPlank	0.89
NearshAssPisc	0.69
Mullets	0.74
Other fishes	0.89
Squid	0.40
Adult Shrimps	2.47
Lobsters	4.31
Large Crabs	0.71
Octopods	0.99
Echinoderms/Large gastropods	0.95
Bivalves	6.33
Sessile epibenthos	0.94
Small infauna	0.94
Small mobile epifauna	0.94
CarnivJellyfish	0.94

APPENDIX 5. GUIDE TO 'DATA PEDIGREE' VALUES

Table A5. Confidence intervals associated with pedigree ranks

Pedigree categories	Index value	Conf. int. (+/- %)
Biomass		
Estimated by *Ecopath*	0	80
From other model	0	80
Guesstimate	0	80
Consumer: Approximate or indirect method Producer: Indirect method (remote sensing)	0.4	50
Consumer: Sampling based, low precision Producer: Locally based, low precision	0.7	30
Consumer: Sampling based, high precision Producer: Locally based, high precision	1	10
P/B and Q/B		
Estimated by *Ecopath*	0	80
Guesstimate	0.1	70
From other model	0.2	60
Empirical relationship	0.5	50
Consumer: Similar group/species, similar system Producer: Similar system, low precision	0.6	40
Similar group/species, same system Producer: Same system, low precision	0.7	30
Consumer: Same group/species, similar system Producer: Similar system, high precision	0.8	20
Consumer: Same group/species, same system Producer: Same system, high precision	1	10
Diets		
General knowledge of related group/species	0	80
From other model	0	80
General knowledge for same group/species	0.2	60
Qualitative diet composition study	0.5	50
Quantitative but limited diet composition study	0.7	30
Quantitative, detailed, diet composition study	1	10
Catches		
Guesstimate	0.1	70
From other model	0.1	70
FAO statistics	0.2	80
National statistics	0.5	50
Local study, low precision/incomplete	0.7	30
Local study, high precision/complete	1	10

APPENDIX 6. EMPIRICALLY BASED CONVERSION FACTORS

Table A6. Conversion factors used in the construction of the West Florida Shelf model

Conversion	Ratio	Source
Chlorophyll a to Carbon	1 to 25	Parsons et al. 1977 in Browder 1993
Chlorophyll a to Carbon (Phytoplankton)	1 to 44.9	Durbin & Durbin 1998
Carbon to dry organic matter	1 to 2.5	Parsons et al. 1977 in Browder 1993
Carbon to dry organic matter (Phytoplankton)	1 to 5.4	Durbin & Durbin 1998
Carbon to dry organic matter (Meiobenthos)	1 to 2.5	Warwick (Plymouth marine laboratory; pers. comm. 12 June 2000)
Carbon to dry organic matter (Benthic macrofauna)	1 to 10	Rowe and Menzel (1971) ("5 to 15 times")
Dry to wet organic matter	1 to 5	Parsons et al. 1977 in Browder 1993
Dry to wet weight (Benthic primary producers)	1 to 7.7	Arreguín-Sánchez et al. 1993
Dry to wet weight (Benthic macrofauna)	1 to 7.5	Rowe and Menzel (1971) ("5 to 10 times")
Dry to wet weight (Shrimp)	1 to 7.7	Bougis 1979 in Cushing 1984
Carbon to dry organic matter (Crustaceans)	1 to 2.5	Bougis 1979 in Cushing 1984
Carbon to wet weight (Shrimp)	1 to 19.2	Cushing 1984

Literature cited (Conversions)

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APPENDIX 7. FUNCTIONAL GROUPINGS AND PARAMETERS FOR FISHES

Table A7. Summary table of all fish group parameters and references

			Biomass t/km2	**Reference**	**Q/B per yr**	**Reference**	**P/B per yr**	**Reference**
1	**Whales and dolphins**	**Whales and dolphins**			40.86	Brown et al. 1991		
2	**Sea birds**	**Sea birds**			80.00	GoM models	5.40	Other GoM model
3	**Turtles**	**Turtles**			3.50	GoM models	0.15	Other GoM model
4	**Manatees**	**Manatees**	0.001	?	36.50	?	0.10	Indep.
5	**Large oceanic piscivores**							
	Xiphias gladius	swordfish	0.00277	B=C/F	2.9184	Brown et al. 1991	0.50	Z=P/B
	Makaira nigricans	blue marlin	0.00019	B=C/F	4.56	Brown et al. 1991	0.40	Z=P/B
	Tetrapturus spp.	white marlin and spearfish	0.00007	B=C/F	6.384	Brown et al. 1991	0.40	Z=P/B
	Istiophorus platypterus	sailfish	0.00039	B=C/F	7.296	Brown et al. 1991	0.45	Z=P/B
	Coryphaena hippurus	dolphin fish	0.05992	B=C/F	4.73	Pred. Palomares and Pauly 1987	0.8	Z=P/B
	Alopias spp.	thresher shark	0.00010	B=C/F	8.97	Other GoM model	0.54	Z=P/B
	Isurus paucus	longfin mako	0.00013	B=C/F	8.97	Other GoM model	0.54	Z=P/B
	Thunnus albacares	yellowfin tuna	0.00354	B=C/F	12.221	Brown et al. 1991	1.2	Z=P/B
	Thunnus alalunga	albacore	0.00000	B=C/F	9.4	Pred. Palomares and Pauly 1987	0.78	Z=P/B
	Thunnus thynnus	bluefin tuna	0.00001	B=C/F	12.16	Brown et al. 1991	0.43	Z=P/B
	Thunnus atlanticus	blackfin tuna	0.00990	B=C/F	15.455	Browder model	0.87	Z=P/B
	Thunnus obesus	bigeye tuna	0.00004	B=C/F	7.9	Pred. Palomares and Pauly 1987	0.64	Z=P/B
	Katsuwonus pelamis	skipjack tuna	0.00161	B=C/F	23.8944	Brown et al. 1991	1.14	Z=P/B
	Hexanchus griseues	Sixgill shark	0.00000	B=C/F	8.975	Pred. Palomares and Pauly 1987	0.49	Z=P/B
6	**Large ocean planktivores**				10.00	GoM models	1.4	Other GoM model
	Mobulidae	Manta ray			1.30	Pred. Palomares and Pauly 1989	0.11	M pred.(Pauly 1980)
	Rhincodon typus	whale shark			0.80	Pred. Palomares and Pauly 1989	0.07	M pred.(Pauly 1980)
	Cetorhinus maximus	basking shark			3.70	Pred. Palomares and Pauly 1989	0.09	M pred.(Pauly 1980)
	Mola mola	ocean sunfish			1.40	Pred. Palomares and Pauly 1989	0.18	M pred.(Pauly 1980)
7	**Coastal sharks**				7.84	GoM models	0.55	Other GoM model
	Sphyrna lewini	scalloped hammerhead	0.00041	B=C/F	2.48	Palomares eqn.	0.43	Z=P/B
	Sphyrna mokarran	great hammerhead shark	0.00058	B=C/F	1.90	Pred. Palomares and Pauly 1989	0.25	Z=P/B
	Carcharhinus plumbeus	sandbar shark	0.02994	B=C/F	4.10	Stillwell and Kohler 1992	0.263	Z=P/B
	Carcharhinus obscurus	dusky shark	0.00086	B=C/F	2.20	Pred. Palomares and Pauly 1989	0.21	Z=P/B
	Carcharhinus acronotus	blacknose shark	0.00055	B=C/F	3.20	Pred. Palomares and Pauly 1989	0.62	Z=P/B
	Carcharhinus brevipinna	spinner shark	0.00001	B=C/F	3.00	Pred. Palomares and Pauly 1989	0.44	Z=P/B
	Carcharhinus falciformis	silky shark	0.00023	B=C/F	2.00	Pred. Palomares and Pauly 1989	0.28	Z=P/B

	Carcharhinus limbatus	blacktip shark	0.00324	B=C/F	3.60	Pred. Palomares and Pauly 1989	0.466	Z=P/B
	Carcharhinus leucas	bull shark	0.00219	B=C/F	2.37	Palomares eqn.	0.21	Z=P/B
	Carcharhinus isodon	finetooth shark	0.00016	B=C/F	3.30	Pred. Palomares and Pauly 1989	0.39	Z=P/B
	Rhizoprionodon terraenovae	Atlantic sharpnose shark	0.00034	B=C/F	6.40	Vidal model	1.04	Z=P/B
	Galeocerdo cuvier	tiger shark	0.00005	B=C/F	1.70	Pred. Palomares and Pauly 1989	0.21	Z=P/B
	Negaprion brevirostris	lemon shark	0.00003	B=C/F	6.00	Cortes and Grubber 1990	0.75	Z=P/B
	Squalidae	Dogfish	0.00000	B=C/F	4.77	Pred. Palomares and Pauly 1989	0.17	Z=P/B
	Odontaspis taurus	sand tiger	0.00000		1.70	Pred. Palomares and Pauly 1989	0.62	Z=P/B
	"all sharks"							
8	**Rays and skates**				7.84	GoM models	0.20	Other GoM model
	Raja texana	roundel skate	0.018	Trawl surveys	19.4	Pred. Palomares and Pauly 1989	0.9	pred. M (Pauly 1980)
	Raja eglanteria	clearnose skate	0.050	Trawl surveys	11.8	Pred. Palomares and Pauly 1989	0.39	pred. M (Pauly 1980)
	Dasyatis spp.	stingray genus	0.009	Trawl surveys	2.5	Pred. Palomares and Pauly 1989	0.26	pred. M (Pauly 1980)
	Aetobatus narinari	spotted eagle ray			2.3	Pred. Palomares and Pauly 1989	0.18	pred. M (Pauly 1980)
	Rhinoptera bonasus	cownose ray	0.158	Trawl surveys	6.4	Pred. Palomares and Pauly 1989	0.24	pred. M (Pauly 1980)
	Rhinobatos lentiginosus	Atlantic guitarfish	0.003	Trawl surveys	11.9	Pred. Palomares and Pauly 1989	0.51	pred. M (Pauly 1980)
	Sphyrna tiburo	bonnethead	0.001	Trawl surveys	5	Pred. Palomares and Pauly 1989	0.45	pred. M (Pauly 1980)
	Ginglymostoma cirratum	nurse shark			1.8	Pred. Palomares and Pauly 1989	0.15	pred. M (Pauly 1980)
9	**Pelagic oceanic piscivores**							
	Trichiurus lepturus (?distribution?)	Atlantic cutlassfish	0.150	NMFS trawl	25.54	Brown et al. 1991	1.06	Browder model (pelagic predators)
	Ruvettus pretiosus	oilfish						
	Merluccius albidus	offshore hake	0.000	NMFS trawl			1.06	Browder model (pelagic predators)
	Brama sps	pomfrets	0.000	NMFS trawl			1.06	Browder model (pelagic predators)
	Lepidocybium flavobrunneum	escolar	0.000	NMFS trawl				
10	**Pelagic coastal piscivores**							
	Acanthocybium solandri	wahoo	0.003	B=C/F	25.54	Brown et al. 1991	0.90	Z
	Sarda sarda	Atlantic bonito						
	Euthynnus alletterus	little tunny	0.009	B=C/F	15.11	Palomares equation	0.90	Z
	Auxis thazard	frigate mackerel						
	Pomatomus saltatrix	bluefish	0.001	Trawl surveys	9.36	GoM models	0.70	Z
	Rachycentron canadum	cobia	0.001	B=C/F	7.30	Brown et al. 1991	0.70	Z
	Caranx crysos	blue runner	0.038	FMRI pelagic surveys	10.00	Independent?	0.47	Goodwin & Johnson 1986 (Z est)
	Caranx hippos	crevalle jack	0.007	B=C/F	10.00	Independent?	0.60	Other GoM model

	Caranx bartholomaei	yellow jack			10.00	GoM models	0.60	Other GoM model
	Caranx latus	horse-eye jack			10.00	GoM models	0.60	Other GoM model
	Caranx ruber	bar jack			6.15	GoM models		
	Seriola zonata	banded rudderfish	0.000	Trawl surveys	10.00	GoM models	0.60	Other GoM model
	Seriola dumerili	greater amberjack	0.021	B=C/F	5.90	Other Q/B	0.40	Z
	Seriola fasciata	lesser amberjack			10.00	GoM models	0.60	Other GoM model
	Seriola rivoliana	almaco jack			10.00	GoM models	0.60	Other GoM model
	Elagatis bipinnulata	rainbow runner			10.00	GoM models	0.60	Other GoM model
	Echeneidae	remora family	0.016	Trawl surveys	32.13	Browder model (pelagic predators)	1.057	Browder model (pelagic predators)
	Belonidae	needlefish family			8.80	GoM models	0.3	Other GoM model
	Lobotes surinamensis	tripletail			3.51	Palomares equation		
	"carangids"							
11	**Mackerels adult**							
	Scomberomorus maculatus	Spanish mackerel	0.083	NMFS assessment (Chris Legult 1998)	10.02	GoM models	0.41	Legult (1998) VPA mort
	Scomberomorus cavalla	king mackerel	0.099	NMFS assessment (Chris Legult 1998)	9.29	GoM models	0.36	Legult (1998) VPA mort
	Scomberomorus regalis	cero mackerel			9.00	Other Q/B	0.99	Other GoM model
12	**Juvenile mackerels**							
	Scomberomorus maculatus	Spanish mackerel	0.019	NMFS assessment (Legult 1998)				
	Scomberomorus cavalla	king mackerel	0.106	NMFS assessment (Legult 1998)				
	Scomberomorus regalis	cero mackerel						
13	**Sardine-herring-scad complex**							
	Opisthonema oglinum	Atlantic thread herring	0.039	FMRI pelagic surveys	13.26	GoM models	1.60	Other GoM model
	Harengula jaguana	scaled sardine	0.048	FMRI pelagic surveys	12.89	GoM models	1.57	Other GoM model
	Sardinella aurita	Spanish sardine	0.139	FMRI pelagic surveys	11.45	GoM models	0.95	Other GoM model
	Brevoortia spp.	menhadens	0.047	Vaughan et al. 1999	13.64	GoM models	0.95	Other GoM model
	Decapterus punctatus	round scad	0.184	FMRI pelagic surveys	10.00	GoM models	0.92	Naughton & Saloman 1986 (Z)
14	**Pelagic oceanic jelly eaters**							
	Ariomma bondi	silver-rag	0.190	NMFS trawl	8.2	Fishbase	1.12	M fishbase
	Peprilus burti	gulf butterfish	2.503	NMFS trawl	8	Fishbase	1.85	M fishbase
	Hyperoglyphe perciformis	barrelfish						
15	**Pelagic oceanic planktivores**							
	Maurolicus weitzmani	hatchet fish						

	Etrumeus teres	round herring	1.065	Houde 1977	11.45	GoM models	0.95	Other GoM model
	Jenkinsia family	dwarf round herring	0.004	Trawl surveys	11.45	GoM models	0.95	Other GoM model
	Trachurus lathami	rough scad	1.352	NMFS trawl	10.00	GoM models	0.60	Other GoM model
	Selar crumenophthalmus	bigeye scad	0.015	NMFS trawl	10.00	GoM models	0.60	Other GoM model
	Scomber japonicus	chub mackerel	0.703	NMFS trawl	11.45	GoM models	1.70	Other GoM model
	Diaphus sp	Lanternfish			14.89	GoM models	0.61	Other GoM model
	Bregmaceros atlanticus	antenna codlet						
	Argentina striata	straited argentine	0.000	NMFS trawl				
	Engraulis eurystole	silver anchovy			14.24	GoM models	0.60	Other GoM model
16	**Demersal oceanic invertebrate feeders**							
	Mullus auratus	red goatfish	0.041	Trawl surveys	15.76	Browder model (demersal fish)	2.17	Browder model (demersal fish)
	Synagrops bellus	blackmouth bass	0.000	NMFS trawl	15.76	Browder model (demersal fish)	2.17	Browder model (demersal fish)
17	**Demersal coastal piscivores**							
	Cynoscion nothus	silver seatrout	0.015	Trawl surveys	6.80	Independ. Est	0.64	Other GoM model
	Cynoscion nebulosus	spotted seatrout	0.011	**VPA estimate**	5.29	Palomares equation	0.64	Other GoM model
	Cynoscion arenarius	sand seatrout	0.042	Trawl surveys	6.73	GoM models	0.64	Other GoM model
18	**Demersal coastal invertebrate feeders**							
	Bairdiella chrysoura	silver perch	0.072	Trawl surveys	9.17	GoM models	0.74	Other GoM model
	Equetus umbrosus	Cubbyu	0.028	Trawl surveys	10.00	GoM models	0.35	Other GoM model
	Leiostomus xanthurus	spot	0.439	Trawl surveys	9.09	Palomares equation	0.35	Other GoM model
	Menticirrhus sp.	kingfish	0.033	Trawl surveys	7.32	Palomares equation	0.35	Other GoM model
	Micropogonias undulatus	Atlantic croaker	0.168	Trawl surveys	5.41	Palomares equation	0.35	Other GoM model
	Sciaenops ocellatus	red drum	0.014	B=C/F	3.67	Palomares equation	0.35	Other GoM model
	Pogonias cromis	black drum	0.002	B=C/F	3.67	Palomares equation	0.35	Other GoM model
	Chloroscombrus chrysurus	Atlantic bumper	0.042	FMRI pelagic surveys	11.70	Independ	0.60	Other GoM model
	Trachinotus carolinus	Florida pompano			11.60	Vidal	0.60	Other GoM model
	Trachinotus falcatus	permit			7.62	Palomares equation	0.60	Other GoM model
	Oligoplites saurus	leatherjacket	0.000	Trawl surveys	3.00	GoM models	0.30	Other GoM model
	Alectis ciliaris	African pompano			10.00	GoM models	0.60	Other GoM model
	Arius felis	hardhead catfish	0.157	Trawl surveys	9.70	GoM models	0.55	Other GoM model
	Bagre marinus	gafftopsail catfish	0.014	Trawl surveys	10.14	GoM models	0.55	Other GoM model
	Calamus arctifrons	grass porgy	0.043	FMRI surveys	5.20	GoM models	0.65	Other GoM model
	Pagrus pagrus	red porgy	0.004	Trawl surveys	5.20	GoM models	0.65	Other GoM model
	Stenotomus caprinus	longspine porgy	0.497	Trawl surveys	5.20	GoM models	0.65	Other GoM model
	Haemulon aurolineatum	tomtate	0.407	FMRI pelagic surveys	9.18	GoM models	0.38	Other GoM model
	Orthopristis chrysoptera	pigfish	0.487	Trawl surveys	10.65	GoM models	1.25	Other GoM model

	Lutjanus synagris	lane snapper	0.095	Trawl surveys	4.95	GoM models	0.68	Manooch & Mason (1984) (Z)
	Eucinostomus sp.	mojarras	0.111	FMRI pelagic surveys	15.34	GoM models	1.25	Other GoM model
	Balistes capriscus	gray triggerfish	0.095	Trawl surveys	9.07	Palomares equation	2.17	Browder model (demersal fish)
19	**Demersal coastal omnivore**							
	Aluterus schoepfi	orange filefish	0.024	Trawl surveys	17.42	Palomares equation	2.17	Browder model (demersal fish)
	Monacanthus ciliatus	fringed filefish	0.123	Trawl surveys	15.10	Fishbase	1.50	M fishbase
	Monacanthus hispidus	planehead filefish	0.002	NMFS trawl	8.20	Fishbase	1.26	M fishbase
	Cantherhines pullus	orangespotted filefish						
	Cantherhines sufflamen	ocean triggerfish						
	Lactophrys polygonia	honeycomb filefish						
	Diplodus holbrooki	spottail pinfish	0.295	Trawl surveys	6.30	Fishbase predicted	1.50	M fishbase
	Lagodon rhomboides	pinfish	0.470	FMRI pelagic surveys	15.21	13.4 (Bioenergetic model); 14.6 (Stoner and Livingstone 1978); 17.8 (Peters and Kjelson)	1.25	Other GoM model
	Chaetodipterus faber	Atlantic spadefish	0.044	Trawl surveys	15.76	Browder model (demersal fish)	2.17	Browder model (demersal fish)
	Lactophrys quadricornis	scrawled cowfish	0.399	Trawl surveys	8.17	GoM modelss	1.26	M fishbase
	Tetraodontidae	puffer family	0.072	Trawl surveys	37.45	Looe key (small reef herbivores)	1.90	Looe key (small reef herbivores)
20	**Benthic oceanic piscivores**							
	Saurida brasiliensis	largescale lizardfish	0.067	Trawl surveys	7.94	GoM modelss	0.30	Other GoM model
	Saurida normani	shortjaw lizardfish	0.023	Trawl surveys	7.94	GoM modelss	0.30	Other GoM model
	Synodus poeyi	offshore lizardfish	0.005	Trawl surveys	7.94	GoM modelss	0.30	Other GoM model
	Hoplunnis spp.	duckbill eels	0.014	Trawl surveys				
21	**Benthic oceanic invertebrate feeders**							
	Halieutichthys aculeatus	pancake batfish	0.004	Trawl surveys	15.80	Fishabse	2.44	M fishbase
	Neomerinthe hemingwayi	spinycheek scorpionfish	0.005	Trawl surveys			2.17	Browder model (demersal fish)
	Peristedion gracile	slender searobin	0.009	NMFS trawl			2.17	Browder model (demersal fish)
	Prionotus stearnsi	shortwing searobin	0.008	NMFS trawl			2.17	Browder model (demersal fish)
	Serranus notospilus	saddle bass	0.006	Trawl surveys	15.80	Fishbase	2.44	M fishbase
	Malacanthidae	tilefish family	0.066	Trawl surveys	15.76	Browder model (demersal fish)	2.17	Browder model (demersal fish)
	Steindachneria argenta	luminous hake	0.023	Trawl surveys			2.17	Browder model (demersal fish)

22	**Benthic coastal piscivores**							
	Synodus foetens	inshore lizardfish	0.138	Trawl surveys	7.94	GoM models	0.30	Other GoM model
	Synodus intermedius	sand diver	0.076	Trawl surveys	7.94	GoM models	0.30	Other GoM model
	Paralichthys spp.	lefteye flounder genus	0.045	Trawl surveys	9.46	GoM models	0.30	Other GoM model
	Ophichthidae	snake eel family	0.003	Trawl surveys				
23	**Benthic coastal invertebrate feeders**							
	Diplectrum bivittatum	dwarf sand perch	0.041	Trawl surveys	15.76	Browder model (demersal fish)	2.17	Browder model (demersal fish)
	Diplectrum formosum	sand perch	0.307	Trawl surveys	9.67	Palomares equation	2.45	M fishbase
	Etropus crossotus	fringed flounder	0.013	Trawl surveys	9.46	GoM models	0.30	Other GoM model
	Etropus rimosus	gray flounder	0.190	Trawl surveys	9.46	GoM models	0.30	Other GoM model
	Syacium papillosum	dusky flounder	0.763	Trawl surveys	9.46	GoM models	0.30	Other GoM model
	Symphurus plagiusa	blackcheek tonguefish	0.006	Trawl surveys	9.46	GoM models	0.30	Other GoM model
	Prionotus roseus	blue spotted searobin	0.019	Trawl surveys	15.76	Browder model (demersal fish)	2.17	Browder model (demersal fish)
	Prionotus scitulus	leopard searobin	0.031	Trawl surveys	15.76	Browder model (demersal fish)	2.17	Browder model (demersal fish)
	Scorpaena brasiliensis	barbfish	0.128	Trawl surveys	8.6	Fishbase	1.01	M fishbase
	Scorpaena calcarata	smoothhead scorpionfish	0.014	Trawl surveys	13.5	Fishbase	2.03	M fishbase
	Polydactylus octonemus	Atlantic threadfin	0.000	Trawl surveys	15.76	Browder model (demersal fish)	2.17	Browder model (demersal fish)
	Urophycis regia	spotted hake	0.020	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
	Urophycis floridana	southern hake	0.005	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
	Ariosoma balearicum	bandtooth conger	0.016	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
	Gobiidae	Gobies			12.30	GoM models	0.30	Other GoM model
	Ophidiidae	cusk-eels (gadiforms)	0.079	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
	Ogcocephalidae	batfish family	0.041	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
24	**Surface pelagics**							
	Hemirhamphidae	halfbeaks	0.000	Trawl surveys	11.70	Independ	2.60	Looe key (small planktivores)
	Exocoetidae	flyingfish family						
25	**Structure associated coastal piscivore**							
	Lutjanus campechanus	red snapper	0.013	B=C/F	16.78	Brown et al. 1991	0.50	Z
	Lutjanus griseus	gray snapper	0.002	Trawl surveys	7.24	Palomares equation	0.57	Other GoM model
	Lutjanus cyanopterus	cubera snapper			4.95	GoM models	0.57	Other GoM model
	Lutjauns analis	mutton snapper			4.95	GoM models	0.57	Other GoM model

	Lutjauns apodus	schoolmaster			4.95	GoM models	0.57	Other GoM model
	Lutjanus buccanella	blackfin snapper			4.95	GoM models	0.57	Other GoM model
	Lutjanus jocu	dog snapper			4.95	GoM models	0.57	Other GoM model
	Lutjanus mahogoni	mahogany snapper			4.95	GoM models	0.57	Other GoM model
	Lutjanus purpureus	caribbean red snapper			4.95	GoM models	0.57	Other GoM model
	Lutjanus vivanus	silk snapper			4.95	GoM models	0.57	Other GoM model
	Pristipomoides aquilonaris	wenchman	0.020	Trawl surveys	4.95	GoM models	0.57	Other GoM model
	Etelis oculatus	queen snapper			4.95	GoM models	0.57	Other GoM model
	Lutjanidae	**snapper family**					0.57	Other GoM model
	"snappers"						0.57	Other GoM model
	Epinephelus cruentatus	graysby	0.001	Trawl surveys	2.30	GoM models	0.40	Other GoM model
	Epinephelus niveatus	snowy grouper	0.001	B=C/F	10.21	Brown et al. 1991	0.61	Z
	Antennariidae	Anglerfish	0.040	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
	Holocentridae	squirrelfish family	0.030	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
	Sphyraena barracuda	great barracuda	0.007	B=C/F	10.21	Brown et al. 1991	0.40	Z
	Muraenidae	moray family	0.495	Trawl surveys	7.30	GoM models	0.95	Other GoM model
	Congridae (conger eels)	conger eel family	0.048	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
	Grammistidae	soapfish	0.064	Trawl surveys	12.92	Browder model (demersal predators)	0.855	Browder model (demersal preds.)
26	**Large groupers**							
	Epinephelus itajara	jewfish			2.52	Palomares equation	0.85	Z
	Epinephelus morio	red grouper	0.080	B=C/F	4.47	GoM models	0.44	Z
	Epinephelus flavolimbatus	yellowedge grouper	0.006	Trawl surveys	4.32	Palomares equation	0.40	Other GoM model
	Epinephelus adscensionis	rock hind			5.58	Palomares equation	0.40	Other GoM model
	Epinephelus drummondhayi	speckled hind	0.000	B=C/F	3.6	Palomares equation	0.63	Z
	Epinephelus guttatus	red hind			2.30	GoM models	0.40	Other GoM model
	Epinephelus nigritus	warsaw grouper			2.69	Palomares equation	0.40	Other GoM model
	Mycteroperca interstitialis	yellowmouth grouper			7.63	Palomares equation	0.40	Other GoM model
	Mycteroperca venenosa	yellowfin grouper			2.30	GoM models	0.40	Other GoM model
	Mycteroperca phenax	scamp	0.007	B=C/F	5.25	Palomares equation	0.32	Z
	Mycteroperca microlepis	gag	0.026	NMFS assessment (Steve Atran memo to Wayne Swingle)	4.15	Palomares equation	0.42	Z
27	**Structure associated coastal invertebrate feeders**							
	Centropristis ocyurus	bank sea bass	0.187	Trawl surveys	9.20	Fishbase	1.12	M fishbase
	Centropristis striata	black sea bass	0.112	Trawl surveys	9.20	Fishbase	1.12	M fishbase

Centropristis philadelphica	rock sea bass	0.221	Trawl surveys	9.20	Fishbase	1.12	M fishbase
Serranus subligarius	belted sandfish	0.000	Trawl surveys	9.20	Fishbase	1.12	M fishbase
Hemanthias leptus	longtail bass	0.000	Trawl surveys	9.20	Fishbase	1.12	M fishbase
Hypoplectrus unicolor	butter hamlet	0.000	Trawl surveys	9.20	Fishbase	1.12	M fishbase
Paranthias furcifer	creole fish	0.000	NMFS trawl	9.20	Fishbase	1.12	M fishbase
Halichoeres bivitattus	slippery dick	0.000	Trawl surveys	9.20	Fishbase	1.12	M fishbase
Halichoeres caudalis	painted wrasse	0.000	Trawl surveys				
Halichoeres garnoti	yellowhead wrasse						
Lanchnolaimus maximus	hogfish	0.039	Trawl surveys	4.66	Palomares equation	0.60	guess
Bodianus pulchellus	spotfin hogfish						
Bodianus rufus	spanish hogfish						
Decodon puellaris	red hogfish	0.006	Trawl surveys			0.60	guess
Thalassoma bifasciatum	bluehead						
Odontoscion dentex	reef croaker			10.00	GoM models	0.35	Other GoM model
Equetus lanceolatus	jackknife-fish	0.036	Trawl surveys	10.21	Brown et al. 1991	0.60	guess
Ocyurus chrysurus	yellowtail snapper	0.007	B=C/F	4.95	GoM models	0.37	Z
Rhomboplites aurorubens	vermilion snapper	0.045	Trawl surveys	4.95	GoM models	0.48	Manooch &Johnson 1998 (Z)
Opsanus pardus	leopard toadfish	0.000	Trawl surveys			0.60	guess
Scorpaenidae	scorpian fish	0.010	Trawl surveys	13.50	Fishbase	2.03	M fishbase
Chaetodon capistratus	foureye butterflyfish						
Priacanthidae	bigeyes	0.031	Trawl surveys	12.80	Looe key (small reef carnivores)	1.60	Looe key (small reef carn.)
Archosargus probatocephalus	sheepshead	0.082	Murphy and McDonald 2000	11.11	GoM models		
Calamus proridens	littlehead porgy	0.203	Trawl surveys	5.20	GoM models	0.65	Other GoM model
Calamus bajonado	jolthead porgy	0.100	Trawl surveys	5.20	GoM models	0.65	Other GoM model
Calamus calamus	saucereye porgy	0.007	Trawl surveys	5.20	GoM models	0.65	Other GoM model
Calamus leucosteus	whitebone porgy	0.101	Trawl surveys	5.20	GoM models	0.65	Other GoM model
Calamus nodosus	knobbed porgy	0.003	Trawl surveys	5.20	GoM models	0.65	Other GoM model
Haemulon plumieri	white grunt	0.127	Trawl surveys	9.38	GoM models	0.66	Z
Haemulon flavolineatum	French grunt	0.005	Trawl surveys	8.14	GoM models	0.38	Other GoM model
Haemulon macrostomum	Spanish grunt	0.005	Trawl surveys	8.14	GoM models	0.38	Other GoM model
Haemulon album	margate	0.005	Trawl surveys	8.14	GoM models	0.38	Other GoM model
Haemulon sciurus	bluestriped grunt	0.005	Trawl surveys	8.14	GoM models	0.38	Other GoM model
Haemulon striatum	striped grunt	0.003	Trawl surveys	8.14	GoM models	0.38	Other GoM model
Haemulon parra	sailor's grunt	0.005	Trawl surveys	8.14	GoM models	0.38	Other GoM model
Anisotremus virginicus	porkfish	0.001	Trawl surveys	8.14	GoM models	0.38	Other GoM model
Gobiosoma oceanops	neon goby			12.30	GoM models	0.30	Other GoM model

28	**Structure associated coastal omnivores**							
	Holacanthus bermudensis	blue angelfish	0.039	Trawl surveys				
	Pomacanthus arcuatus	gray angelfish	0.001	Trawl surveys	37.45	Looe key (small reef herbivores)	1.90	Looe key (small reef herb.)
	Centropyge argi	cherubfish						
	Holacanthus tricolor	rock beauty						
	Pomacentrus variabilis	cocoa damselfish	0.000	Trawl surveys	37.45	Looe key (small reef herbivores)	1.90	Looe key (small reef herb.)
	Pomacentrus partitus	bicolor damselfish	0.000	Trawl surveys	37.45	Looe key (small reef herbivores)	1.10	Looe key (small reef herb.)
	Pomacentrus leocostictus	beau gregory	0.000	Trawl surveys	37.45	Looe key (small reef herbivores)	1.10	Looe key (small reef herb.)
	Microspathodon chrysurus	yellowtail dameselfish	0.000	Trawl surveys	37.45	Looe key (small reef herbivores)	1.10	Looe key (small reef herb.)
	Parablennius marmoreus	seaweed blenny	0.000	Trawl surveys	12.80	GoM models	1.60	Other GoM model
	Acanthuridae	ocean surgeons						
	Scarus croicensis	striped parrotfish	0.020	Trawl surveys	22.80	GoM models	1.55	Other GoM model
	Coryphopterus glaucofraenum	bridled goby			12.30	GoM models	0.30	Other GoM model
	Kyphossus sectarix	bermuda chub						
29	**Structure associated coastal planktivores**							
	Apogon pseudomaculatus	twospot cardinalfish	0.002	Trawl surveys				
	Phaeoptyx xenus	sponge cardinal fish	0.000	Trawl surveys	10.00	Looe key (small planktivores)	2.60	Looe key (small planktivores)
	Chromis scotti	purple reeffish	0.000	Trawl surveys	10.00	Looe key (small planktivores)	2.60	Looe key (small planktivores)
	Chromis enchrysurus	yellowtail reeffish	0.000	Trawl surveys	10.00	Looe key (small planktivores)	2.60	Looe key (small planktivores)
	Chromis cyanea	blue chromis	0.000	Trawl surveys	10.00	Looe key (small planktivores)	2.60	Looe key (small planktivores)
	Opisthognathus aurifrons	jawfish	0.000	Trawl surveys	10.00	Looe key (small planktivores)	2.60	Looe key (small planktivores)
30	**Nearshore associated piscivores**							
	Tarpon atlantica	Atlantic tarpon			9.20	Palomares equation	1.06	Browder model (pelagic preds.)
	Elops saurus	ladyfish	0.002	B=C/F	9.13	Palomares equation		
	Centropomus undecimalis	common snook	0.003	B=C/F	5.44	Palomares equation		
	Albula vulpes	bonefish						
31	**Mullets**							
	Mugil cephalus	striped mullet	0.010	B=C/F	12.30	Vidal	0.60	Z
	Mugil spp.	other mullets	0.319	B=C/F	10.37	GoM models	0.90	Other GoM model
32	**Nearshore planktivores**							

	Anchoa mitchilli	bay anchovy	0.177	Brown et al. 1991	14.24	GoM models	0.60	Other GoM model
	Anchoa hepsetus	striped anchovy			14.24	GoM models	0.60	Other GoM model
	Atherinidae	silverside family (e.g. Menidia sp.)	0.000	Trawl surveys	26.02	Palomares equation	0.60	Other GoM model
	Alosa spp.	alewife	0.005	NMFS trawl	10.91	Palomares equation	0.60	Other GoM model
33	**Other fishes**	Other fish	3.877	Trawl surveys	7.04	GoM models	0.70	Other GoM model