

**SEASONAL ECOSYSTEM MODELS OF THE LOOE KEY
NATIONAL MARINE SANCTUARY, FLORIDA**

by

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Abstract

Five mass-balance trophic models (1 annual and 4 seasonal) were constructed of the Looe Key National Marine Sanctuary ecosystem, Florida, USA using the ECOPATH approach and software package in order to increase our understanding of its, and other coral reefs', general and seasonal function. Input parameters were obtained from published data on Florida and additional coral reef areas. The Looe Key Sanctuary (18 km²) was chosen as a representative reef of the Florida Reef Tract system which runs for 580 km offshore of the Florida Keys and contributes greatly to South Florida's economy.

Looe Key receives heavy use by SCUBA divers and snorkelers throughout the year, and contains many habitats and a high diversity of organisms. Modeling the ecosystem provides a way to synthesize available information from the Keys in order to increase our understanding of how these fragile and important ecosystems function, which can contribute to our ability to manage them effectively.

The ways that coral reef ecosystem structure and function change seasonally is poorly understood. It is clear that all measured states and rates, such as biomass, primary productivity, coral and fish growth, grazing and recruitment exhibit marked seasonality on reefs throughout the world.

In general, the Looe Key ecosystem is large in terms of primary productivity and energy flow. The production at higher trophic levels was found to be strongly dependent upon the secondary production of detritus, from which 75% of all flows originate. The majority of production of most groups is directly consumed within the system and non-predation losses are small. Many groups feed at more than one trophic level which indicates a great degree of interdependency within the system.

Compared with other reef systems, the overall maturity of Looe Key was intermediate, although the two Caribbean systems (Looe Key and the USVI) appeared more mature than those modeled in the Pacific. Apparently Pacific reefs have more specialized organisms than those in the Caribbean. Looe Key seems to be relatively large in terms of energy flow when compared with other reef systems, and transfers this energy up the food web more efficiently. Secondary production by detritus was important in most systems compared, and thus may be a general feature of coral reefs throughout the world.

When seasonal models of Looe Key were compared, total system flow was much larger in summer, when biomasses were higher, than in winter. The system was also autotrophic during the warmer seasons and heterotrophic during winter, and was supported throughout the winter by detritus, which accumulated during the more productive seasons.

A simulation routine was also run on the Looe Key ecosystem to investigate the changes in biomass which would result from the introduction of spearfishing on the top predators. The outputs suggest that the total system biomass would not change, but that a shift in its distribution to small carnivores and large herbivores would occur. This change at Looe Key simulated by the model is consistent with reports of what the system was like before spearfishing was outlawed in 1981.

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1 General Introduction

It has long been appreciated “that nearly all [species] either prey on or serve as prey for others [...and] that each organic being is either directly or indirectly related in the most important manner to other organic beings” (Darwin 1872). More recently, much emphasis has been placed on understanding the structure and function of ecosystems through the study of their parts, especially in the face of global human population growth. Indeed, there is a rising need to manage resources on the ecosystem level (Christensen 1995) for both the preservation of species diversity and for other uses which these systems provide (McClanahan 1995).

Coral reefs, besides being among the most complex, diverse and productive ecosystems in the world (Odum 1971), provide humans with aesthetic value, support major world fisheries (McClanahan 1995) and are responsible for half of the world’s calcium carbonate precipitation (Smith 1978), thus sheltering shorelines from erosional processes. As a result, they contribute to the economies of countries throughout the tropics, notably through both the tourist and fishing industries. However, coral reefs are also fragile and easily disturbed. The exploitation of coral reef resources on a global scale signifies the need for an improved understanding of coral reef ecosystem function and structure in order to be able to better manage them (Polovina 1984). This need for understanding applies particularly to the reefs of the Florida Keys, which are under pressure from a variety of sources and where the regulatory process is strongly science-driven.

Thus, the objectives of this study are:

1. To describe the Looe Key National Marine Sanctuary ecosystem by identifying and quantifying its trophic flows. The description will allow interactions between the various components or groups within the system to be ascertained and will also enable comparisons to be made with other coral reef ecosystems throughout the world. Thus, a greater understanding of the Looe Key system and coral reefs in other areas will be achieved;
2. Demonstrate, through the construction of seasonal models, that system-level seasonal changes do occur in the Looe Key National Marine Sanctuary. This should reduce biases which occur when rates are expressed as annual averages when, in reality, they were collected from one season. This part of the study, based on the global literature on seasonal changes in coral reefs will lead to the first comprehensive description of seasonal changes in a coral reef ecosystem;
3. Predict, through the use of a dynamic simulation model, changes in ecosystem structure when perturbations are introduced (i.e., increases in fishing mortality) and thus, for example, forecast the changes which could occur at the Looe Key sanctuary when spearfishing on the large predators is introduced.

1.1 The Florida Reef Tract

1.1.1 *Geography*

The Florida Reef Tract consists of a narrow band of large bank-barrier reefs and smaller patch reefs which parallels the Florida Keys in a southwesterly direction from Fowey Rocks in Biscayne National Park off Miami (25°35'N; 80°05'W) to Loggerhead Reef west of the Dry Tortugas (24°42'N; 82°49'W) (Fig. 1; Marszalek *et al.* 1977; Porter and Meier 1992; U.S. Department of Commerce 1996). Its total length is approximately 580 km (Porter and Meier 1992), and the reefs lie 5-11 km offshore of the Keys (U.S. Department of Commerce 1996) near the shelf edge. The Florida Reef Tract is not considered a true barrier reef system because there are numerous and large gaps between many reefs (U.S. Department of Commerce 1996).

The reefs are located between the Florida Current (see below) offshore and Hawk Channel inshore. Hawk Channel runs for approximately 240 km from Key Biscayne to just west of Key West and is about 3-6 km wide (Pitts 1994). The depth of the channel varies from 8.5-14 m (U.S. Department of Commerce 1996) and its bottom consists mostly of seagrass meadows dominated by *Thalassia testudinum*, with some soft and hard coral patches (Jones 1963). The majority of the 6000 patch reefs in the Keys are located within or along the Hawk Channel boundaries, and 80% are concentrated in the Upper Keys (Marszalek *et al.* 1977; U.S. Department of Commerce 1996).

Shoreward of the Keys there are shallow water environments which cool considerably in the winter. They include the Gulf of Mexico in the Lower Keys, Florida Bay in the Middle and lower Upper Keys and Barnes Sound, Card Sound and Biscayne Bay in the Upper Keys. The capacity for heat storage in these areas is limited and they are, therefore, highly variable in terms of temperature (Roberts *et al.* 1982). Numerous passes between the Keys allow for exchange of water between the shallow environments and Hawk Channel (see below).

1.1.2 *Reef Development*

Reef development is greatest in the Upper Keys, where disturbances are at a minimum. Here, the combined effect of a more north-south orientation and the large size of the islands separating Florida Bay, Card Sound, Barnes Sound and Biscayne Bay buffer the reefs from cold water intrusions from shallow inshore areas (Marszalek *et al.* 1977). In the Middle Keys, reef development is reduced (Marszalek *et al.* 1977) because of increased exchange of detrimentally cold or hot water between shallow Florida Bay and the outer reef tract (Walker *et al.* 1982; Szmant and Forrester 1996). Increased mixing of water between Florida Bay and the reef tract is facilitated by a great number of tidal passes between the Keys and the east-west orientation of the tract (Marszalek *et al.* 1977). When severe winter fronts move in from the north, they decrease Florida Bay water temperatures and wind-induced currents

can cause this cold water to flow south through the tidal channels and onto the reef tract, thus stressing the reef environment (Hudson *et al.* 1976; Marszalek *et al.* 1977; Walker *et al.* 1982; 1987). In summer, when Florida Bay water temperatures and salinity increase, warm, highly saline water can flow out of the Bay and over the reef tract. These natural disturbances have been shown to cause high mortality in reef corals (Hudson *et al.* 1976; Hudson 1981; Davis 1982; Porter *et al.* 1982; Roberts *et al.* 1982; Walker *et al.* 1982) and, because they repeat themselves due to the annual climatic cycle (White and Porter 1985), they are probably the main reason for the absence of well developed reefs in the Middle Keys. Off of the Lower Keys, where land area increases again and tidal flow is reduced between Florida Bay, the Gulf of Mexico and the tract, reef development increases once again, although to a lesser extent than in the Upper Keys (Marszalek *et al.* 1977). Here, as in the Middle Keys, the orientation of the reef tract is east-west; thus cold water masses from the north can still intrude out onto the reefs during the winter months, although with less detrimental effects.

Zonation of habitats within the Florida Reef Tract from inshore to offshore consists of offshore patch reefs, seagrass beds, bank reefs and intermediate/deep reefs. Each of these areas is distinct in terms of species composition and diversity.

Offshore patch reefs are dominated by stony corals, with a vertical relief between 1 and 5 meters, and octocorals (U.S. Department of Commerce 1996). They lie at the seaward boundary of Hawk Channel and are often located in the lee of the larger bank reefs (Shinn 1963). The hard corals are dominated by large heads of *Montastrea annularis* (Shinn 1963), which is typically the species which forms the highest relief (Marszalek *et al.* 1977). Branching corals (*Acropora* spp.) are rarely found on patch reefs, although the shallow water hydrocoral *Millepora complanata* often grows on dead coral surfaces (Jones 1963). Alcyonaria commonly grow between coral heads and are often encrusted with *Millepora alicornis* (Jones 1963).

Seagrass beds comprised of *Thalassia testudinum* surround the patch reefs and continue seaward toward the bank reefs (U.S. Department of Commerce 1996). Voss and Voss (1955) described the extent of seagrass beds in South Florida stating that they formed "almost unbroken dense matted beds" over most of the continental shelf south of Miami "from the mainland to the keys and offshore to the outer reef." *Thalassia* beds extend into the back reef areas of bank reefs and are important nursery and transitional habitats for many species of reef fishes and invertebrates. Numerous soft coral areas are located within seagrass beds.

The bank reefs of the Florida Reef Tract may be divided into several different zones, i.e., the back reef, reef flat, spur and groove zone (fore-reef) and buttress zone. The zonation described here is similar to that of the classic Caribbean reef zonation study of Goreau (1959), with shallow zones dominated by *Acropora palmata* and deeper sections by *Montastrea annularis* (Porter and Meier 1992). The most conspicuous feature of the protected the back reef, located immediately behind the reef flat, is

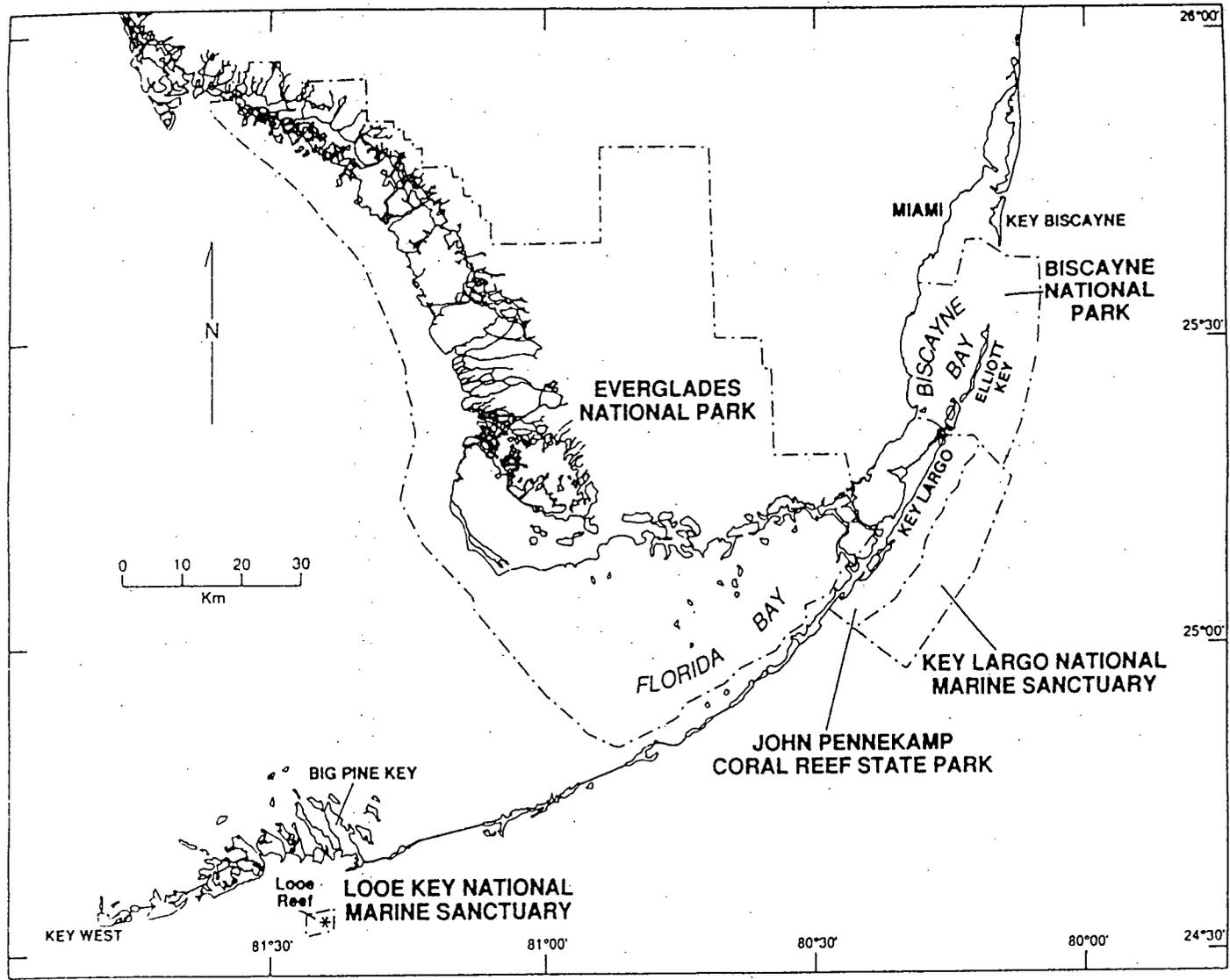


Figure 1. General geography of the South Florida/Florida Keys region. Note the location of the Looe Key National Marine Sanctuary as well as other areas protected for the preservation of the reefs. The Marquesas and Dry Tortugas are not shown (see Figure 2). From Porter and Meier (1992).

unconsolidated coral rubble deposited during storms. The depth of this area is usually very shallow (0-3 m; Bohnsack *et al.* 1987) and scattered about the rubble are large colonies of the branching corals *Acropora palmata* and *A. cervicornis* (Shinn 1980). Some colonies of *A. palmata* are overturned (Dustan 1985; Wheaton and Jaap 1988), probably due to heavy storm surge (Dustan 1985). Also located sparsely within this area are large heads of the massive corals *M. annularis*, *Diplora strigosa* and *Colpophyllia natans* (Shinn 1980).

The reef flat zone is the shallowest area of the reef and may break above the surface at low tide. It is composed mostly of a dead *A. palmata* framework (Shinn 1980; Dustan 1985) with some live cover. Coralline red algae is a common encrusting organism in this area (Dustan 1985). Live cover is dominated by *M. complanata* and the gold sea mat anemone *Palythoa carbaeorum* interspersed with the corallimorph *Ricordea florida* and another colonial anemone, *Zoanthus sociatus* (Wheaton and Jaap 1988). On some reefs, live *A. palmata* forms a band on the leeward side of the reef flat and is apparently actively growing into the back reef area (Shinn 1980). Coral spurs and sand grooves originate in this area and progress out into the prevailing seas.

The spur and groove zone is the region immediately seaward of the reef flat. Coring of the spurs reveals that they formed historically through growth of *A. palmata*, *Montastrea* spp. or a combination of both (Shinn 1963; 1980; Shinn *et al.* 1977; 1981; Dustan 1985). On some reefs, especially in the northern Keys, the upper parts of the spurs are dominated by uniformly oriented colonies of *A. palmata* (Shinn 1963; 1980). In the Lower Keys, *A. palmata* is much less abundant and *Agaricia agaricites*, *Millepora complanata*, *Porites astreoides*, *Acropora cervicornis* and *Porites porites* become the dominant species (Wheaton and Jaap 1988). As the spurs progress down in depth, coral dominance changes to large heads of *Montastrea annularis* with *Millepora complanata* still remaining common on some reefs (Shinn 1963; 1980; Dustan 1985; Wheaton and Jaap 1988). Octocorals become more common in this zone as well (Wheaton and Jaap 1988). The spurs eventually taper out as they move seaward and lead into the buttress zone.

The buttress zone is a flat area with large heads of *Montastrea annularis*, *Colophyllia natans*, *Siderastrea* spp. and *Diploria* spp. interspersed on a *Halimeda* sand bottom (Shinn 1963; 1980; Wheaton and Jaap 1988). Large sponges and octocorals are also common in this area (Wheaton and Jaap 1988).

Intermediate/deep reefs are located seaward of the shallow bank reefs (U.S. Department of Commerce 1996). They contain spurs and grooves of tighter spacing and lower vertical relief than the spur and groove zone of bank reefs (Wheaton and Jaap 1988). A high diversity of benthic organisms is characteristic of these areas including many species of stony corals, soft corals and sponges (U.S. Department of Commerce 1996). Growth forms of massive corals are usually platelike (U.S. Department of Commerce 1996), thus maximizing light exposure.

1.1.3 Hydrography

The major controlling hydrographic feature of the Florida Reef Tract is the Florida Current which flows along the continental shelf seaward of the Keys (Fig. 2). The water moving past the Keys in the upper layers originates in the South Atlantic (Schmitz and Richardson 1991) and flows into the Caribbean through the Lesser Antilles. The general flow of water curves north-northwest at the Central American coast, proceeds along the Yucatan Peninsula and, depending on the prevailing conditions, either proceeds into the Gulf of Mexico to form the Loop Current, or shifts to the east and enters the Straits of Florida where it becomes the Florida Current. The Florida Current is part of the Gulf Stream system and connects the Loop Current to the Gulf Stream off the southeastern Florida coast (Cha *et al.* 1994). Off of the Dry Tortugas and the Lower Keys the Florida Current axis is located offshore and its distance is dependent upon the condition of the Loop Current in the Gulf (Lee *et al.* 1994). When the Loop Current is weak, the axis is closer to shore, but when the current is strong, the axis moves further offshore and this axis shift results in the formation of the cold, cyclonic Tortugas Gyre (Lee *et al.* 1994). The gyre lasts for approximately 100 days and eventually is forced to the east when Loop Current or Yucatan Current patterns shift (Lee *et al.* 1994). As the gyre moves eastward it gradually reduces in size and is generally gone before it reaches the Upper Keys (Lee *et al.* 1994). Frontal eddies can also form and move up the Keys which carry the gyre waters (Lee *et al.* 1994).

Upwelling occurs in the center of the Tortugas Gyre; it increases nutrient supply to the surface waters, thus enhancing primary productivity and zooplankton populations (Lee *et al.* 1994). This phenomenon enhances the food supply for commercially important larval invertebrates, as shown for penaeid shrimps by Criales and Lee (1995), and fishes and, since the duration of the gyre lasts for about 100 days, many species are retained in a food-rich area for their entire planktonic existence (Lee *et al.* 1994). The gyre and its frontal eddies, along with the westerly winds characteristic of this area, also provide for onshore advection of larval organisms to the coral reefs of the Lower and Middle Keys (Lee *et al.* 1994). The reefs of the upper Middle and Upper Keys no longer receive onshore Ekman transport of surface waters, and the larvae contained therein, due to the southeasterly winds, the shift in the direction of the Florida Current from east-west to north-south and the narrowing of the Straits of Florida in this area which eliminates coastal gyres (Lee *et al.* 1994).

The width of the Straits of Florida in the Upper Keys, despite causing the dissipation of the Tortugas Gyre, keeps the axis of the Florida Current close to the reefs. This phenomenon, along with reduced transport of cold shelf water due to fewer tidal channels, facilitates the greater development of coral reefs in this area as disturbances and variation in water quality are reduced. However, Leichter *et al.* (1996) have shown that cold, high-salinity, nutrient-rich water can flow up the slope from below the thermocline and stay on the reef slope for up to 4 hours before mixing occurs. Temperature fluctuations of up to 5.4°C are associated with this phenomenon and the frequency of occurrence is greater from mid-

spring (May) to mid-fall (November) with peak activity during the summer months. These internal bores cause physical variability that increases with depth and this finding is in contrast to the general consensus that the deeper reef slope environments are more stable. They increase the concentrations of dissolved nutrients, suspended particles and plankton from seaward of the reef tract which flow over the reef and become available for organisms to utilize. At the same time, they dramatically decrease temperature and increase salinity, both of which stress reef organisms. Although they studied one specific reef off the Upper Keys, Leichter *et al.* (1996) speculate that the spatial scale of these internal bores can be large enough to affect other reefs along the Florida Reef Tract. Similar events have been noted from Tahiti (Wolanski and Delesalle 1995) and from reefs located near the shelf break in the central Great Barrier Reef (GBR), although these studies do not show seasonal variations (Andrews and Gentien 1982; Wolanski and Pickard 1983).

Inshore hydrography consists of along-channel and cross-channel flow in Hawk Channel and tidal exchange of waters north (Gulf of Mexico and Florida Bay) and west (Barnes and Card Sounds and Biscayne Bay) with the Atlantic through passes between the Keys. Along-channel flow changes seasonally in both the Upper and Lower Keys where the flow is southwesterly in the fall and winter but shifts to a more northeasterly pattern in spring and summer (Pitts 1994). This pattern is not as well defined in the Lower and Middle Keys during spring and summer as periodic reversals are common (Pitts 1994). Tidal flow is both into (ebb) and out of (flood) waters north and west of the Keys, but net flow is into the Atlantic as the ebbs are consistently stronger than floods (Ogden *et al.* 1994). Smith (1994) speculates that the net flow out of the Gulf of Mexico may be due, in part, to the fact that mean sea level is higher there than in the Atlantic. As discussed above, the physical parameters of the nearshore waters fluctuate much more than the deeper waters seaward of the reef tract and their influence on the outer reefs is evident in the large fluctuations in sea surface temperature measurements at reefs in the Middle Keys (Ogden *et al.* 1994). Smith (1994) found that there is greater across-channel flow at a Lower Keys site when compared with a site in the Upper Keys due to the proximity of this site to tidal passes and to the return flow of shoreward directed Ekman transport over the shelf.

1.1.4 *Nutrients*

Lapointe and Clark (1992) investigated human induced coastal eutrophication in the Keys due to groundwater discharge from the widespread use of septic tanks. They found that inshore areas showed elevated concentrations of nitrogen (N), phosphorus (P) and chlorophyll *a* (Chl *a*) and that these levels decreased with increasing distance from shore. The lower concentrations farther from shore indicate that most of the nutrients were taken up by organisms in canal and seagrass communities before they reached the reefs. However, dissolved organic phosphorus (DOP) levels remained elevated further from land than other nutrients, which suggests that this may provide P to offshore patch and bank reefs. Nutrient

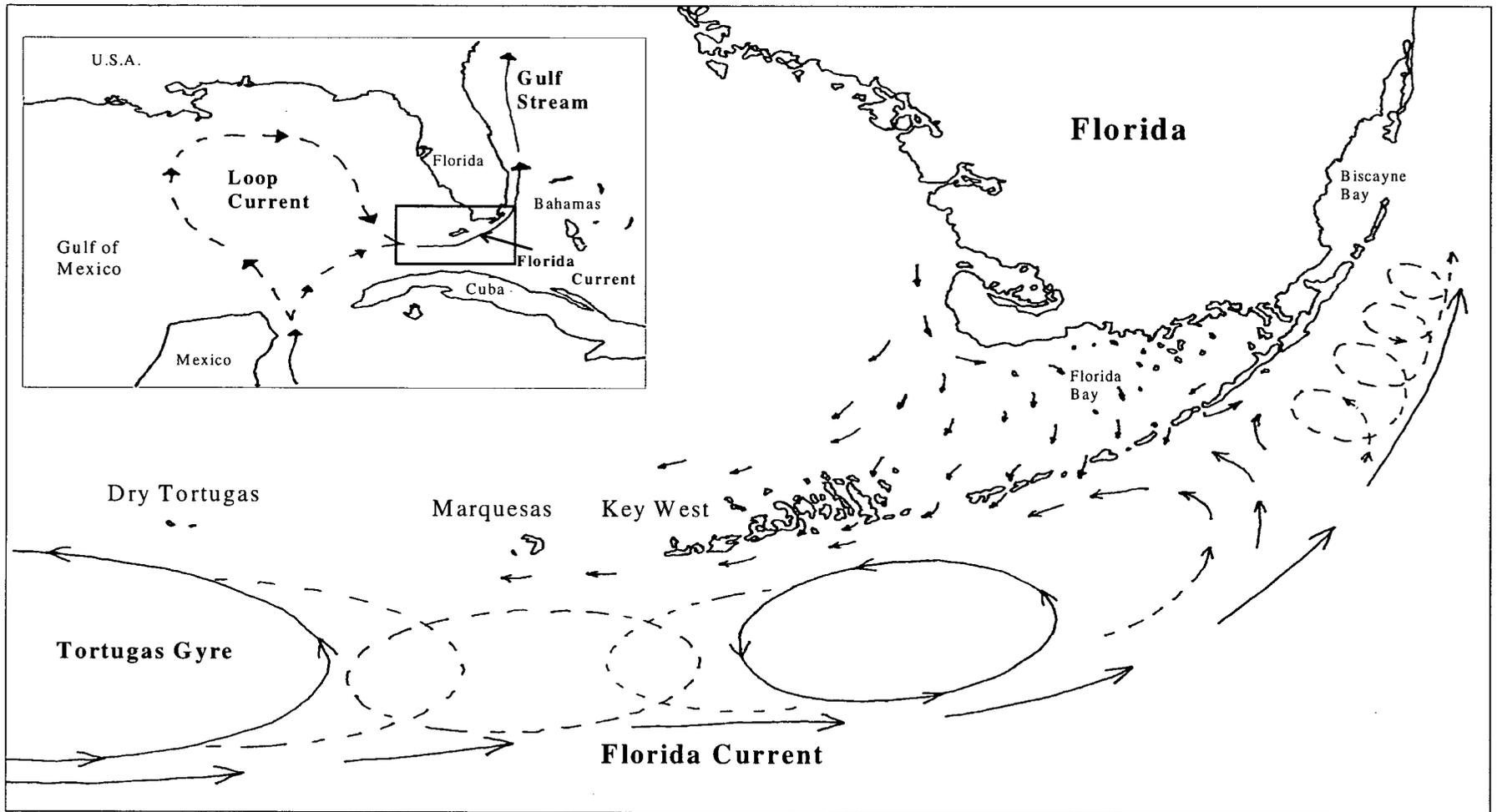


Figure 2. Hydrography of the Florida Keys showing the major currents and their directions of flow. Inset shows where the Florida Current/Gulf Stream system is formed. Modified from U.S. Department of Commerce (1996).

discharge from land is increased during the summer due to increased rainfall, reduced evaporation, annual maximum ebbing tides and the delayed discharge of winter deposits of nutrients - a 68% increase in Keys residents occurs from summer to winter and tourism greatly increases during this season as well (Lapointe *et al.* 1990). This, in turn, increased Chl *a* concentrations due to increased phytoplankton biomass. In contrast, Lapointe and Clark (1992) found that turbidity was higher in the winter due to winds coming out of the north, which resuspended bottom sediments. Combined high turbidity levels and high offshore transport of this material through increased tidal flow through channels could potentially increase the turbidity of offshore reef areas in winter.

Ogden *et al.* (1994) and Szmant and Forrester (1996) found similar patterns in nutrient distribution. In the Upper and Lower Keys, where tidal exchange with estuarine water from Biscayne Bay and Florida Bay is reduced, nutrient concentrations followed the same pattern as those from Lapointe and Clark (1992) with increased nutrients close to land and a decrease to more oligotrophic levels farther from shore. However, Szmant and Forrester (1996) found that water column nutrients increased during winter storms when resuspension of sediments occurred. In the Middle Keys, the gradient of nutrient concentration from inshore to offshore was much less pronounced which was probably due to the large tidal passes in this area which allow exchange with Florida Bay. Both Ogden *et al.* (1994) and Szmant and Forrester (1996) measured higher P concentrations offshore than inshore which suggests inputs other than from the Keys. Gyre upwelling (Ogden *et al.* 1994; Szmant and Forrester 1996) or tidal bores (Leichter *et al.* 1996) are possible sources for the increased levels of P.

1.1.5 *Climatology*

The Florida Keys generally have a more moderate climate than the rest of Florida as continental cold air masses are buffered by the Gulf of Mexico and the Atlantic Ocean (Jones 1963). Winds are predominantly out of the southeast in the summer rainy season and from the northeast in the winter dry season (Smith 1994; U.S. Department of Commerce 1996). Air temperature is greatly influenced by the warm waters surrounding the small islands (U.S. Department of Commerce 1996). The Florida Current moderates the upper temperature limits when winds are out of the southeast and when winter cold fronts move into the region, their intensity is reduced by the warmer waters of the Gulf of Mexico (Walker *et al.* 1987). Average annual maximum air temperature in Key West is 28°C and the average minimum is 23°C (U.S. Department of Commerce 1996). Waters in the Lower Florida Keys are commonly calm during summer, as the prevailing winds and seas are from the east/southeast, which is parallel to the reef tract axis. This facilitates heating of the water column and, as a result, water temperatures in the Lower Keys are usually slightly warmer than those in equivalent areas in other parts of the reef tract, where reefs have a greater amount of water exchange due to their orientation to the winds and seas (Jaap 1985).

Most of the annual rainfall ($124.5 \text{ cm} \cdot \text{year}^{-1}$; Schomer and Drew 1982 as cited in U.S. Department of Commerce 1996) occurs during summer.

1.2 Looe Key National Marine Sanctuary

The Looe Key National Marine Sanctuary ($24^{\circ}32'N$, $81^{\circ}24'W$) is located approximately 13 km southwest of Big Pine Key in the Lower Keys (Fig. 1; Wheaton and Jaap 1988) and is bordered to the north by Hawk Channel and to the south by the Straits of Florida. Although there is very little patch reef formation in Hawk Channel near the Sanctuary (Lidz *et al.* 1985), there is a considerable amount of low relief hard bottom environment which support a high diversity of reef fishes and invertebrates, especially alcyonarians (pers. obs.). Looe Key Reef, an outer bank reef located near the shelf edge, is noted for its large size and well developed, high relief spur and groove formations (Bohnsack *et al.* 1987). A sanctuary of approximately 18 km^2 was established in January 1981, to protect the fragile fore-reef environment (Bohnsack *et al.* 1987), to preserve commercially important resources and to provide for education and recreational activities (White and Porter 1985). In April 1981, spearfishing at Looe Key was outlawed (Bohnsack 1982), but hook and line fishing continued until July 1997 (J. Bohnsack, National Marine Fisheries Service, Miami, FL, pers. comm.).

The Sanctuary receives heavy recreational use throughout the year which mostly consists of snorkeling and SCUBA diving activities. The number of visitors that Looe Key receives is not as high as those reefs in the northern Keys, which are in closer proximity to the major population center of Miami and endure heavy weekend use (Tilmant 1987). Due to the large number of boats associated with diving activities, mooring buoys were installed to reduce anchor damage to the reef. It is illegal to touch anything within the Sanctuary and the reef is frequently patrolled by rangers to ensure that this is not done. In addition, a National Oceanographic and Atmospheric Administration (NOAA; the lead agency with jurisdiction of Sanctuary waters) patrol boat is constantly present during daylight hours to prevent illegal activities and ward against boat groundings. Thus, Alevizon and Gorham (1989) have described Looe Key as a well-patrolled reef.

The dimensions of Looe Key Reef are approximately $0.2 \times 1.2 \text{ km}$ and it lies in the southern part of the center of the Sanctuary, i.e., forming its 'core area' (Fig. 3; Lidz *et al.* 1985), delineated by buoys. The area outside of the core reef zone encompasses sand flats, seagrass beds and hard bottom environments (Bohnsack *et al.* 1987) as well as a deeper intermediate reef and a deep reef (Fig. 4). The sand flats substrate is composed mainly of fragments of corals, molluscs and *Halimeda* (Lidz *et al.* 1985) and is the dominant habitat within the Sanctuary (Bohnsack *et al.* 1987). Seagrass beds consist mostly of *Thalassia testudinum* mixed with *Syringodium filiforme* (Bohnsack *et al.* 1987). Scattered alcyonarians, sponges and small, individual head corals attached to a hard calcium carbonate substrate with little or no vertical relief constitute hard bottom habitats within the Sanctuary (Lidz *et al.* 1985; Bohnsack *et al.*

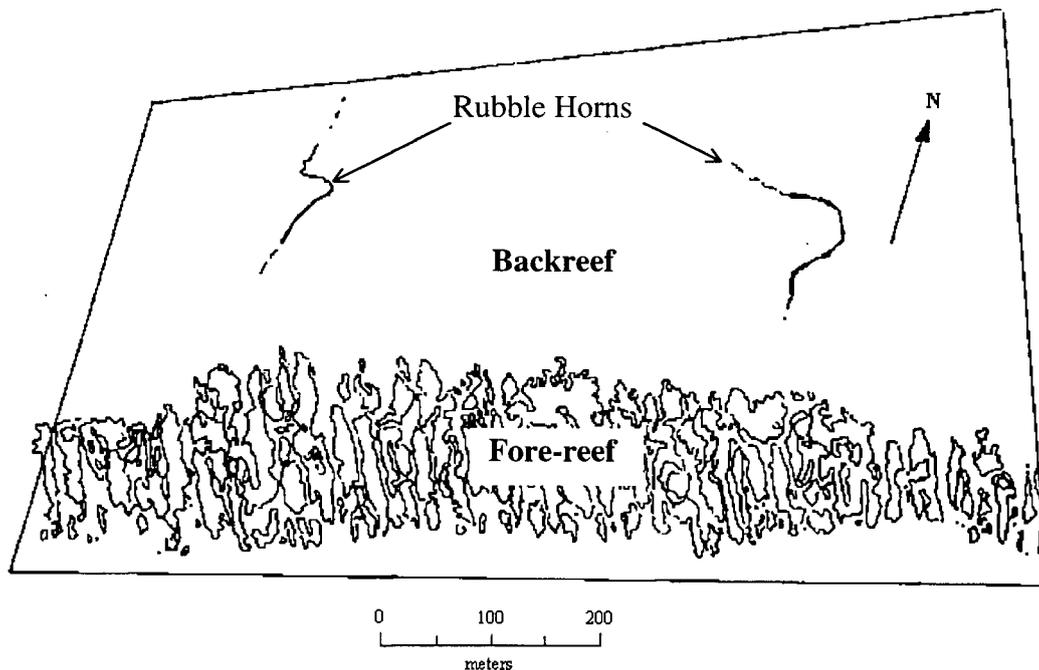


Figure 3. The core area of the Looe Key National Marine Sanctuary which encompasses the fore-reef and backreef habitats. The map shows the spur and groove formations in the fore-reef and the rubble horns in the backreef formed by hurricanes. Modified from Lidz *et al.* (1985).

1987). An intermediate reef exists at Looe Key just below the buttress zone of the fore-reef. It consists of low-relief spur and groove formations which extend from the ends of the buttress zone spur and groove community at about 10 m (Bohnsack *et al.* 1987) down a gradually sloping bottom to about 20 m (U.S. Department of Commerce 1996). The intermediate reef is highly diverse and contains numerous alcyonarians, stony corals and large sponges (U.S. Department of Commerce 1996). Many reef fish species not found in shallower habitats occur in this zone (U.S. Department of Commerce 1996; pers. obs.). The deep reef environment begins as the shelf begins to slope at a greater angle at about 20 m (U.S. Department of Commerce 1996) and ends in a horizontal sand flat at 30 m (Shinn *et al.* 1981). This environment has low-relief spur and groove formations like the intermediate reef, but species composition changes somewhat to deeper water octocorals and sponges and massive coral growth is plate-like (U.S. Department of Commerce 1996). The deep reef fish community changes once again to an abundance of deep water species which are not found in any other zone (U.S. Department of Commerce 1996). The central portion of both the intermediate and deep reefs have been buried by a coralline sand lobe which extends from the buttress zone of the central fore-reef seaward (Shinn *et al.* 1981; Lidz *et al.* 1985).

The core area of Looe Key incorporates the well developed fore-reef zone as well as the shallow reef flat and back reef zones. The fore-reef zone is characterized by high relief spur and groove formations with spurs of 3-5 m high (Shinn *et al.* 1981). The spurs extend from the reef flat in a seaward

direction for approximately 150 m (Shinn *et al.* 1981) before tapering out at about 10 m depth (Bohnsack *et al.* 1987). The fore-reef is approximately 1200 m wide and runs east to west (Wheaton and Jaap 1988) with coral spurs facing the shelf margin at a slightly less than perpendicular angle (Shinn *et al.* 1981). The coral spurs consist of *Acropora palmata* which began growing over a carbonate sand substrate approximately 6500 years ago when sea levels were much lower than today (Shinn *et al.* 1981). *A. palmata* is no longer a significant reef builder at Looe Key, or at any other reef in the Lower Florida Keys, and began to die off 800-1000 years ago, probably due to the flooding of, and the subsequent influx of unfavorable water from Florida Bay (Shinn *et al.* 1981). Although *A. palmata* is still present at Looe Key, it does not exist in flourishing mono-specific stands as it does on Upper Keys reefs which lack the tidal water influence of Florida Bay (Shinn *et al.* 1981). In contrast, the reef flat/back reef zone was not formed by *A. palmata*, but instead consists of consolidated coral rubble (Wheaton and Jaap 1988).

The corals and other benthic cnidaria of Looe Key have been described in detail by Wheaton and Jaap (1988). The first zone of the fore-reef is the reef crest which is almost entirely encrusted with *Millepora complanata* and *Palythoa caribaeorum* with a few small heads of *Porites asteroides* (Shinn *et al.* 1981; Wheaton and Jaap 1988). These two species also extend into and dominate the upper spur and groove zone (Wheaton and Jaap 1988). The reef crest is a high energy zone which receives the full force of the waves and sections of the crest are emergent during spring low tides (Shinn *et al.* 1981; Wheaton and Jaap 1988). Therefore, benthic invertebrate species which occupy this zone must be adapted to the severe physical forcing of waves as well as to dessication during spring low tides. Historically, this area was a small, sandy island, described by Agassiz (1880), but which has since eroded away.

As the spurs progress down in depth, the increased relief provides more area for organism settlement and *A. palmata* occurs on the upper surfaces of some spurs and *Agaricia agaricites* becomes abundant on the vertical sides of the spurs (Wheaton and Jaap 1988). *M. complanata* continues to remain abundant as the spurs gradually become deeper (Wheaton and Jaap 1988). Octocorals become abundant as the heights of spurs diminishes and massive colonies of *Montastrea*, *Diploria*, *Colpophyllia* and *Siderastrea* come to dominate the stony corals (Wheaton and Jaap 1988). Numerous caves exist underneath the spurs which provide refuge for a variety of reef fish and invertebrates (Wheaton and Jaap 1988; pers. obs.) The last fore-reef habitat is the buttress zone which is characterized by massive *Montastrea annularis* heads lying on the bottom in about 10-12 meters of water (Bohnsack *et al.* 1987; Wheaton and Jaap 1988).

Immediately behind (shoreward of) the fore-reef is rubble-covered back reef or reef flat. This area contains coral rubble of 4 to >256 mm (Lidz *et al.* 1985) which has been deposited here after storms. The rubble forms two 'horns' which border the reef flat and meet to the north to form a crude triangle (Shinn *et al.* 1981) which shelters the back reef from prevailing winds and seas. These features are common on Florida reefs (Shinn *et al.* 1981) and have been shown by Ball *et al.* (1967) to be due mainly

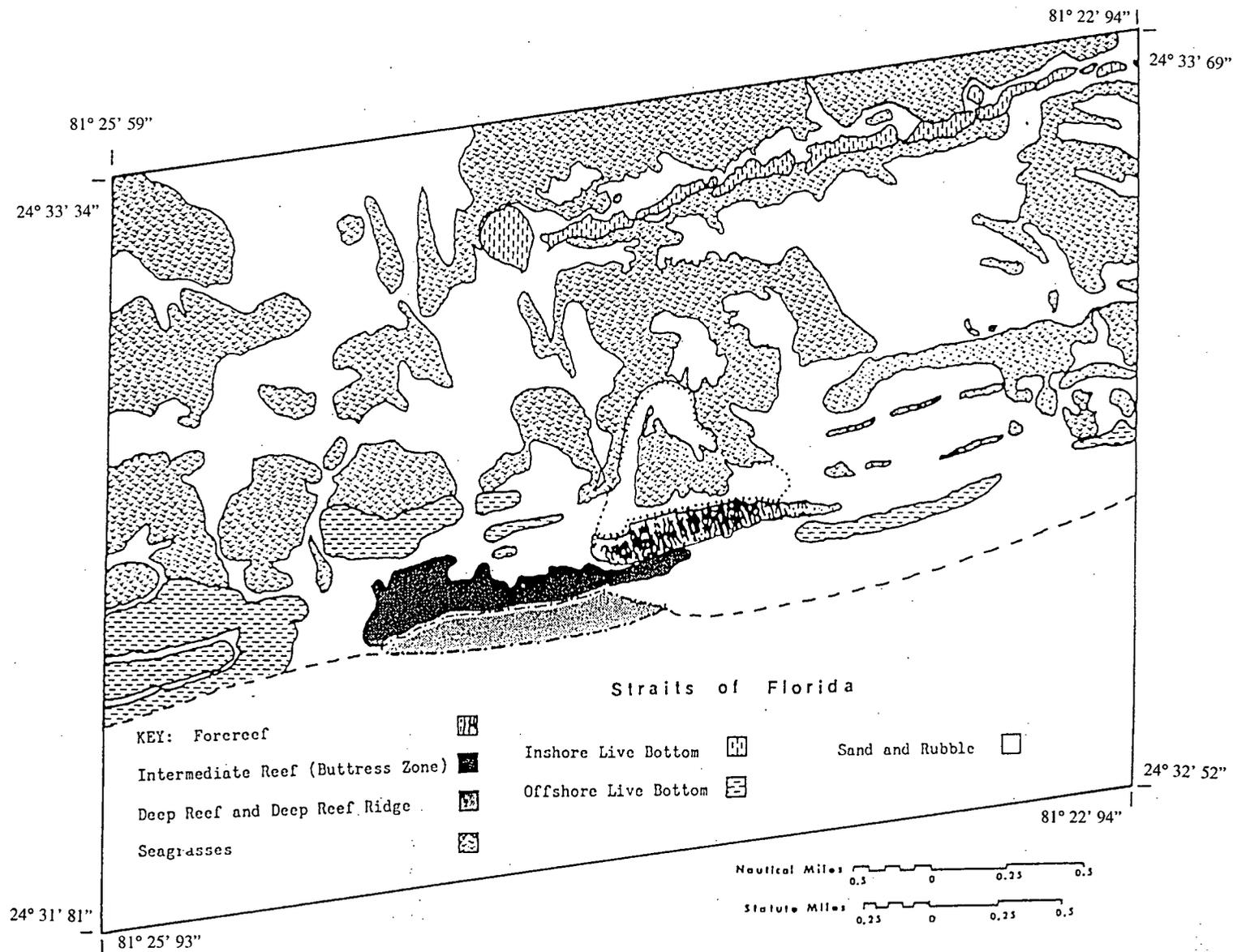


Figure 4. Habitats of the Looe Key National Marine Sanctuary distinguished from aerial photographs from Bohnsack *et al.* (1987). Habitats in the area deeper than 13 m seaward of dashed line were not distinguishable from the photographs.

to the passage of hurricanes. The back reef community consists of many patches of coral growth interspersed in the coral rubble. Large, unoriented colonies of *Acropora palmata* are common (pers. obs.) and many upended colonies exist, presumably overturned during storms. They provide shelter for a highly diverse and abundant reef fish population which utilizes the branches as a diurnal resting place. Just shoreward of the reef flat, within the rubble triangle, a seagrass community exists which is broken in many places by sand-filled blowouts 25-30 cm deeper than the surrounding seagrass bed (Shinn *et al.* 1981) which were formed during hurricanes (Ball *et al.* 1967). The entire back reef community, including the seagrass beds, is shallow with depths ranging from 1 to 4 m (Shinn *et al.* 1981).

The fish community in the Looe Key National Marine Sanctuary have been described by Bohnsack *et al.* (1987). They divided the Sanctuary into 10 separate zones based on bottom habitats and fish species composition and, quantified fish species abundance and percent frequency occurrence using a visual sampling technique. Zones deeper than 13 m (~31% of the Sanctuary) were not sampled due to the limitations of time when SCUBA diving at depth. A total of 188 species of fish were observed within that Sanctuary of which 14% of the counted individuals were herbivores, 48% planktivores, 2% browsers, 10% microinvertivores, 24% macroinvertivores and 2% piscivores. The forereef zone contained the highest abundance of fishes followed by the back reef area and live bottom habitats. Seagrass beds and sandy areas had relatively low abundances of fishes.

Studies conducted specifically within the Looe Key National Marine Sanctuary are considered to be representative of the entire reef tract because species found there are generally found in similar habitats throughout the Florida Reef Tract (U.S. Department of Commerce 1996). Therefore, a model describing the trophic interactions of the Looe Key ecosystem will also be applicable to the outer bank reefs of the Florida Keys.

1.3 Why We Model Ecosystems

Ecology is the study of organisms and their interactions with each other and with their environment. Each individual living in a certain area survives by outcompeting its competitors for limited resources, avoiding predation and enduring the environmental conditions which surround it. Populations of organisms persist in a similar fashion and also perpetuate their numbers by successfully reproducing. Ecosystems thus consist of a multitude of populations occurring in a given area, interacting with each other through direct and indirect processes with limited exchange with the outside (adjacent ecosystems). Within an ecosystem, complex processes occur between organisms and populations which govern the structure and functioning of the system as a whole.

Ecologists study and describe these processes to gain an understanding of specific species or groups of species in order to increase knowledge or suggest possible avenues for future research. However, most ecological work is conducted on single species or on specific processes in small areas

with some general relations to the surrounding environment and organisms such as diet compositions, primary productivity, feeding rates, etc. Hence, there is a great deal of information available for the many different organisms or components of ecosystems. The fluxes of energy which connect these components can be quantified in a rigorous fashion through studies which describe the rates at which they occur. The problem is that most studies done only focus on certain aspects of the ecology of specific organisms. Unfortunately, these studies also describe the fluxes between two species, or small groups of species, and not in a larger ecosystem context.

Modeling of whole ecosystems provides a way to link the components together and make use of all available data for a given area. Thus they serve to tie in information from various disciplines and force the modeler to review the literature outside her/his specific discipline (Christensen and Pauly 1993). Through the use of computers, mathematical models can be constructed which describe the various components of the system and the various biological rates which occur within and between populations, or system level rates, such as exchange with neighboring ecosystems (Christensen and Pauly 1993).

Coral reefs are characterized by a high complexity of trophic interrelationships and they are more diverse than any other type of aquatic ecosystem. Hence, describing a coral reef ecosystem in quantitative terms through the use of modeling may seem a difficult task. However, most work done on coral reefs are based on the assumptions - generally implicit - that the states and rates measured are applicable to a certain period in time (Pauly and Christensen 1994). Through the application of quantitative ecosystems models, these measured state and rate estimates are compared and tested to see if they can generate new knowledge on the functioning of the system from which they were measured (Pauly and Christensen 1994). In addition, the parameters which have not been measured can be identified and estimated through the construction and balancing of the models (Christensen and Pauly 1993; Pauly and Christensen 1994). Two types of models have emerged and been applied to coral reef systems: simulation models (McClanahan 1995) and mass-balance models (Polovina 1984; Christensen and Pauly 1992; Venier and Pauly 1997; see Appendix 5). Recently, it has been shown that mass-balance models, which are generally less data intensive than simulation models, can be re-expressed as dynamic simulation models (Walters *et al.* 1997), thus bridging the gap between these two types of models.

I present here several mass-balance ecosystem models of the Looe Key National Marine Sanctuary, a coral reef in the Florida Keys, USA. One model was constructed using data averaged over an entire annual period and is based on a preliminary version described in Venier and Pauly (1997). Four additional models were constructed which take into account seasonal changes in system structure and function. These models are then compared with other mass-balance models of coral reef systems. Finally, the response of the ecosystem to a specific change in management policy is evaluated using the EcoSim module of the ECOPATH software package.

2 Seasonality in Coral Reefs

To date, few comprehensive studies of seasonal variations in processes affecting coral reef ecosystems have been published. The literature does show, however, that, when measured for long enough periods (i.e., through seasons), most states and rates within reef systems fluctuate seasonally and tend to peak during the summer months. These changes have been correlated with a variety of environmental factors (e.g., temperature, light intensity, daylength, seasonal weather patterns, etc.) specific to the area and species or groups examined. What this means is that the function of coral reef systems probably changes with the seasons such that the way energy flows within them also fluctuates on an annual basis. On the other hand, many measurements have been taken of reef states and processes during a single season and then applied to pertain to the entire year. If these rates and processes change seasonally, then the 'averages' which are reported do not adequately represent yearly means at all, but apply solely to the time period in which they were measured. The objective of this chapter is, therefore, to synthesize available seasonal estimates for major states and processes of coral reef ecosystem function through a comprehensive review of the coral reef literature.

2.1 Primary Producers

Kinsey (1985) provided a summary of total system level studies on metabolic processes such as productivity, respiration and calcification for seven different reefs in both summer and winter. These studies encompassed sections of whole reef and productivity was measured for both the resident algal communities and symbiotic dinoflagellates (zooxanthellae) associated with the corals (Table 1). He noted an overall pattern of higher productivity during the summer that was roughly two times greater than that measured in winter. Note that many reef areas also include seagrass communities with associated epiphytes and macroalgae which are important contributors to the overall productivity of the system.

2.1.1 Seagrass Communities

Seagrass communities are common in both temperate and tropical regions, and because of this broad distribution, they have been studied extensively. Productivity and biomass have been measured for many species using a variety of techniques, and seasonal trends have emerged when studies of seagrass productivity and biomass, lasting for at least an annual period, have been compared between regions. Nearly all studies have shown that productivity and biomass are higher during the season with the greater light intensities (see below). However, when temperate and subtropical/tropical seagrasses were compared, seasonal variability was found to be less pronounced at lower latitudes (Hillman *et al.* 1989).

Barber and Behrens (1985) showed that productivity of *Thalassia testudinum* and *Syringodium filiforme* was significantly correlated with temperature in an inshore area near Tampa Bay, Florida (28°

Table 1. Seasonal differences in metabolic processes of reef systems (P = production; R = respiration). (Modified from Kinsey, 1985).

Location	P (gC · m ⁻² · day ⁻¹)		R (gC · m ⁻² · day ⁻¹)		P/R		Source
	summer	winter	summer	winter	summer	winter	
Kauai, Hawaii (22°05'N) Fringing reef	8.3	7.7	7.6	7.6	1.1	1.0	(1)
One Tree Reef, GBR (23°30'S) Patch reef	4.1	1.7	3.8	2.4	1.1	0.7	(2)
One Tree Reef, GBR (23°30'S) Reef flat	9.0	3.6	7.9	5.3	1.1	0.7	(3)
Lizard Island, GBR (14°30'S) Reef flat	9.7	4.1	11.8	3.8	0.8	1.1	(4)
Kaneohe Bay, Hawaii (21°26'N) Fringing reef	11.0	5.5	15.1	6.4	0.7	0.9	(4)
Houtman Abrolhos, Austr. (28°30'S) Lagoon coral shoal	21.0	12.1	19.6	14.4	1.1	0.8	(5)
French Frigate Shoals, Hawaii (24°50'N) Reef flat	8.5	4.3	4.9	2.6	1.8	1.7	(6)

Sources:

(1) Kohn and Helfrich (1957); (2) Kinsey and Domm (1974); (3) Kinsey (1977); (4) Kinsey (1979); (5) Smith (1981); (6) Atkinson and Grigg (1984).

12'N). Both species showed an increase in productivity with increasing temperatures, with a maximum reached in late spring and a general decline throughout the rest of the year to a minimum in January - February. They estimated the optimum temperatures of *T. testudinum* to be between 23 and 31°C, and *S. filiforme* had its optimum productivity between 23 and 29°C. At an offshore backreef site (Looe Key; 24°32'N), where seasonal temperature fluctuations are dampened, Lapointe *et al.* (1994) found that *T. testudinum* exhibited marked seasonality in areal production with a maximum value in summer and minimum in winter. Areal biomass showed a similar trend at this site, but the summer value was only slightly higher than the winter value.

Fong *et al.* (1997) measured seasonal changes in both biomass and productivity of *T. testudinum* through a modeling approach and verification studies at inshore stations in Biscayne Bay, Florida (25°25'N). Biomass was higher in July than it was in January at both sites where it was measured. As Zieman *et al.* (1989) have shown that a consistent relationship exists between *Thalassia* standing crop and areal leaf productivity, it follows that if biomass (as measured by leaf standing crop) is higher in summer, then productivity should be higher as well. In their model, Fong *et al.* (1997) predicted that, except in winter, light levels and temperatures were within the ranges of optimal values for *T. testudinum* at one site within in Biscayne Bay where this species dominated the seagrass community. The winter season showed the lowest biomass and productivity values and may, therefore, be correlated to suboptimal light and temperatures.

In Shark Bay, Western Australia (26°S) growth and productivity of seagrasses have also been correlated with light and temperature (Walker 1989). In Walker's study, *Amphibolus antarctica* showed maximum productivity and specific growth rates that coincided with annual highs in light intensity, while *Posidonia australis* showed lowest specific growth rates in winter. These results for *P. australis* agree with those of Silberstein *et al.* (1986) who found that leaf production was highest in the summer months and lowest in winter and spring at the northern end of Cockburn Sound, Western Australia. In a review of the Australian seagrass literature, Hillman *et al.* (1989) found that standing crop in temperate seagrasses generally shows a unimodal annual variation with a high in the late spring/early summer, but that this pattern is less pronounced in lower latitudes, probably due to the moderation of seasonal fluctuations in abiotic factors (e.g., light and temperature). However, Duarte *et al.* (1996) showed that in a Kenyan backreef lagoon (4°25'S), growth of the vertical shoots of *Thalassodendron ciliatum* exhibit a bimodal pattern wherein growth was reduced during the two rainy seasons per year occurring in this monsoon area. They attributed this reduced growth to the increased freshwater input and turbidity associated with the monsoons (McClanahan 1988). This observation implies that, even at low latitudes where seasonal changes in light intensity are small, local conditions can reduce the amount of available light to seagrasses and thus reduce their growth rates and productivity. Since most tropical areas have a season in which rains or winds are strong and the resultant turbidity increased, seagrasses are likely to experience a period of lower growth and productivity rates regardless of latitude.

Seagrasses growing in very shallow areas may also experience seasons of lower growth corresponding to tidal patterns. Heijs (1987a) found that shallow beds of seagrasses in Bootless Bay, Papua New Guinea (9°S) showed a declining abundance during the SE monsoon due to increased exposure during seasonal daytime spring tides, an effect that became less pronounced with depth. At the same site, seagrasses occurring at depths where they were never exposed followed a similar trend, with highest abundance during the NW monsoon (December - April) and lowest values during the SW monsoon, but their overall abundances remained higher than at exposed locations. Heijs (1987a) suggested that this trend may be related to temperature. At a protected back-reef site in deeper water, seagrasses did not show a seasonal trend: this was probably a result of the overall stability of this area with protection from waves and low turbidity throughout the year (Heijs 1987a). However, biomass of seagrass was generally higher from February to May at this site, though Heijs (1987a) presented no explanation for this observation. It could be due to much reduced algal biomass during this period which would reduce competition, or to seasonally favorable water temperatures.

The epiphytes growing on seagrass leaves also show seasonal oscillations regarding their relative abundance, biomass and productivity. In a mixed seagrass meadow (5 spp.) in a Papua New Guinean backreef lagoon, Heijs (1987b) found that the epiphytic community reached its highest abundance and diversity between May and August (fall - winter), with a decline thereafter. The decline was

hypothesized to be a result of increased temperatures associated with low daytime spring tides and/or heavy precipitation caused by storm events which occurred at the times of the lowest tides. Biomass and productivity peaked in July and declined rapidly from September through November to an annual low. Heijs (1987b) speculated that this observed pattern possibly relates to seasonal changes in tidal regime and/or temperature.

Kendrick and Burt (1997) compared the epiphyte assemblages growing on *Posidonia sinuosa* at two locations, separated by 8 km, which experienced different wave exposures in Western Australia (32° 05'S). They reported a general summer-autumn peak in species richness and abundance, although slightly different seasonal patterns were observed between the two sites. The exposed site showed peaks in the fall (February - March) while the protected site peaked over a longer period (December - June) (Kendrick and Burt 1997). The differences were apparently linked to the growth of *Posidonia* leaves as colonization by epiphytes occurred after spring growth peaks. In a different location in Western Australia, Silberstein *et al.* (1986) found that epiphyte loads on *P. australis* at a site influenced by oceanic waters peaked in winter then declined to a low in summer. The only correlation they found was with water column chlorophyll concentrations, and they suggested that controls of phytoplankton and epiphyte abundance may be similar.

In a model of seagrass dynamics, Fong *et al.* (1997) found that epiphytes in low nutrient conditions were limited primarily by the rate of seagrass senescence and secondarily by water column P concentrations. Support for these predictions come from the data of Heijs (1987b) and Lapointe *et al.* (1994) who found that epiphyte levels on seagrasses growing in low nutrient backreef areas were highest in winter. During this season, Lapointe *et al.* (1994) measured increased turnover time for seagrasses and significantly higher level of water column P concentrations. The combined conditions of stable substrate (seagrass leaves) and higher nutrients are conducive to increases in epiphyte abundance.

Macroalgae growing in seagrass communities also seems to show seasonal fluctuations in some areas. In shallow sites in Papua New Guinea, Heijs (1987a) found that macroalgae generally showed trends opposite to the seagrasses, with low abundance or complete absence during the NW monsoon (December - April) and high abundance during the SE monsoon (May - November). Both species richness and abundance increased at this time coincidentally. Total algal biomass was extremely low from January to May and then increased to a high value in the spring (October - November). The apparent seasonality was speculated to result from seasonal changes in temperature, although competition with seagrasses for space, light and nutrients may also be important (Heijs 1987a). Also, algae growing in the shallow sites were unaffected by exposure during the SE monsoon, an effect which appeared to control the abundance of seagrasses. The life cycle of the macroalgal species present may also play a role in the observed seasonal patterns in richness and abundance. Many species, even in deeper sites, were not present all year, and were only seen during the SE monsoon season (Heijs 1987a).

At higher latitude sites in Florida, both *Caulerpa paspaloides* (O'Neal and Prince 1988) and *Sargassum pteropleuron* (Prince and O'Neal 1979; Prince 1980) show peak growth rates in summer and reduced growth in winter. These authors attribute this apparent seasonality to changes in temperature, with growth increasing with rising temperatures. In contrast, Lapointe *et al.* (1994) found that there was no significant change in macroalgal biomass at three backreef sites along the Florida Reef Tract. Although these studies were conducted in different areas (i.e., inshore and offshore, respectively), the apparent discrepancy between them warrants further investigation.

2.1.2 Reef Macroalgae

Macroalgae have been recognized as important primary producers in reef ecosystems and, indeed, some forms may dominate total reef primary production (Wanders 1976; Hatcher 1981; Rogers and Salesky 1981; Hatcher and Larkum 1983; Carpenter 1985; Morrissey 1985; Klumpp and McKinnon 1989). In general, reef macroalgae can be broken down into four categories based on morphological and functional characteristics *sensu* Morrissey (1985): large fleshy algae, encrusting calcareous algae, erect calcareous algae and turf algae. Algal turf and cructose coralline algae have also been referred to in the coral reef literature as the epilithic algal community (EAC) (Hatcher 1981; Hatcher and Larkum 1983; Klumpp *et al.* 1987; Scott and Russ 1987; Klumpp and McKinnon 1989) which consists of small, mainly filamentous greens, reds and blue-greens (turf) in addition to encrusting calcareous algae (mainly reds). There are a variety of habitats in reef ecosystems that support algal populations ranging from shallow, often intertidal reef crests and flats, to deep reef slopes. Coral reef macroalgae have been hypothesized to be the main source of the primary production which is cycled through the trophic webs of reef systems (Hatcher 1981; Carpenter 1985). Morrissey (1985) found that turf algae were the most productive, followed by large fleshy algae, erect calcareous algae and cructose coralline algae. Many studies have documented the seasonality of growth and production of macroalgal species associated with coral reefs

The effects of seasonality on reef algae seems to vary between zones. Tsuda (1974), in an investigation of brown algae in Guam, and Hatcher and Larkum (1983), studying the EAC at One Tree Reef, Great Barrier Reef (GBR), found that at very shallow sites, winter peaks in abundance do occur. Tsuda (1974) attributed this peak to the combined effects of desiccation due to daytime spring tides in summer and reduced salinity due to increased precipitation during the summer/fall rainy season. Hatcher and Larkum (1983) correlated the winter bloom in the shallow lagoon to decreased water temperatures. They found that when water temperatures fell below 20°C, algal growth was enhanced, but when temperatures rose above 20°C, the algae senesced. However, they also found that some algae species showed an increased abundance in late summer on the shallow reef crest. Algal biomass also seemed to follow this general trend at One Tree Reef. Hatcher and Larkum (1983) observed an increase in biomass

in the summer on the crest and in winter in the lagoon. Where seasonal temperatures were more stable at deeper sites, they found that algal biomass was more constant throughout the year.

At Heron Reef, GBR, a site adjacent to One Tree Reef, Rogers (1997) observed a higher cover of brown algae during the summer, with a subsequent decline throughout the rest of the year. Green algae at this site appeared to show more variable effects with some species exhibiting higher cover in summer, and some in fall and winter (Rogers 1996). In addition to possible temperature effects, seasonal variation in light intensity may also be a factor. Marsh (1970) found that photosynthesis in samples of calcareous red algae taken from the reef at Eniwetak Atoll, Marshall Islands increased with increasing light intensity. Similar light relationships were found for algae taken from a shallow reef in Curaçao, Netherlands Antilles (Wanders 1976).

At Davies Reef, central GBR, a site further north than Heron and One Tree Reefs, Klumpp and Polunin (1989) found that the density, biomass and net primary productivity of turf algae within damselfish territories was higher in summer (November - March) than in winter (June - August). Similarly, Klumpp and McKinnon (1989) and Polunin and Klumpp (1992) measured the highest net areal and biomass-specific production rates in summer and the lowest in winter in all reef zones at the same site. They correlated this seasonality to reduced irradiance in winter and the response of the algae to seasonal temperature fluctuations, with the highest production coinciding with the highest temperatures. This observed seasonality does not apply to all algal taxa as Drew (1983) found that the highly variable growth rates of two species of the erect calcareous algae *Halimeda* at Davies Reef masked possible seasonal oscillations.

At Tague Bay Reef, St. Croix, Carpenter (1985) found that production of algal communities was higher in the summer than in winter. Total daily production was reduced by 18% between July and October, 26% by November and 30% by December. Carpenter (1985) believed that the decrease in production rates was due to a seasonal decrease in algal biomass, as it also was higher in summer than in winter. The increase in biomass could have been due to increased summer production relative to the amount of algae removed by herbivory (Carpenter 1984). A correlation of both with daylength seems to occur, so that an increase in daylength increases production which, in turn, raises biomass. At a similar site on Tague Bay Reef a year later, in a herbivore exclusion experiment, Carpenter (1986) found that instantaneous productivity rates were generally lower in early summer and highest in the spring and fall. These rates were not correlated with water temperature. However, integrated daily biomass production rates were highest in summer and seemed to result from an increase in daylength, and not from increases in primary productivity (Carpenter 1986). Biomass production was generally lowest during the winter months. The causal relationships appear to be similar to those found in Carpenter (1985).

2.1.3 Whole Reef Productivity

Many studies have been conducted which attempted to measure the total production of coral reefs or of zones within them. These studies did not differentiate between different types of primary producers and thus incorporated algae, corals and phytoplankton. However, the duration of only a few of these allows for seasonal trends to be identified. Since primary production can be used as an index of available energy to coral reef consumers, it is important for modeling purposes, to be able to understand how it changes throughout the year.

One of the first studies to incorporate measurements of reef productivity on a seasonal basis was that of Kohn and Helfrich (1957) in Kauai, Hawaii. They found that July productivity was 10% greater than November productivity. The reefs were autotrophic during both seasons with P/R values of 1.1 and 1.0 in summer and winter, respectively. In an investigation into the productivity of a Florida patch reef, Jones (1963) found that spring (May) and summer (August) productivity were about twice as high as that measured in fall (November) and winter (March). Jones' measurements were taken in water adjacent to a patch reef over a *Thalassia testudinum* bed. He felt that these were representative of the patch reef environment as he found that duplicate samples directly over the reef were not significantly different. His values are extremely low, however, when compared with other reef productivity values, and may therefore represent only phytoplankton production rather than whole patch reef production. Although the investigators in these two studies measured several environmental factors, they did not attempt any correlations with the variable productivity they observed, perhaps due to the short duration of their within-season measurements.

At a patch reef in One Tree Reef lagoon, southern GBR net production appears to increase steadily from a late spring (June) minimum to a peak in the late summer/early spring (March/April), followed by a sharp decline in May (Kinsey and Domm 1974). Respiration seems to follow the same trend, but resulting P/R values are generally lower than 1 (heterotrophic: $P/R \approx 0.7$) in fall and winter, and the reef becomes autotrophic in October to a high P/R value of approximately 1.1 in summer. For the reef flat, identical P/R values for summer and winter are evident, but overall productivity and respiration rates are over two times as large (Kinsey 1977). However, at Lizard Island, a site 9° lower in latitude than One Tree Reef, the reef flat community shows an opposite trend with autotrophy occurring in the winter ($P/R = 1.1$) and heterotrophy in the summer, with $P/R = 0.9$ (Kinsey 1977). Productivity is, however, roughly two times as high in summer than in winter. Kinsey (1977) attributes the observed seasonality at both sites to seasonal changes in light intensity and not to temperature changes. He does recognize the possibility of seasonal temperature effects on the productivity of benthic algae, which may be important to higher latitude reef systems.

Smith (1981) measured production and respiration rates of the coral reefs of the Houtman Abrolhos Islands, off of Western Australia. He found that gross production and respiration were higher

in summer (March) than in winter (September), and that the community P/R ratios were 1.07 in summer (autotrophic) and 0.84 in winter (heterotrophic). These data agree with those of Kinsey and Domm (1974) and Kinsey (1977) for One Tree Reef. Smith (1981) attributed the seasonal rates to varying light levels. At French Frigate Shoals, Hawaii, Atkinson and Grigg (1984) obtained similar results for a reef flat environment. Both production and respiration were about two times as high in summer as they were in winter, although the reef was apparently a net producer throughout the year (P/R = 1.8 in summer and 1.7 in winter). Atkinson and Grigg (1984) suspected that the seasonality in reef metabolic processes was probably the result of seasonal temperature and light level fluctuations. In contrast, Kinsey (1979) found the fringing reef in Kaneohe Bay, Oahu to be a net consumer in both seasons with P/R values of 0.7 in summer and 0.9 in winter. There was, however, marked seasonality in both production and respiration rates.

In his review of the metabolism of coral reef areas, Kinsey (1985) noted that the production and respiration rates for almost all reefs he reviewed showed values two times greater in summer than in winter. He also noted that there seems to be no trends with respect to latitude as one might expect given the greater temperature ranges encountered at higher latitudes. Although no studies have incorporated seasonality into their measurements of total reef production at sites below 14°, seasonal fluctuations in productivity and respiration rates are likely to occur given the uniform nature of the data presented for mid to high latitude reefs, and the observations of seasonal effects on other primary producers, such as seagrasses, at low latitudes.

2.2 Coral Growth Rates

Both live tissue growth and the deposition of CaCO₃ have been measured for many different coral species on reefs throughout the world. Although they are different processes, calcium carbonate accretion which increases the linear extension of the coral skeleton will also increase tissue growth (and the biomass accumulation rate). The phenomenon of density bands forming annually when two different accretion processes occur at different times of the year is well established in the coral literature. High density bands appear to be accreted during times of extreme water temperatures and low density bands are formed during optimal conditions (e.g., when temperatures range between 25 - 30°C; Buddemeier and Kinzie 1976) (Highsmith 1979). In a review of the literature on coral growth, Buddemeier and Kinzie (1976) highlighted its complexity by stating: "Environmental or ecological factors which could influence coral growth are almost unlimited in number; only slightly less numerous are literature references to qualitative relationships between some aspect of growth and environmental factors."

Many studies have concentrated on measuring the growth of corals while disregarding the accretion of density bands. Shinn (1966) showed that linear growth of *Acropora cervicornis* in the Florida Keys was positively correlated with temperature. Growth was highest when temperatures were

between 28 and 30°C and the rate slowed when temperatures fell below 28°C. Shinn (1966) demonstrated this seasonal growth pattern in a graph of growth rate versus temperature which showed two different slopes: one associated with an increase in growth during May when water temperatures rose, and the other reflected a decrease in growth towards the end of summer (September) when water temperatures began to decline. Linear growth of *A. cf. formosa* and *Pocillopora damicornis* on the reefs in the Houtman Abrolhos Islands, Western Australia were similarly correlated with temperature (Crossland 1981). Maximum elongation of these two species occurred during the summer months when water temperatures were higher than during the rest of the year. Crossland (1981) also suspected that light played a secondary role, as the season of maximum growth was also the one with increased light levels in relation to other seasons.

In contrast, Yap and Gomez (1984) found that linear growth was negatively correlated to temperature and daylength for *A. pulchra* in Bolinao, N.W. Luzon, Philippines. Both growth rate and branch initiation were greater during the cooler months from October to February, and growth rate was highest when temperature was at an annual low (26°) in January and February. The reason seemed to be that longer days and clear skies in summer caused shallow water to heat up, which probably stressed the corals (Yap and Gomez 1984).

Bak (1974) found that the growth rate (measured by the change in weight of the coral colony/head) of two species of corals (*Madracis mirabilis* and *Montastrea annularis*) showed positive correlations with the number of hours with full sunlight in Curaçao, Netherlands Antilles. Another species (*Agaricia agaricites*) showed only a weak correlation. All three species exhibited maximum growth in August and two showed minimums in October and one in January (Bak 1974). No correlations were found between growth and temperature or daylength. Gladfelter (1984) found a similar correlation between sun-hours and growth in *A. cervicornis* at Buck Island, St. Croix. She found that calcium carbonate accretion (mean specific accretion times linear extension, $\text{mg} \cdot \text{tip}^{-1}$) showed two peaks; one in winter and one in summer, with a minimum in spring.

Both Highsmith (1979) and Wellington and Glynn (1983) showed that the different density bands characteristic of many corals can be correlated to growth rates. High density bands were shown to be associated with slower growth rates than low density bands in the coral *Porites lutea* at two depth ranges in Eniwetak Atoll (Highsmith 1979). In Pacific Panamá, Wellington and Glynn (1983) have shown that the low density band in *Pavona clavus* has a greater width (linear skeletal extension) and a higher rate of tissue growth. The results of these two studies indicate that the seasonal deposition of low density bands should coincide with the season with the highest formation of coral tissue.

In a study of numerous species of corals which deposit annual density bands taken from 31 localities throughout the Caribbean and Indo-Pacific regions, Weber *et al.* (1975) found a positive correlation between high density bands and water temperature, but not light levels. They suggested that

high density bands are deposited at times of higher than average temperatures. Weber *et al.* (1975) also noted that many coral species exhibit skeletal banding even in places where annual temperature change is minimal. At Eniwetak Atoll, high density bands formed in a number of species when water temperatures were high or declining, from July to January (Buddemeier *et al.* 1974; Highsmith 1979). Since this period coincides with the time of highest average rainfall, from July to November (Buddemeier *et al.* 1974), and assuming that precipitation and cloud cover are correlated, Highsmith (1979) also suspects that high density banding may also be associated with lower light availability. Low density banding shows the opposite pattern: it occurs throughout the remainder of the year, when water temperatures are lower and light availability is higher (less cloud cover) (Buddemeier *et al.* 1974; Highsmith 1979).

In a comparison of 24 reefs, broken into three groups (equatorial, transitional and high latitude) based on their banding pattern similarity in relation to water temperatures and light availability, Highsmith (1979) suggests that high density bands form in response to periods of extreme temperatures and low light availability. Low density bands appear to be produced during times of high light availability and when water temperatures fall within the range of 24 - 29°C. Wellington and Glynn (1983) compared the density banding of *Pavona clavus* between two locations off the Pacific coast of Panamá, one subjected to seasonal upwelling of cold water and the other more stable. Coral in both locations showed consistency with regard to the timing of the deposition of density bands, despite differences in water temperature, and the authors hypothesized therefore that the banding was correlated with light levels. Cloud cover was lowest during the time of low density band formation and Wellington and Glynn (1983) suspected that density band formation may be independent of temperature changes.

2.3 Herbivore Grazing Rates

The food webs of coral reefs rely mainly on the grazing of reef macroalgae (Hatcher 1981; Choat 1991). Despite low biomass, algal communities (particularly turf algae) on coral reefs are among the most productive systems in the sea, due to their extremely high growth rates (Hay 1991). The majority of this production is consumed by various fish and invertebrate grazers (Hatcher and Larkum 1983; Carpenter 1986; Hay 1991) and fish alone have been estimated to consume from half to almost all of algal production (Hatcher 1981; Carpenter 1986; Klumpp and Polunin 1989). The abundances of herbivores on coral reefs are very high with over 60 species of fish and invertebrates (excluding microherbivores) recorded on a single Caribbean reef (Carpenter 1986). Thus, herbivores have a profound impact on reef algal communities and, therefore, on reef primary productivity in general.

A number of studies have shown that the grazing rates of reef herbivores are not constant, and vary seasonally throughout the year. At One Tree Reef, GBR, Hatcher (1981) found that the grazing rates of fishes were highest in summer (27 bites · min⁻¹) and lowest in winter (9.6 bites · min⁻¹). He attributed the change in rates to seasonal changes in water temperature. Further north at Davies Reef,

Klumpp and Polunin (1989) found that the grazing rates of the damselfish *Stegastes apicalis* within its territory in winter were almost half of what they were in summer ($773 \text{ mg C} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}$ and $1433 \text{ mg C} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}$ in winter and summer, respectively). These rates were equivalent to 0.9% of algal biomass and 25% of daily primary production within the damselfish territories in winter, and 1.5% of algal biomass and 38% of the primary production in summer. Farther, the fish ingested 11.1% of its weight per day in winter and 20.5% in summer. Ingestion by the territorial surgeonfish *Acanthurus lineatus* at Davies Reef was $7.5 \text{ gC} \cdot \text{day}^{-1}$ in winter and $14.3 \text{ gC} \cdot \text{day}^{-1}$ in summer (Polunin and Klumpp 1992). Total herbivory by all associated herbivores (fishes and invertebrates) in *A. lineatus* territories accounted for 43% of net primary production in winter and 65% in summer. Although net primary productivity was 120% greater in summer than in winter, grazing increased by 180%, which resulted in the higher proportion of algal production ingested by herbivores in summer (Polunin and Klumpp 1992).

Polunin and Brothers (1989) found that the damselfish *Plectroglyphidodon lacrymatus* on a fringing reef off of southern Papua New Guinea showed a bimodal pattern of daily bite rates over a year. The peaks were strongly correlated with temperature and occurred in April (fall) and December - January (late spring/summer) when water temperatures were high. Carpenter (1986) also found elevated grazing rates to be positively correlated with water temperature. In St. Croix, USVI, he found that grazing intensity was generally high during the summer when water temperatures were high, with a peak in September when herbivorous fish abundance was also at a maximum. Grazing rates were generally lowest in the late fall and winter (Carpenter 1986).

Invertebrates are also important grazers of reef algae, especially in the Caribbean where echinoids have been considered the dominant coral reef herbivores (Berner 1990). Carpenter (1986) has suggested that grazing by *Diadema antillarum* is much more intense than grazing by fishes due to the faster turnover time of algae grazed by the urchin compared with algae grazed by only fishes. Although grazing by *D. antillarum* (+ microherbivores) did not appear to show a strong seasonal pattern, the mean amount of algal biomass removed per day in experimental treatments seemed to be slightly higher in the spring and summer (based on seasonal averages from Carpenter's 1986 data) than in fall and winter.

In moderately exposed habitats in the San Blas Islands, Panamá, grazing by *D. antillarum* was reduced during periods of high wave action which are associated with greater wind speeds in the dry season (January - April) (Foster 1987). Apparently, during these times, the urchins move deeper into shelter sites among the corals to avoid being swept away by waves (Foster 1987).

On Davies Reef, GBR, Polunin and Klumpp (1992) have shown that the various groups of invertebrate grazers associated with *Acanthurus lineatus* territories have higher feeding rates in summer and winter, although the differences appear to be relatively smaller than those observed for fishes. The invertebrate grazers consumed considerably less than associated fish herbivores, which suggests that

fishes in Indo-Pacific coral reef systems may be more important as trophic conduits of primary production than in Caribbean systems.

2.4 Spawning and Recruitment of Reef Fishes

2.4.1 *Spawning*

Almost all reef fish have complex life cycles which involve the release of vast quantities of eggs or larvae into the water column (Sale 1980; Doherty and Williams 1988). Johannes (1978) divided the spawning strategies of coral reef fishes into four categories: migrating spawners, which are generally larger species (>25 cm TL) that aggregate in deeper water and release pelagic eggs; smaller, non-migrating fishes (<25 cm TL), which produce pelagic eggs, but release them well above the reef; demersal egg layers which typically guard their nests; and live-bearers which release their young at an advanced stage. Regardless of spawning type, once released, the eggs and/or larvae go through a pelagic existence which can last from 0 days (for 1 species of damselfish which broods its young) to over 3 months, but typically falls into the range of 3 - 6 weeks (Brothers *et al.* 1983; Victor 1986c; Thresher *et al.* 1989; Wellington and Victor 1989). Once in the plankton, these larvae and eggs are transported passively by oceanic or estuarine currents (Fairweather 1991), often away from reefs. This behavior may appear counterproductive at first glance, as in these open systems (Forrester 1990; Hughes 1990), the organisms must eventually find their way back to suitable settlement substrates either at their place of origin or to other favorable locations. These apparent contradictions will be discussed further below.

2.4.2 *Dispersal/Retention of Eggs and/or Larvae*

Many reef fish undergo extended spawning seasons with certain peaks in spawning activity (Munro *et al.* 1973; Johannes 1978 and refs. therein; Williams *et al.* 1984; Colin and Clavijo 1988; Robertson *et al.* 1988; Lobel 1989). Johannes (1978) reviewed the literature on the spawning behavior of coral reef fish and concluded, among other things, that many species breed during times of the year when winds and currents are at their weakest. This behavior, he suggests, facilitates the retention of eggs and larvae close to reef environments and reduces the risk of their being transported away from settlement habitats. In addition, spawning is common during new/full moons when offshore transport of eggs and larvae on spring tides is greatest. Spawning at this time reduces the risk of eggs and larvae falling victim to the high benthic predation rates associated with reefs. Many species were also found to spawn in the vicinity of nearshore gyres which can serve to retain larvae close to reef settlement areas (e.g. Sale 1970) and may also increase larval food supply by upwelling nutrients (Lee *et al.* 1992; 1994).

Indeed, many of the processes discussed by Johannes (1978) will serve to limit or control the planktonic dispersal or retention of eggs and larvae locally, and will vary from region to region, or even

among individual reefs. Oceanographic processes are believed to be the major controlling factor for the spatial and temporal patterns of both spawning and recruitment (Robertson *et al.* 1988), although larval behavior may also be important for recruitment (Victor 1986b; Richards and Lindeman 1987). In addition, Meekan *et al.* (1993) have found that the timing of spawning may greatly influence the annual temporal variability in recruitment events. Hensley *et al.* (1994) found that the bluehead wrasse (*Thalassoma bifasciatum*) in Puerto Rico spawned at sites and at times which increased the chances of their eggs being transported off the reef platform. They hypothesized that this phenomenon reduced the risk of egg predation by reef associated planktivores (i.e., Johannes 1978). Both Hunt von Herbing and Hunte (1991) and Appeldoorn *et al.* (1994) suggest that current speed may influence the site selection and timing of spawning to maximize this effect. However, Appeldoorn *et al.* (1994) did not find that transport of the eggs off the shelf occurred and instead, eggs appeared to remain within the vicinity of the reef, or at least inshore where predation pressure from reef, seagrass and mangrove associated predators is high. Thus, these inshore populations of bluehead wrasse probably do not survive to contribute to future populations (Shapiro *et al.* 1988).

According to Bakun (1996), three elements are necessary for the successful spawning and subsequent recruitment of a cohort of juveniles which involve both spatial and temporal patterns. The first is enrichment where food for the larvae becomes abundant. The second is the concentration of this food and the third is the retention of the larvae within this food patch. Gyres meet all three criteria for Bakun's 'fundamental triad': they enrich prey supply to the larvae by upwelling cool, nutrient-rich water which promotes plankton growth, they concentrate the plankton in the center of the gyre where nutrients are being brought to the surface, and retain larvae within their elliptical currents for a good proportion of their larval existence. The potential for gyral systems to retain larvae within localized areas was suggested by Johannes (1978). In the Lower Florida Keys, the Tortugas Gyre exists for approximately 1 month periods during the year (Lee *et al.* 1992; 1994). These authors suggest that the gyre has the potential to retain larvae of reef organisms for their entire planktonic existence, increase their food supply by upwelling cold, nutrient rich waters in its center and to facilitate their local recruitment when combined with onshore Eckman transport. Lee *et al.* (1994) point out that since there is a local spawning occurrence of mutton snapper (*Lutjanus analis*) within the vicinity of the gyre in May and June, co-occurrence of the two events may serve to retain larvae within the area and facilitate local recruitment, a hypothesis still to be tested. Sale (1970) found that larval acanthurids were retained within an offshore gyre southwest of Oahu. He believes that these fish would pass the island every 5 - 6 days where they could potentially settle onto the reefs. Lobel (1989) correlated the spawning in Hawaiian reef fishes to seasonal cues (proximate causes such as daylength and temperature) and seasonal oceanographic conditions which can serve to retain larvae within the archipelago or near a given island (ultimate or evolutionary causes). Both he and Walsh (1987) observed that many reef fish had peak spawning times

from January to July, which corresponds to the season with the highest wind velocities that cause the generation of ocean eddies around the islands. One of these eddies was hypothesized to entrain larvae and concentrate their food (Lobel and Robinson 1986). In an analysis of previous oceanographic data (surface drift bottles), Lobel (1989) found that the probability of loss of surface drifting larvae was lowest during the spawning season. He concluded that the oceanographic data support the hypothesis that these fishes spawn during the season when their larvae will have an increased chance of survival and recruitment into the Hawaiian reef system. He also hypothesized that the timed spawning and gyres could possibly be a mechanism for the high degree of endemism associated with Hawaiian reef fish. This hypothesis is further supported by the observations of Stimson (1990), who believes that the timing of spawning in *Chaetodon miliaris*, an endemic butterflyfish, determines the time of recruitment. However, Lobel and Robinson's (1986) hypothesis lacks the biological data to support it since they do not describe any reef fish larvae being caught in this eddy (Leis 1991).

Temporal coupling of spawning and recruitment in damselfish (Pomacentridae) has been found in both Panamá (Robertson *et al.* 1988) and on the GBR (Meekan *et al.* 1993). Lunar patterns in reproductive output and recruitment have been found in both studies. By observing spawning and egg guarding behavior and subsequently monitoring settlement for 3 years in *Stegastes partitus*, Robertson *et al.* (1988) showed correlations between both activities, but not in the magnitude of either event. Similarly, Meekan *et al.* (1993) monitored spawning output and recruitment for *Pomacentrus amboinensis*, but also measured larval supply using light traps at Lizard Island, northern GBR for two summers (spawning and recruitment season). They also found that the spawning patterns greatly influenced larval supply and the timing of recruitment, but not its magnitude. However, they found that larval supply and recruitment were generally more strongly correlated to each other than they were to patterns of spawning. Both Robertson *et al.* (1988) and Meekan *et al.* (1993) speculated that this difference in correlation, and the differences in the magnitude of settlement events, could be a result of planktonic processes acting on the larvae. Meekan *et al.* (1993) also point out that confounding difficulties occur with the interpretations of coupling between spawning and recruitment when the sources of the larvae are not local or are unknown. If the larvae derive from upstream sources, and the spawning patterns of these fish differed with those measured on the downstream reef, coupling might not be detected. However, short larval durations and semi-enclosed systems would increase the chances of self-recruitment and the detection of coupling (Meekan *et al.* 1993).

In contrast, Robertson (1990) and Robertson *et al.* (1993) found a relationship between seasonal peaks in reproductive output and subsequent recruitment for only one (in one study, but not the other) of several species of reef fishes from both the Pacific side (Robertson 1990) and the Caribbean side of Panamá. They found that although all species showed seasonal cycles of recruitment, seasonality in spawning output was weaker. Robertson *et al.* (1993) concluded that oceanographic processes acting on

the larvae of these species control their subsequent recruitment strength. If coupling does exist, then seasonal environmental stresses can affect the reproductive output of these fishes so that they are forced to spawn when larval survival is not optimal (Robertson 1990), which would increase the variability in annual settlement pulses.

In Barbados, Cowan and Castro (1994) have found that local retention of larvae exists without the formation of gyres. They chose Barbados to test for local retention because of its upstream location within the Caribbean region with no potential distant sources for replenishment of reef fish. These authors did not find a leeward eddy as expected, but instead found that local currents were controlled by the local topography and that reef fish larvae followed this flow, and thus may be retained locally. If nearshore circulation and/or tidal excursions influence the spawning of local reef fish populations, as suggested by Robertson *et al.* (1988) and Hunt von Herbing and Hunte (1991), then these events may be coupled with fish behavior to facilitate transport of eggs/larvae away from reefs and/or settlement pulses of recruits from the offshore current to the reefs (Cowan and Castro 1994).

Doherty (1983a) observed seasonal spawning in two species of damselfish (Pomacentridae) on One Tree Reef, GBR and found that both species bred during the warmest and calmest months of the year (October - March). In contrast to Johannes (1978), Doherty hypothesized that the observed seasonality probably correlates to times of better ocean survival of the larvae and not to times of weaker offshore currents. Ocean survival is greatest when patches of food for larvae are not mixed by wind-generated turbulence (Lasker 1975). Such situations occur in summer on the GBR with the creation of a shallow thermocline (Wolanski 1981) which allows food particles (plankton) to build up and remain stable (Bakun 1996). Thus, summer spawning might be an adaptation to increase larval survival by increasing their food availability (Doherty 1983a).

Also, with regard to larval retention near natal reefs, Williams *et al.* (1984) suggest that the spring/summer spawning, which occurs for most species of reef fish and invertebrates on the GBR, maximizes the transport of eggs and larvae away from their home reefs. In an investigation of the current patterns of the central region of the GBR, they concluded that the majority of planktonic eggs and larvae will be transported off the reefs and into the main shelf current, and will travel tens to hundreds of kilometers away from their natal reefs in a southward direction during summer. In contrast to Johannes (1978), who suggested that reef fish spawn when currents are at their weakest, Williams *et al.* (1984) found that the summer spawning season coincides with the time of the strongest southward currents. Thus, most of the recruitment in southern reefs arrives from the north while most of the eggs and larvae in the north are transported south. Downstream recruitment, such as occurs in the southern portions of the GBR, is likely to explain how some isolated areas receive recruits. A similar situation occurs in Bermuda (32°N) which is probably fed by larvae spawned in the Caribbean, Florida and the Bahamas via the Gulf Stream and at Rottneest Island (32°S), off Perth, Western Australia, which receives its larvae

from the Houtman Abrolhos via the Leeuwin Current (Hutchins and Pearce 1994). These observations agree with the hypothesis of Barlow (1981) which states that reef fish have been selected to disperse eggs and larvae because of the patchiness of their environment and the fact that most of these fishes do not migrate between patches. Doherty *et al.* (1985) suggest another alternative; this states that larval dispersal could be due to the extreme patchiness and unpredictability of their survival in the pelagic environment. They reason that these species have been selected to disperse large numbers of progeny in order to “spread the risk of failure among members of a cohort” (Doherty *et al.* 1985). Small demersal fishes, such as *Pomacentrus wardi*, studied on the GBR, could have a genetic stock which encompasses 15° of latitude and has a distribution of “perhaps a million local breeding units on several thousand coral reefs” (Doherty 1987). Doherty (1987) sums up the potential reason for spreading the risk by stating, “the success of a cohort of larvae and its eventual destination depend on a long chain of events which must include a great deal of chance.” However, if larval durations are relatively short (<15 days), localized sub-populations could exist (Thresher *et al.* 1989) via self-recruitment. Nonetheless, survivorship during the brief pelagic duration of these fishes will be largely unpredictable, and both of these hypotheses could still apply.

2.4.3 Patches and Their Significance

Patches of larvae in the plankton (Victor 1984; Doherty 1987) are believed to cause the pulses of recruitment events that many reefs experience during the recruitment season (Williams 1983; Doherty and Williams 1988). One such patch, which measured at least 6 km across and contained many species, was found near Myrmidon Reef, GBR (Williams and English 1992). These authors speculate that it was caused by a meso-scale eddy. The observations of Victor (1984) of a large, simultaneous recruitment event of the bluehead wrasse of different ages in Panamá, over an area which covered approximately 1000 km², indicate that these patches can contain many cohorts of larvae spawned over the period of several weeks. The multispecificity and multi-cohort characteristics of these patches indicate that some mechanism, either oceanographic or behavioral, is acting to aggregate larvae during these times. This patch formation, and their subsequent transport over suitable settlement sites, probably cause the seasonality of recruitment events observed at so many reefs throughout the world.

In a series of studies on the larval supply from Exuma Sound to the Lee Stocking Island area of the Great Bahama Bank (Shenker *et al.* 1993; Thorrold *et al.* 1994a,b,c), it was found that patches of larvae probably exist. These studies, done both in winter and summer, used a series of moored plankton nets in tidal passes and noticed significant pulses of larval fishes moving in both temporal and spatial scales consistent with the existence of patches. They found that movements of most larvae taxa correlated with various meteorological and hydrographic phenomenon, although they were not the same for all fishes. For example, Shenker *et al.* (1993) found that in the winter of 1991, the movement of

Nassau grouper (*Epinephelus striatus*) occurred during two storm events which increased onshore current flow and accounted for 86% and 10% of the species' total recruitment. In 1992, these pulses did not occur and Nassau grouper numbers were much lower (Thorrold *et al.* 1994c). Stochasticity with regard to meteorological and hydrographic events could help to explain the high interannual variations in recruitment associated with most reef fishes throughout the world (Shenker *et al.* 1993; Thorrold *et al.* 1994b). These authors also found that, in contrast to the winter of 1991 when fish larvae were concentrated near the surface (Shenker *et al.* 1993), vertical distributions were greater in 1992 (Thorrold *et al.* 1994c). The majority of fishes were caught in flood tides on nights during new moons with low lunar intensity in all years and seasons (Shenker *et al.* 1993; Thorrold *et al.* 1994a,b). Other studies have shown that reef fishes settle during dark nights (Victor 1983; 1984; 1986a; McFarland *et al.* 1985; Robertson *et al.* 1988). The conclusion reached by Shenker *et al.* (1993) and Thorrold *et al.* (1994a,b,c) is that larval behavior can facilitate their onshore transport by vertical migrations into favorable currents during optimal periods (i.e., dark nights). In addition, the numbers of larvae captured during the summer was much higher than both of the winter samples (Thorrold *et al.* 1994b), which indicates that spawning peaks in this area in the spring.

2.4.4 Spawning Cues

Most species of fishes and invertebrates studied in Jamaica spawned throughout the year, or at least for extended periods, and maximized their seasonal output during a few months which coincided with the calmest periods of the year (Munro 1983c; contributions in Munro 1983a). Spawning periods generally were highest from January to May with a peak in March-April and a secondary rise in spawning activity in September-October (Munro 1983b; contributions in Munro 1983a). Munro *et al.* (1973) suggest that the two observed peaks in spawning of Jamaican fishes might be timed so that subsequent recruitment of juveniles coincides with the annual peaks of primary productivity observed in late spring and fall by Beers *et al.* (1968). This mechanism, if true, would serve to increase the food supply, and probably growth and survival, of recruits. Russel *et al.* (1977), working in the GBR, suggested the same thing might occur there, where maximum juvenile settlement appears to occur two months prior to the time of greatest primary productivity. They suggest that growth rates will be optimized as food supply becomes increasingly abundant. Beers *et al.* (1968) also found that primary productivity was relatively high during summer in Barbados when settlement of the bluehead wrasse was greatest (Hunt von Herbing and Hunte 1991), which suggests the same mechanism there as well. In addition, McFarland *et al.* (1985) in an investigation of the recruitment patterns of French grunts (*Haemulon flavolineatum*) on Tague Bay Reef, St. Croix, United States Virgin Islands (USVI), found that although settlement does occur throughout the year, the number of postlarval fish showed two peaks of different sizes during two seasons. The larger one occurred in the spring (May/June) and the second,

Table 2. Spawning times for some species of serranids in the western Atlantic. Spawning was either directly observed or inferred from gonadal samples.

Species	Region	Spawning Times	Peak Times	Source
Jewfish (<i>Epinephelus itajara</i>)	Gulf of Mexico	June-December	July-September	1
Red hind (<i>E. guttatus</i>)	Puerto Rico		January-February	2, 3, 4
Snowy grouper (<i>E. niveatus</i>)	Lower Florida Keys	April-July		5
Tiger grouper (<i>Mycteroperca tigris</i>)	Puerto Rico	January-April		6
Gag (<i>M. microlepis</i>)	South Atlantic Bight	March-April		7
"	Gulf of Mexico	December-May	February-March	8
Scamp (<i>M. phenax</i>)	South Atlantic Bight	April-August	May-June	9
Sand perch (<i>Diplectrum formosum</i>)	Gulf of Mexico	all year	April-June	10

Sources:

1 Bullock *et al.* (1992); 2 Colin *et al.* (1987); 3 Shapiro *et al.* (1993); 4 Sadovy *et al.* (1994); 5 Moore and Labisky (1984); 6 Sadovy and Domeier (1994); 7 Collins *et al.* (1987); 8 Hood and Schleider (1992); 9 Matheson *et al.* (1986); 10 Darcy (1985).

smaller peak occurred in the fall (October/November); the same times as high productivity on Jamaican reefs (Beers *et al.* 1968).

Because of their commercial importance, groupers (Serranidae) have been particularly well studied. Groupers generally aggregate to spawn, and thus peak spawning is limited to a few weeks per year (e.g., Sadovy *et al.* 1994). Thompson and Munro (1978) and Munro (1983b) found that spawning occurs from December to April in eight species of serranids in Jamaican waters and most takes place in February and March (Munro *et al.* 1973). Shapiro (1987) reviewed the literature on grouper spawning, and from the information he presented, it is clear that the potential to spawn, as measured by the period with ripe gonads, lasts for an extended period of time, but peak spawning occurs for only 1 - 2 months during that time (see Table 2). He also concluded that there appear to be no definitive causes which can explain the timing of the spawning events. However, Colin (1992) and Tucker *et al.* (1993), in reviews of the known spawning times of *Epinephelus striatus* in the Caribbean region, found that the species tends to spawn when water temperature approaches 26°C (possible proximate cues of Lobel 1989). The data presented are remarkably consistent, despite the broad geographic scope of the studies they reviewed. In general, the spawning of the Nassau grouper occurs earlier in the year at lower latitudes and later in the year at higher latitudes, presumably due to the geographical differences in seasonal temperatures. This temperature-related pattern does not seem to apply to all species of serranids as Munro *et al.* (1973) found that the graysby (*Epinephelus cruentatus*) in Jamaica spawned when the water temperature was approximately 26°C and Nagelkerken (1979) found that spawning occurred when temperatures were between 27.4 and 28.4°C in Curaçao.

In contrast to the above hypotheses, Colin and Clavijo (1988), in an investigation of the spawning activity of 26 species of reef fish off Puerto Rico, found no correlations between peak spawning times and oceanographic conditions. Like the fish of Jamaica (Munro *et al.* 1973), the fish of Puerto Rico had extensive spawning seasons with peak activity in the winter, but these authors suggest

that the timing of the migrations to the shelf edge and the subsequent spawnings they observed, could be an adaptation developed during the last glacial period when sea levels were lower and shallow shelf habitat was virtually non-existent. During the glacial period, the shelf edge habitat was the only habitat available, and they hypothesize that this is the reason that fish aggregate there.

2.4.5 Recruitment

2.4.5.1 Recruitment Hypotheses

It is perhaps relevant to discuss some of the issues which have arisen over the last 25 years and have served to drive the study of coral reef fish recruitment. Recruitment, in ecological terms, is defined as the addition of a new cohort of juveniles to a population (Sale 1990) or the abundance of age 0+ fish resulting from settlement (Doherty and Williams 1988). Since most coral reefs are not self-recruiting, with some exceptions (see above), the regulation of their populations must occur during or after recruitment (Doherty 1983b). The importance of understanding how recruitment and subsequent post-settlement processes affect reef fish abundance and community structure has been noted by all researchers in this field of study (see review by Doherty and Williams 1988 and reviews in Sale 1991). Many hypotheses have arisen which attempt to explain the population dynamics of coral reef fish. Doherty (1983b) and Doherty and Williams (1988) discussed three which are outlined below:

- 1) Single-species equilibrium hypothesis. This hypothesis assumes that, if the carrying capacity of the environment is stable, then the population dynamics of each species will be governed by density-dependent factors and that competition by species for shared limiting resources is unequal (competitive exclusion and niche partitioning) (Smith and Tyler 1972; Gladfelter *et al.* 1980; Ogden and Ebersole 1981).
- 2) Multispecies equilibrium hypothesis. Also termed the 'lottery hypothesis' by Sale (1978), this model also assumes that resources are limited, but for several competing species, instead of just one. Sale explains that coexistence occurs because individuals can regulate the recruitment of all competing species, and that as space is made available due to mortality of some fish within the population, this space is quickly filled by stochastic recruitment events.
- 3) Nonequilibrium hypothesis. In this model, densities of reef fishes are assumed to be below carrying capacity and are controlled by external forces. Thus, reef fish abundances are governed by two opposing phenomenon: recruitment adding fish to the population and mortality removing them. Important sources of mortality which could keep populations below carrying capacity are predation (Talbot *et al.* 1978; Hixon and Beets 1993) and

environmental processes, such as cold temperature events (Bohnsack and Talbot 1980). The densities of fish will vary over time unless recruitment and mortality rates are constant.

Both 1 and 2 assume that reef environments are saturated and, therefore, stable and at carrying capacity which is in contrast to 3. These hypotheses all generate testable predictions which will be discussed below.

If one 1 or 2 are correct, one would expect to find that the number of recruits/post-recruits surviving would be inversely related to the density of conspecifics or other competitors present at the time of settlement (Doherty 1983b; Jones 1991) in the case of 1 and 2, and to the total amount of suitable substrate not already occupied by conspecifics or other competitors in the case of 2 (Jones 1987b; 1991). Hypothesis 3 predicts that there will be no evidence of density-dependent effects after settlement (Doherty and Williams 1988), and that changes in populations and age structure will reflect recruitment variation (Jones 1991).

2.4.5.2 Density-Dependent Recruitment

In the past it was assumed that due to the complexity of interactions and the diversity of organisms in coral reef ecosystems, reef fish assemblages, and indeed all reef-associated communities, were resource-limited (Smith and Tyler 1972; Sale 1978; reviewed in Doherty and Williams 1988). In a review of the reef fish literature, Sale (1980) found that many researchers concluded that the two most limiting resources are food and space. Most of the support for density-dependent recruitment concentrates on correlations between these resources and settlement parameters.

Although many researchers have dismissed the hypothesis that recruitment can be limited by the density of resident (all fish already settled or adults) conspecifics or other competitors (Jones 1991), a few studies have succeeded in identifying density-dependent effects. Hunt von Herbing and Hunte (1991) found that spawning of *Thalassoma bifasciatum* was highest during the spring and summer months on several reefs in Barbados and that subsequent recruitment peaked in the summer. They found that the densities of bluehead wrasses greater than 30 mm were greatest in December and January, declined during the post-recruitment period (January - May) and then rose again during the summer. They attribute this winter/spring decline to density-dependent post-recruitment mortality and not to migration out of the study areas.

Several studies have investigated the population dynamics of gobies and blennies and found density-dependent effects. Forrester (1995) examined the survival of the bridled goby (*Coryphopterus glaucofraenum*), a territorial, short-lived species, in the British Virgin Islands by manipulating densities which encompassed the natural range that was established from prior censusing. He found that there was a strong negative relationship between the recruitment of juveniles and the density of residents. Forrester

(1995) also found that adult survival was reduced at higher densities, but that their growth was not. He, therefore expects that the limiting resource was not food availability, and he attributed apparent density-dependence to a shortage of shelter sites. Forrester (1995) agrees with Shulman's (1984) conclusion that because of shelter limitation at high densities, recruits and adults become more susceptible to predation and their mortality is greatly increased. The suppression of settlement due to density-dependent effects for this species will likely override the influence of the supply of larvae, and hence this population probably does not reflect the relative abundance of potential recruits from the plankton (Forrester 1995). Although Forrester's study did not measure seasonality of recruitment, the bridled goby, in Barbados, was found to settle primarily in the spring (Sponaugle and Cowen 1994). The work of Forrester (1995) suggests that if seasonal pulses in recruitment exist for the British Virgin Islands bridled goby populations, their effects on density and total population size are likely to be dampened by post-settlement processes.

Hunte and Côté (1989) investigated recruitment hypotheses by monitoring the characteristics of both pre- and post-recruitment populations of the redlip blenny (*Ophioblennius atlanticus*), a small territorial herbivore, which, in Barbados, exhibits peak recruitment in May. Adults defend larger territories than juveniles, and the authors assumed that the number of adults would be an index of available space. Recruitment was apparently negatively correlated with the total number of adults, which may imply some space limitation that might increase with increases in the density of adult blennies. They found that recruit mortality was correlated with the number of recruits and the total number of blennies present. This led them to conclude that the mortality of the recruits may have been density-dependent. Following the May recruitment pulse, the mean territory size of adult fishes was reduced by 50% from pre-settlement size. In addition, territory size, which was not correlated to the total length of adults before recruitment, became highly correlated with adult length after settlement of juveniles. Also, aggression (monthly mean rate of chases) was most common during the post-recruitment period and was significantly correlated with the density of recruits and the total blenny density. These results also imply density-dependence, as space appears to be limiting. Most recruitment occurred when space was most available on the reef, in May, and although it may be coupled with the spawning period of redlip blennies, Hunte and Côté (1989) believe that the relationship is not causal, but that it relates to the high mortality rate of adult blennies throughout the year. They found that the mortality rate was relatively constant, and the numbers of residents on the reef decreased steadily during 5 of the 8 months that they monitored the population. A rise in total numbers of adults, in June, they believe, indicates that the recruits which settled in May began to mature at this time. Therefore, in terms of total population size, good spring recruitment may have a substantial influence on the redlip blenny with summer peaks in density, and subsequent declines during the rest of the year. This implies that the intensity of the recruitment pulses can influence the total density of the population regardless of density-dependent

effects regarding space. Hunte and Côté (1989) caution against categorizing such a species as 'recruitment-limited' or 'space-limited' and instead suggest that both processes may be acting on different temporal scales.

Some density-dependent effects have been found for larger fish from a variety of families, including Pomacentridae, to which the non-equilibrium model has been frequently applied (see below). In a study of the recruitment and post-settlement survival of two planktivorous damselfish (*Pomacentrus amboinensis* and *Dascyllus aruanus*) which show peak settlement rates during January and February (Jones 1987a) at One Tree Reef, GBR, Jones (1988) found weak negative effects of density on *D. aruanus*, but positive effects of density on *P. amboinensis*. However, density had less of an effect on survival than coral substratum type: both species were found to survive better in *Pocillopora damicornis* when compared to *Porites* sp. substratum.

A stronger density-dependent relationship was found for *Chaetodon miliaris*, a non-territorial planktivore, in Kaneohe Bay, Oahu. Stimson (1990) studied the recruitment of *C. miliaris* to patch reefs and also censused the populations throughout the year for seven years. He found that recruitment generally occurs from April - June during new moon periods and that there is a steady rate of mortality outside of the recruitment season which causes corresponding density per reef to fall. Consequently, summer population densities are the highest per year and the lowest are reached just prior to the recruitment season. Due to differences in the rates of mortality between reefs, and to trap fishing, pre-settlement densities on different reefs varied such that density-dependent effects could be identified. Recruitment was inversely correlated with initial density of residents and settlement increased on those reefs affected by trap fishing, which had removed some residents (Stimson 1990). The mechanisms for this phenomenon are unknown.

Hunt von Herbing and Hunte (1991) found that spawning of *Thalassoma bifasciatum* was highest during the spring and summer months on several reefs in Barbados, and that subsequent recruitment peaked in the summer. They found that the densities of bluehead wrasses greater than 30 mm were greatest in December and January, declined during the post-recruitment period (January - May) and then rose again during the summer. Mortality of recruits during the post-recruitment period was both correlated to pre-recruitment population densities on the reefs and the recruitment strength. They attribute this winter/spring decline to density-dependent post-recruitment mortality and not to migration out of the study areas. The results suggest that strong density-dependent effects influence the population dynamics of the bluehead wrasse in Barbados and that these fish are near carrying capacity (Hunt von Herbing and Hunte 1991).

A study by Robertson (1988a) in Caribbean Panamá showed that recruitment variability does not have a large effect on the population size of the queen triggerfish (*Balistes vetula*) when compared to other affects. A huge recruitment event occurred in April 1985 that was 50 - 100 times greater than in

any other year measured, but only a 1.5 fold increase in the adult population resulted from the event, and the species remained uncommon (Robertson 1988a). The poor population response of the queen triggerfish to this large recruitment event implies that some factor(s) affects post-recruitment survival (such as lack of suitable shelter sites and the resultant competition for them).

2.4.5.3 Density-Independent Recruitment

Much of the original work which has supported the non-equilibrium model of fish population dynamics came from studies of damselfishes (Pomacentridae) (e.g., Williams 1980, Doherty 1981; 1983b; Robertson *et al.* 1981) and wrasses (Labridae) (e.g., Victor 1983; 1986a). These studies show that resources are generally not limiting and that future population sizes should track trends of recruitment. However, these studies were limited to small spatial scales (i.e., patch reefs) and relatively short temporal scales (i.e., less than the life span of the fishes studied) and have received much criticism as a result (Jones 1987a,b; 1990). Jones (1991) suggested that studies need to encompass many spatial scales, because different processes may work on different scales and, therefore, might not be detected if only one is considered. The original studies mentioned above have all been reviewed in Doherty and Williams (1988) and I will try to restrict my discussion to studies published after that review appeared.

A large scale project was initiated in 1981 in the Capricorn-Bunker Group, a region of reefs within the southern GBR. The study stemmed from the expansion of standardized recruitment surveys which were being conducted at One Tree Reef to encompass six other reefs within 70 km (Doherty and Fowler 1994a). The study spans both large spatial, as well as temporal scales (9 years). Some preliminary results from this study are presented for labroids (Labridae and Scaridae: 2 years) from lagoon sites (Eckert 1984), 62 spp. from 13 families from reef slope sites (1 year), 76 spp. from 11 families (1982) and 86 spp. from 12 families (1983) from lagoon sites (Sale *et al.* 1984) and *Pomacentrus wardi* (Pomacentridae: 6 years) from lagoon sites (Doherty 1987). These studies also outline the general sampling methods used which apply to later studies (i.e., Doherty and Fowler 1994a,b) which consisted of censusing post-recruitment densities in April, after the settlement season. Eckert (1984) explains that April was chosen because the recruitment season had ended, many fishes, such as labroids and pomacentrids (Williams 1980), have relatively high mortality in their first 3 months following settlement so that by April, most early mortality had already taken place, and recruits were still small enough to be distinguishable from older individuals. This method has been shown by Williams *et al.* (1994) to be a robust sampling technique to determine recruitment patterns of most fishes they studied on the GBR, and Sale *et al.* (1984) suggest that, depending on the species, from 45 to 75% of all fish which settled in their sampling sites during the recruitment season were detected by this technique.

From the annual census data collected, a clear picture of year-class strength should be evident in the abundances of older fishes if the non-equilibrium hypothesis is to be supported. In 1989 10 patch

reefs from each of the seven lagoons were defaunated using Rotenone (Doherty and Fowler 1994a,b). An aging technique (reviewed by Victor 1991) was used to estimate the ages of individuals of *P. moluccensis* and *P. wardi* to obtain the age structures of their populations. It was found by Doherty and Fowler (1994a,b) that the recruitment records were well preserved in the age structures of the populations of both species which supports the non-equilibrium hypothesis that the population dynamics are a reflection of recruitment variability. The evidence listed by Doherty and Fowler (1994b) include: "correlations at the reef scale pooled across years; correlations between final and initial year-class size within individual reefs; and the presence of dominant cohorts in the age structures still detectable after a decade or more of mortality." In 1979, Williams (1983) noted a large pomacentrid recruitment event at One Tree Reef (one of the seven reefs in this study). Remarkably, this large recruitment event was preserved at both One Tree Reef and nearby Wistari Reef in the abundances of age 10+ *P. moluccensis* caught in 1989 which made up 12% and 20% of the standing stocks of these populations, respectively, despite the contributions of 14 other age classes (Doherty and Fowler 1994a,b). Williams (1983) also showed that the 1980 recruitment event at One Tree Reef was very small. This pattern is also evidenced in the age structures of the populations at One Tree and Wistari Reefs (Doherty and Fowler 1994a). The linear trend between recruitment and year class strength identified by these authors is suspected to derive from the constant mortality schedule of these fishes after their first few months on the reefs (Doherty and Fowler 1994a,b), and the similar rate at which the recent four year classes decline in abundance, indicates the density-independence of their mortality (Doherty and Fowler 1994a).

They conclude that the abundances that were observed of *P. moluccensis* and *P. wardi* on the seven reefs sampled support the non-equilibrium hypothesis and resulted from variable recruitment events interacting with density-independent mortality. Moreover, Doherty and Fowler (1994b) believe that the monitoring of recruitment and the forecasting of future abundances can be achieved, and that this could be useful for fisheries management, a suggestion with which many fisheries scientists would disagree (D. Pauly, UBC Fisheries Centre, pers. comm.).

Milicich *et al.* (1992) studied the relationship between larval supply and recruitment for three species of pomacentrids at Lizard Island, northern GBR. Utilizing both light traps to catch pre-settlement larvae and weekly visual surveys of new recruits to artificial patch reefs during the summer recruitment season, they found that larval supply and recruitment were highly correlated over two years at the whole reef scale. This presents potential evidence that recruitment patterns may be induced even before settlement and post-settlement processes have occurred. These correlations were present despite the high mortality that damselfishes on the GBR have been shown endure during their first week of benthic life (Doherty and Sale 1985), which suggests that larval supply may have long-term consequences on the abundance and demography of the populations of these fishes (Milicich *et al.* 1992). These results, they claim, are good support for the non-equilibrium hypothesis.

In order to test effects on juvenile demography of *Dascyllus aruanus*, a small, social planktivorous pomacentrid on One Tree Reef, southern GBR, Forrester (1990) manipulated juvenile densities on replicate and natural habitats in the presence or absence of adults during the summer recruitment season and monitored them for a series of interactive effects. These included initial recruit density, presence of adults, and he also supplied additional food to test its effects on the growth, survival and maturation time of the recruits. Mortality of recruits was highest at high densities in the absence of adults (Forrester 1990). This might suggest potential density-dependent effects, but at the same density of recruits with adults present, survival was greatly enhanced. Jones (1987a) found similar effects on this species at One Tree Reef, but his correlations were weaker. The beneficial effect of the presence of adults was thought to be related to predation since adults were found to swim farther away from cover than juveniles (Forrester 1991), and thus detect predators at greater distances. At one of his sites, Forrester (1990) found that mortality was significantly higher than at the others, and speculated that proximity to contiguous natural reef increases the risk of larger reef-associated piscivores preying on *D. aruanus*. Food limitation was deemed to have no effects on the survival of recruits as supplemental feeding did not increase post-settlement abundances. The results indicate that, because initial recruit densities were preserved at the end of the experiment, these populations reflect the level of recruitment. However, Forrester (1990) cautions against accepting this hypothesis because of the short duration of the experiment and the fact that it only measured effects on one cohort of fish.

Victor (1983; 1986a) found that the recruitment of *T. bifasciatum* to the reefs of the San Blas Islands, Panamá was highest from August - December and was not reflective of their spawning patterns, since spawning occurs throughout the year (Warner and Robertson 1978). Post-recruitment mortality was apparently not density-dependent as the densities of adults was directly proportional to the densities of recruits. Victor speculates that if juvenile mortality rates are density-dependent, then the adult population size would most likely be stable and not reflective of settlement patterns. On the other hand, if juvenile mortality is not density-dependent, then recruitment patterns would determine adult population size (Victor 1986a). The latter seems to be true of the reefs he studied in Panamá while the former is more reflective of the bluehead wrasse populations in Barbados (Hunt von Herbing and Hunte 1991; see above). Hunt von Herbing and Hunte (1991) attributed the difference in population regulation to higher densities of blueheads in Barbados.

2.4.5.4 Density-Dependent and Seasonal Growth

The growth of a cohort of fish after they settle during their recruitment season is very important in determining total population biomass. When newly settled, individuals are small and contribute little, in terms of mass, to the entire population. Only when they gain biomass through growth do they make a significant contribution to their population. Thus increases in biomass associated with the recruitment

season, probably have a time lag of a few months, by which time the recruits have grown large enough to augment the population biomass. Although many studies have concluded that reef fish populations are not limited by density-dependent processes, density-dependent growth of juveniles can potentially have great effects on their structure (Jones 1987b; 1988; 1990; 1991; Forrester 1990; Kerrigan 1994). A number of studies have documented density-dependent growth in planktivorous pomacentrids from the GBR. Working with *P. amboinensis*, Jones (1987a,b; 1988) found that intraspecific competition reduced the growth rates of juveniles. Late recruits grew more slowly in the presence of those which had settled earlier in the summer recruitment season (Jones 1987a). Competition between juveniles also reduced the growth of age 0+ *P. amboinensis*, although this effect was weak in one study (Jones 1987b), but stronger in another (Jones 1988), and as these fish approached the age of 1 year, the densities of adults present reduced their growth: thus, the effect was apparently density-dependent (Jones 1987b). Also, significantly more 0+ year and 1+ year fish reached maturity in the absence of adults, but seemed to be independent of initial juvenile density. In the study by Forrester (1990) presented earlier, it was also found that the growth of *D. aruanus* was suppressed at higher densities of both juveniles and adults. The time to maturation was thus affected because maturity is size-dependent.

The mechanisms involved in density-dependent growth appear to be related to food density, as implemented in EcoSim (see Walters *et al.* 1997 and Section 5.4). Supplemental feeding has been shown to increase the growth rates of juvenile *D. aruanus* (Forrester 1990). Dominance hierarchies are apparently established in planktivorous damselfishes (Forrester 1991). In *D. aruanus*, Forrester (1991) found that, despite higher feeding rates in smaller fishes, they were generally ranked lower in the dominance scheme and received smaller prey of less animal matter than larger, higher ranked fish. In addition, larger fishes fed further in the water column and gained first access to the food which drifted by the group on the currents. Kerrigan (1994) measured the biochemical compositions of juvenile *P. amboinensis* in both the field and laboratory, and found that dominant and well-fed fish had higher lipid content (principal energy reserves) and somatic growth than did poorly fed fish. Higher fat reserves will enhance the fishes' response to stress and thus increase their chance of survival.

In addition to the density-dependent processes affecting the growth of coral reef fishes, temperature also plays a role. Through detailed analyses of length-frequency and tagging-recapture data in a number of tropical and coral reef fishes, Pauly and Ingles (1981) and Pauly (1991) have shown that growth oscillates seasonally and that the intensity of these oscillations is dependent on temperature (see also Longhurst and Pauly 1987). Growth is fastest during the warmest periods of the year (the time when many recruits are beginning to contribute to total population biomass after the settlement season) and slowed by some degree during the cooler months in all species examined. The degree to which the growth rate slows appears to be related to the difference between the highest summer and lowest winter temperatures. Thus, fishes living in an environment in which the annual change in temperature is

relatively large will show higher amplitudes of seasonal growth oscillations than fishes living in areas with lower temperature changes.

2.4.6 Conclusion

In conclusion, many reef fish throughout the world exhibit marked seasonality in spawning which appear to be governed by local effects, although some species in some areas seem to spawn continuously throughout the year. Thus, no global generalities regarding spawning season can apply. In contrast, recruitment in most species studied, regardless of spawning behavior, appears to be highly seasonal with settlement occurring in the spring and summer, with few exceptions.

The dispersal or local retention of larvae appear to be related to hydrographic phenomenon occurring at various spatial scales. Thus, in a region where the majority of larvae are entrained in longshore currents and carried to adjacent or distant sites, some reefs may retain their larvae if local currents or meteorological conditions are permitting. Similarly, isolated oceanic islands with no upstream source of recruits are most likely self-recruiting systems with local hydrographic features that facilitate the retention of their own progeny.

The hypothesis that larvae are distributed in patches in the pelagic environment has been supported in most of the studies of recruitment reviewed here. The exact mechanisms of patch formation have yet to be found, but it is clear that both hydrography and larval behavior both play significant roles. These concentrations of larvae can be small or large, and seem to be the cause of the various pulses of settlement events observed during the recruitment seasons at many spatial scales from individual patch reefs, to several adjacent areas up to hundreds of kilometers. For most fishes studied, the magnitude and timing within the season of these pulses changes from year to year. The causes of these changes, because they are stochastic, remains unknown, but could be related to variations from year to year in weather or hydrography which cause the transport of the patches over the reefs. In at least one case, temporal variations in spawning output were linked to changes in larval supply and settlement (Meekan *et al.* 1993).

Perhaps the most relevant aspect of recruitment studies to general ecosystem function is the question of whether fish populations are stable entities or reflect the stochastic nature of recruitment. The contrasting evidence in this area allows no generalizations to be made across all species of reef fish. However, from this review of literature it seems that a few can be presented for certain groups of fishes. For small species with short life spans such as gobies and blennies, the specific nature of their habitat requirements and their total reliance on this space for survival, plus the high turnover of their populations, necessarily invokes the idea of density-dependent mortality. Shulman (1985) and Jones (1987b) stated that there is an increased probability of the populations of short-lived species to reflect changes in recruitment strength since their adult populations consist of only one or two year classes.

This observation does not hold true, at least for the species studied in the work reviewed here, although it may apply to less habitat-specific fishes. Specific types of shelter sites (size, shape, location, etc.) are bound to all be occupied by residents or earlier recruits in populations which require such structures. The observation that these shelter sites are more available at the time of recruitment (Hunte and Côté 1989) is important, because it means that they are available only for the first recruits to arrive during the spawning season or for the best competitors. These sites then appear to become quickly saturated and density-dependent effects come into play.

For larger, more mobile species, adult habitat and juvenile habitat often differ (Jones 1991). Therefore, the scale at which populations are measured will greatly influence conclusions reached. Adult habitats are often colonized by immigration of juveniles and these can be deemed loss from juvenile populations, when in reality it is probably just an ontogenetic shift in habitat. Settlement patterns might thus be overridden by the relocation of individuals (Robertson 1988b) and some habitats, which do not seem to receive settlement of juveniles, might be solely populated by immigration of previously settled fish (Jones 1988; Robertson 1988b; Forrester 1990).

The majority of pomacentrids studied on the GBR appear to be relatively long lived and relatively sedentary throughout their lives. At first glance, these characteristics would appear to facilitate strong density-dependent effects on recruitment. In fact, the opposite has been found in most studies: recruitment success and future population size appear to be reflective of the variation in settlement patterns that are evident a decade or more later (Doherty and Fowler 1994a,b). However, other density-dependent effects have been identified for some species (e.g., growth; see above) which partially reduces the effects of recruitment variation by altering adult densities by affecting the time required to reach maturity.

Compounding effects on the population dynamics of reef fishes and the probability that both recruitment and post-settlement events affect their populations are the reasons why Jones (1987b; 1990; 1991) believes that hypotheses based on single factors should be replaced by hypotheses that incorporate both density-dependent and density-independent processes. Jones (1987a) states that the reflection of recruitment variability in adult numbers is not enough to reject hypotheses regarding density-dependent effects (e.g., competition), and vice versa. He believes that different processes can act at different temporal and spatial scales and that at any given instant, one might be more important than the other (Jones 1990).

Regardless of the processes governing populations, the seasonality of recruitment can be deemed a general phenomenon. Thus, as recruitment events occur, the total biomass of individual populations should increase, albeit slightly in most instances (see Bohnsack *et al.* 1994) as individual fish grow. If mortality acts on a population throughout the year (e.g., as documented by Stimson (1990) for *Chaetodon miliaris*), then increases in the numbers of fishes via recruitment will increase the total biomass of the

population to some degree relative to what it was before the settlement of juveniles. In general terms, if the recruitment season in a certain area is in the spring, then summer biomasses should be higher than other seasons, especially since summer growth is most rapid as well.

3 Construction of Ecosystem Models

3.1 The ECOPATH Approach

The first ECOPATH model was constructed to estimate the biomass and production budgets of the components (species or species groups) of the French Frigate Shoals coral reef ecosystem, in the northern Hawaiian Islands (Polovina 1984). Its basic assumption is that for the period of time that is studied, the system exhibits equilibrium conditions (i.e., it is in a 'steady-state'). This assumption implies that for each species or group within the system, input (biomass production) equals output (various sources of mortality) (Polovina 1984). For each species or group, a simple linear equation can express this condition:

Production of biomass for species/group i - all predation on species/group i - nonpredatory biomass mortality for species/group $i = 0$ for all i1)

Thus, a number of such equations (one for each species/group i in the system) can be used to model the ecosystem during a certain period of time (Christensen and Pauly 1993a).

The original ECOPATH modeling software was enhanced and modified during the late 1980s and early 1990s (and subsequently named ECOPATH II) to be more user-friendly, and to incorporate various techniques regarding network analysis and information theory (Christensen and Pauly 1992a,b). In addition, ECOPATH II (and the more recent Windows version, ECOPATH 3.0; Christensen and Pauly 1995; 1996a) incorporates techniques to quantify several aspects of ecosystem maturity (*sensu* Odum 1969) (Christensen and Pauly 1992a). The newer versions of ECOPATH still rely on the master equation of Polovina (1984) to describe the steady-state condition of the ecosystem being modeled.

Equation (1) can be expressed as:

$$P_i - M_{2i} - P_i (1 - EE_i) - EX_i = 0 \quad \dots 2)$$

where P_i is the production of (i), M_{2i} is the predation mortality of (i), EE_i is the ecotrophic efficiency of (i) (fraction of production of (i) consumed within the system or exported), $(1 - EE_i)$ is the 'other mortality' and EX_i is the export of (i).

Equation (2) be re-expressed as:

$$B_i * P/B_i - \sum_j B_j * Q/B_j * DC_{ji} - P/B_i * B_i (1-EE_i) - EX_i = 0 \quad \dots 3a)$$

or

$$B_i * P/B_i * EE_i - \sum_j B_j * Q/B_j * DC_{ji} - EX_i = 0 \quad \dots 3b)$$

where B_i is the biomass of (i), P/B_i is the production/biomass ratio, Q/B_j is the consumption/biomass ratio of predator (j) and DC_{ji} is the fraction of prey (i) in the average diet of predator (j).

For an ecosystem with n groups, n linear equations can be presented explicitly based on equation (3):

$$B_1P/B_1EE_1 - B_1Q/B_1DC_{11} - B_2Q/B_2DC_{21} - \dots - B_nQ/B_nDC_{n1} - EX_1 = 0$$

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$$B_2P/B_2EE_2 - B_1Q/B_1DC_{12} - B_2Q/B_2DC_{22} - \dots - B_nQ/B_nDC_{n2} - EX_2 = 0$$

-
-
-

$$B_nP/B_nEE_n - B_1Q/B_1DC_{1n} - B_2Q/B_2DC_{2n} - \dots - B_nQ/B_nDC_{nn} - EX_n = 0$$

This system of simultaneous linear equations can be solved through matrix inversion (Pauly and Christensen 1992a).

Definition of the ecosystem to be modeled is the first step in ECOPATH modeling. The ecosystem should be defined such that the sum of trophic flows within the system is greater than the flow exchange between it and the surrounding systems (Christensen and Pauly 1992a). The various components (species or species groups) of the system should then be identified, and if necessary, aggregated into ecologically similar 'boxes,' i.e., groups of species with similar sizes, mortality rates and diet compositions (Christensen and Pauly 1992a; 1993a). A box simply refers to a specific component of the ecosystem to be modeled (i.e., a state variable). The energy balance of a box, assuming steady-state conditions, can be achieved through application of equation (2) with the addition of other flows that link predators and prey (Christensen and Pauly 1995) such that consumption = production + respiration + unassimilated food (Christensen and Pauly 1992a; 1993a). From this equation, respiration can be estimated (Christensen and Pauly 1992a,b; 1993a).

For any group (i), one of the input parameters B_i , P/B_i , Q/B_i or EE_i may be left unknown to be estimated by the model (Christensen and Pauly 1993a; Pauly and Christensen 1996a). Diet compositions and exports (e.g., fisheries catches) must always be entered for all groups (Christensen and Pauly 1993a; Pauly and Christensen 1996a).

The data required to parameterize an ECOPATH model is the kind usually collected by fisheries scientists and marine ecologists working in the field (e.g., consumption rates, biomass estimates,

mortality, etc.) (Christensen and Pauly 1995; Polunin *et al.* 1996). Estimates for several aspects of marine ecosystems are, therefore, relatively easy to obtain.

3.2 Input Parameters

Estimates used to parameterize the models presented herein of the Looe Key National Marine Sanctuary ecosystem were obtained from published reports and papers from Looe Key and other Florida Reefs, or from other Caribbean and Indo-Pacific reefs where necessary. Some inputs were derived through published empirical formulae. The currency used to describe the ecosystem was $t \cdot km^{-2} \cdot year^{-1}$, with tonnes referring to wet weight. Data not reported in this currency were converted before entry into the models through conversion factors from Atkinson and Grigg (1984) and the contributions in Christensen and Pauly (1993b). Organisms and detritus were organized into 20 groups (9 fish and 11 non-fish) following Opitz (1993; 1996). The dimensions of the Sanctuary and its relative area are described Chapter 1. The entire area was divided into 7 habitat zones according to Bohnsack *et al.* (1987): forereef (1%), intermediate reef (1.8%), deep reef (1.2%), inshore live bottom (1.4%), offshore live bottom (3.9%), sand and rubble (34%), seagrasses (26%) (see also Fig. 4. The remaining 30.7% of habitat was deeper than 13 m, and thus not sampled in the fish censuses of Bohnsack *et al.* (1987). From the sampling site descriptions of Lidz *et al.* (1985), the area left undescribed by Bohnsack and co-workers deeper than 13 m consists largely of mud and fine sediment covered bottom. In the vicinity directly south and southeast of the core area, coarse sand recedes down the slope with grain sizes diminishing to a muddy substrate (Lidz *et al.* 1985). The deep reef does extend beyond the 13 m boundary of the fish survey and was not sampled (Bohnsack *et al.* 1987).

The definition and biomass estimates of the fish boxes were based on the visual census study of Bohnsack *et al.* (1987) which estimated the abundances of 188 species reported from within the Sanctuary boundaries. In addition to abundance data, the survey presented estimates of the mean size of each species recorded. Length-weight relationships from Bohnsack and Harper (1988), and additional data kindly supplied to the author by J. Bohnsack (pers. comm.; Appendix 1), were used to derive biomass estimates from the visual census survey abundance and average length estimates. Criteria for the aggregation of fish groups followed Opitz (1993; 1996) and were based on the clustering of species with similar activity levels, size, food and habitat (pelagic or demersal) preferences (Appendix 2). P/B and Q/B values were estimated using the empirical relationships of Pauly (1980), Pauly and Ingles (1981) and Palomares and Pauly (1989) which were derived based on data from a wide range of fishes, including Caribbean reef fishes. Diet compositions were adopted from Randall (1967).

Non-fish taxa input parameters were difficult to estimate due to the scarcity of studies which have examined ecological characteristics needed for the model and the vast number of species involved.

The input data for non-fish taxa were from a diverse array of sources, many of which are documented in Opitz (1993; 1996). The various groupings of non-fish organisms follows Opitz (1993; 1996).

Once input data was entered into the model, the parameter estimation routine was run in order to estimate missing values and to evaluate the validity of the inputs. Since the balance of the model requires that production + respiration and consumption are equal, EE values should all be ≤ 1 . This was not the case for a number of groups so adjustments were necessary to obtain a thermodynamically balanced model. For 7 of the 9 fish groups, EE values close to unity were, as most of the production in coral reefs can be assumed to be consumed within the system. This allowed biomass to be estimated. The model estimated biomass values higher than those estimated from Bohnsack *et al.* (1987). This is not surprising as the stationary visual sampling technique used for Looe Key fishes (see Bohnsack and Bannerot 1986; Bohnsack *et al.* 1987) tends to provide minimum estimates of relative abundance (J. Bohnsack, pers. comm.).

Biomasses were also left to be estimated by the model for crustaceans and worms/molluscs, as the original input values were not large enough to accommodate predation pressure by the fish groups. Also, the initial gross efficiency (ratio between production and consumption) of worms/molluscs was too high; as a remedy, the group's Q/B was increased.

3.3 Seasonal Changes in Input Parameters

Construction of four new models followed the initial mean annual model described above. Each new model represents a 3 month period coincident with the northern hemisphere summer (July - September), fall (October - December), winter (January - March) and spring (April - June). Summer and winter models were parameterized first as these represented the extremes of environmental conditions, while spring and fall models were done as transitional descriptions of the system. Annual temperature at Looe Key averages 26.5°C, with a winter minimum of 24°C and a summer maximum of 29°C (Lee *et al.* 1992).

For most groups, P/B and Q/B values were adjusted from the annual means in the original model (i.e., 100%). Summer P/B was 104% of the mean and winter P/B was 96%. For Q/B, the summer value was 105% of the mean and the winter value was 94%. These percentages were calculated through the empirical formulas in Pauly (1980) for P/B and Palomares and Pauly (1989) for Q/B, both of which having a temperature dependent term, viz

$$\log_{10}M = -0.0066 - 0.279 \log_{10}L_{\infty} + 0.6543 \log_{10}K + 0.4634 \log_{10}T \quad \dots 4)$$

where M is the natural mortality, equal to P/B in a steady-state (Allen 1971), unexploited system, L_∞ is the asymptotic total length in cm, K is the von Bertalanffy growth coefficient and T is the environmental temperature in $^\circ\text{C}$; and

$$\ln Q/B = -0.1775 - 0.2018 \ln W_\infty + 0.6121 \ln T + 0.5156 \ln A + 1.26 f \quad \dots 5)$$

where Q/B is the daily food consumption per unit biomass, W_∞ is the asymptotic weight in g; T is the environmental temperature in $^\circ\text{C}$; A is the aspect ratio of the caudal fin and f represents food type (0 for carnivores, 1 for herbivores). Percent changes in P/B were thus proportional to $T^{0.4634}$. Similarly, percent changes in Q/B were proportional to $T^{0.6121}$; both were applied to most boxes.

For the herbivorous fish groups, changes in Q/B were made based on the findings of Polunin and Klumpp (1992) for herbivores on the GBR where grazing rates increased 1.8 times from winter to summer.

Changes of P/B for the primary producer groups (phytoplankton and benthic producers) were derived from a least squares plot of summer/winter ratios of gross primary production versus temperature range for 11 different coral reef areas throughout the world (Fig. 5). Temperature change at Looe Key from winter to summer was 5°C , corresponding to a summer/winter ratio $\approx 2:1$.

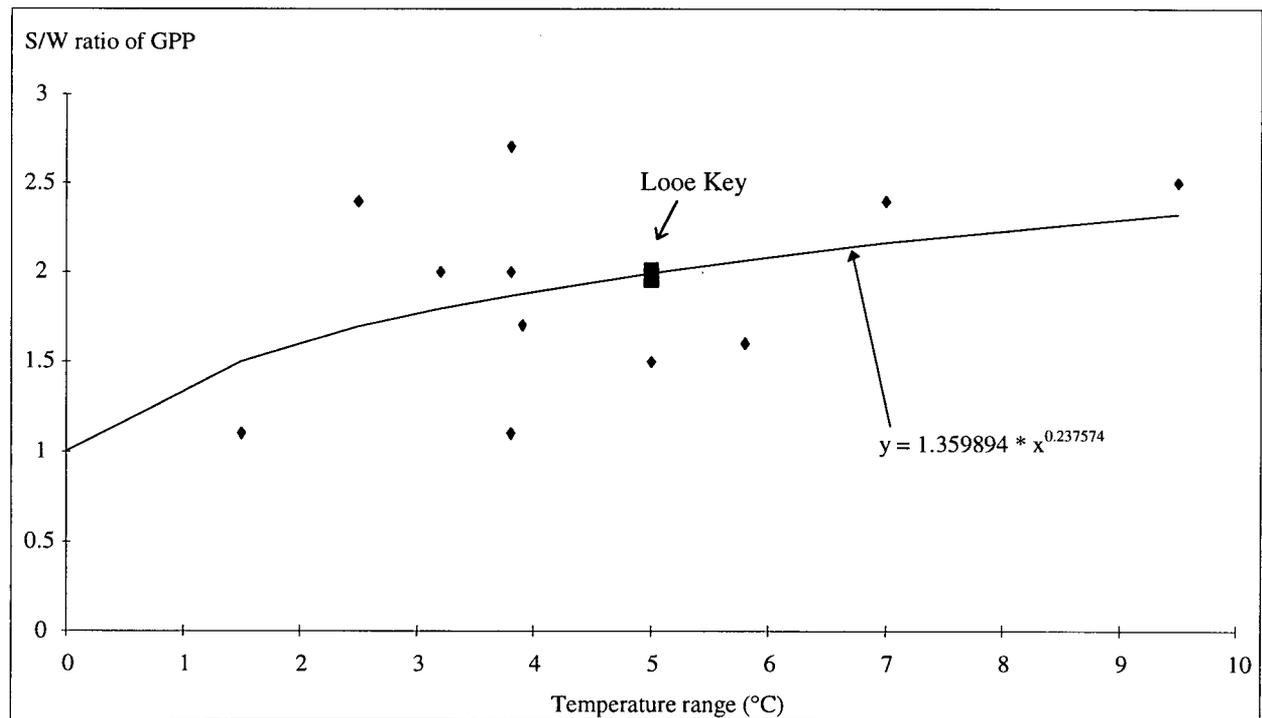


Figure 5. Summer/winter ratio of gross primary production (GPP) vs. temperature range based on data from 11 reefs throughout the world (see Appendix 3 for details). The line depicts the best fit for least squares found using the Solver function of Microsoft Excel.

Phytoplankton and zooplankton biomasses were adjusted seasonally based on the work of Bsharah (1957), who found that Florida Current phytoplankton were 7 times more abundant in summer than winter and zooplankton were 3 times more abundant in spring than the rest of the year.

Since a biomass value was entered into the model for benthic producers, summer - winter differences were not estimated and had to be entered. The biomass of this box was increased by 27% from winter to summer. A 3% increase from winter to summer in the biomass of seagrass at Looe Key was noted by Lapointe *et al.* (1994) and seagrasses account for 26% of the area of the Sanctuary (Bohnsack *et al.* 1987). There appears to be an increase of about 35% (range 33-40%) from winter to summer for algal biomass as estimated by Carpenter (1985) in St. Croix, USVI (33%) and Klumpp and McKinnon (1989) at Davies Reef, GBR (40%). Benthic producers for much of the remainder of the Sanctuary area are dominated by macroalgal species, and thus the rest (besides areas of seagrass) of the Looe Key area was assumed to undergo a 35% increase from winter to summer. The overall value of 27% was thus a weighted average of the two estimates of the seasonal changes of benthic producer biomass according to the proportion of habitat within the Sanctuary that they occupied.

To balance the summer and winter models, the proportions of prey items in the diets of predators had to be adjusted in many cases. Thus, in winter, the plankton groups could not support the same amount of predation as in summer: their EE's were greater than 1. To adjust for this imbalance, the diet compositions of several of their predators were modified to reflect increased consumption of the decomposer/microfauna group and detritus. I assumed that the food preference of each group would remain largely unchanged throughout the different seasons and implemented this by maintaining the initial (mean annual) estimates of Ivlev's electivity index, which is also estimated by Ecopath (see Christensen and Pauly 1992; Appendix 4). This index is defined by values between -1 and 1, where -1 corresponds to total avoidance of, 0 to non-selective feeding on and 1 to exclusive feeding on a given prey (Ivlev 1961).

The spring and fall models were constructed to represent transitional periods between the summer and winter extremes. Thus, the inputs for B, P/B, and Q/B were taken as the averages between winter and summer. However, to account for biomass change, a non-zero biomass accumulation term

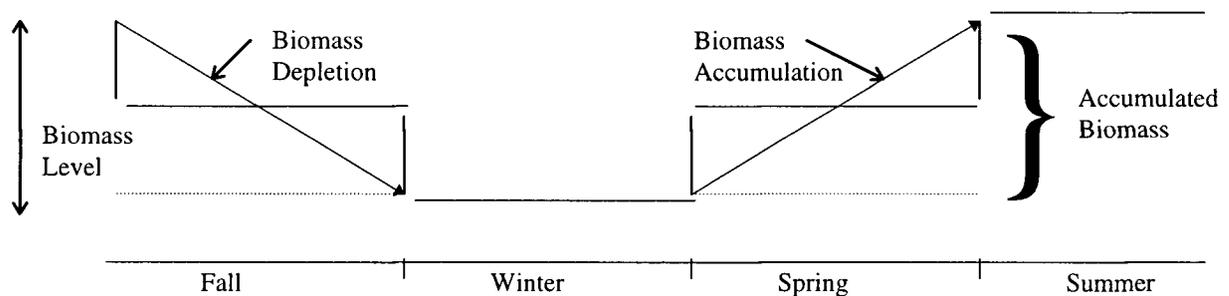


Figure 6. Schematic diagram of seasonal changes in relative levels of biomass. Triangles represent increases (spring to summer) and decreases (fall to winter) in biomass accounted for in the spring and fall ECOPATH models by the biomass accumulation term. Biomass accumulation is negative in the fall and positive in the spring.

was required. This is a rate and is expressed in $t \cdot km^{-2} \cdot year^{-1}$. To obtain this value, the differences between summer and winter biomass values were calculated and then multiplied by four (seasons), i.e., to scale the biomass accumulation so that it could be expressed as an annual rate. Biomass accumulation values were positive in spring, as there is a build-up of biomass to reach the summer maximum from winter minimums, and negative in the fall (Fig. 6). Balancing these models was then achieved by adjusting the diet compositions until all predation could be sustained, i.e., until all EE_i values were ≤ 1 .

4 Results

4.1 General Model

A brief description of the annual average Looe Key ECOPATH model was originally presented in Venier and Pauly (1997; Appendix 5). Since that preliminary model was presented, it has been slightly modified. For example, the proportion of ingested food not absorbed via digestive processes (unassimilated food) was increased from the default value of 20% to 70% for herbivorous fishes, based on the findings of Klumpp and Polunin (1989) and Polunin and Klumpp (1992). In addition, the gross food conversion efficiency ($GE = P/Q$) of the worms/molluscs group was reduced from an initial value >0.5 . Since the GE for most groups should fall within the range of 0.1 - 0.3 (Christensen and Pauly 1992a), the Q/B value had to be increased from 7 year⁻¹ to 8 year⁻¹, which yielded a (still high) value of $GE = 0.45$.

Results from the balancing of the model (outputs) are shown in bold in Table 3, along with the inputs. Many of the biomass values were estimated by the model itself and original inputs obtained from the literature are listed in a separate column in Table 3 for comparison. In general, estimated EE values are high ($>90\%$), which indicates a high degree of turnover within the system and very little excess biomass production.

Figure 7 illustrates the relative impact that an increase in biomass of one group will have on all others within the system. This figure depicts both direct (feeding) and indirect relationships between groups, and can thus be used as a sort of sensitivity analysis for perturbations to the system and as an index of the interdependencies that exist within the ecosystem.

The Looe Key ecosystem appears to be a net producer, at least on an annual basis, with a P/R value of 1.3 (Table 4). A gross primary production value of $30124 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ ($= 8.3 \text{ gC} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and a respiration rate of $22767 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ ($= 6.2 \text{ gC} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) were estimated by the model. Thus, about $7400 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ ($= 2 \text{ gC} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) was available for consumers. In this model, all excess production was accounted for, either as food for consumers or flow to the detritus. Total system throughput (sum of all flows) was $142618 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ of which consumption by organisms accounted for 39%, respiration 16% and flow to detritus 45%.

The system omnivory index (variance of mean trophic level; Pauly *et al.* 1993) is 0.237 which indicates that many of the components in the Looe Key ecosystem feed on a broad range of trophic levels.

4.2 Seasonal Models

The model was parameterized such that the general structure of the Looe Key ecosystem remains the same throughout the year, but with seasonally varying rates and biomasses. Summer is the

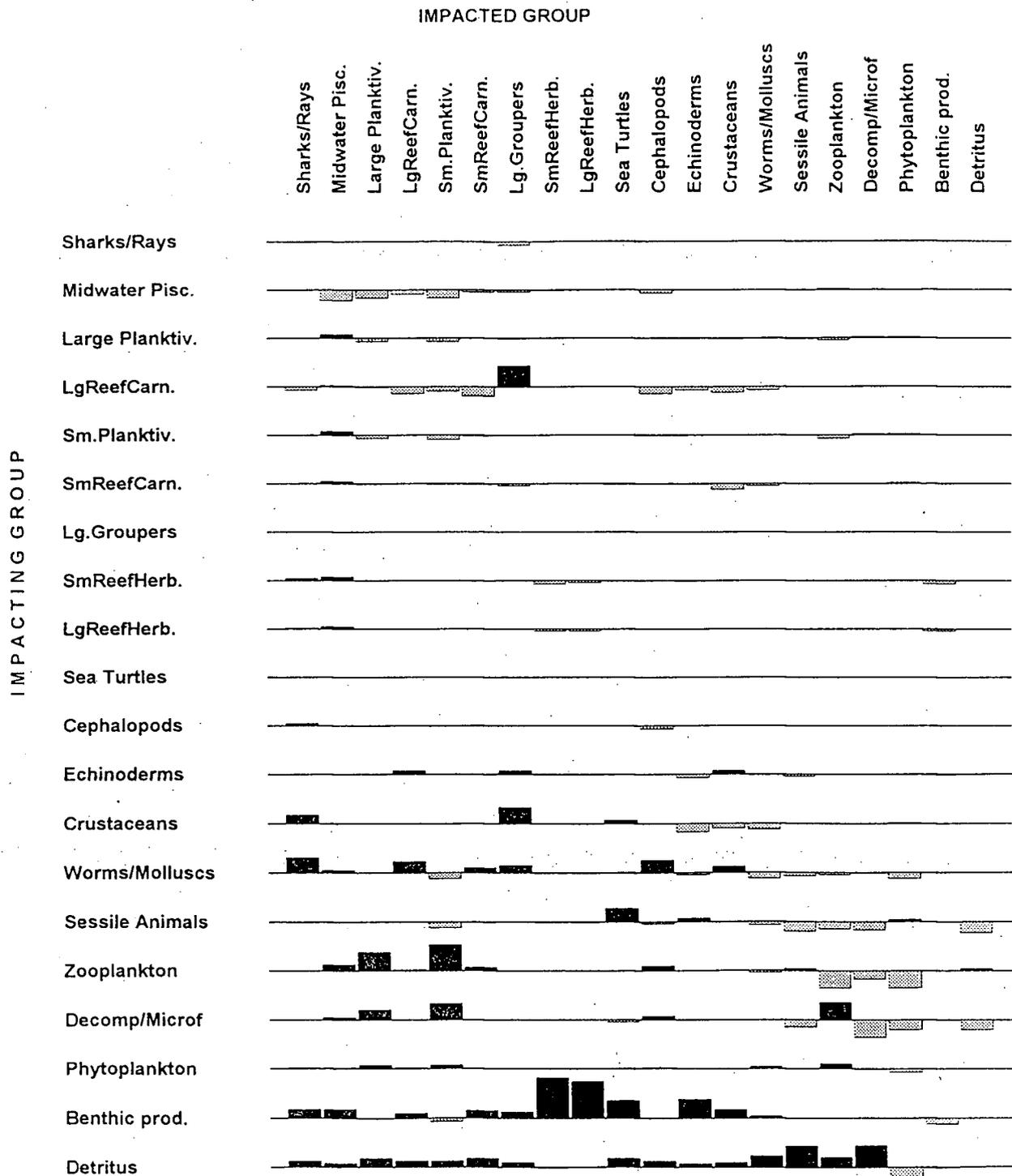


Figure 7. Relative impacts that an increase in biomass of a given group will have on all other groups within the system. Positive impacts (increases in biomass) are black and above the lines, and negative impacts are gray and below the lines.

Table 3. Inputs and outputs (in bold) of the Looe Key National Marine Sanctuary annual average ECOPATH model.

Group	B (t·km ⁻²)		P/B (year ⁻¹)	Q/B (year ⁻¹)	EE
1. Sharks & Rays	1.75	2.69 ^a	0.18	3.80	0.47
2. Midwater Piscivores	85.00	114.59 ^a	1.00	8.90	0.91
3. Large Planktivores	91.54	12.08 ^a	1.40	10.00	0.92
4. Large Reef Carnivores	235.74	247.32 ^a	0.95	7.30	0.95
5. Small Planktivores	76.23	2.01 ^a	2.60	10.00	0.98
6. Small Reef Carnivores	128.61	8.97 ^a	1.60	12.80	0.98
7. Large Groupers	2.08	0.70 ^a	0.40	2.30	0.20
8. Small Reef Herbivores	69.71	10.88 ^a	1.90	37.45	0.98
9. Large Reef Herbivores	94.54	19.27 ^a	1.55	22.80	0.96
10. Sea Turtles	0.02	0.02 ^b	0.15	3.50	0.00
11. Cephalopods	16.55	-	3.50	11.70	0.95
12. Echinoderms	475.00	474.00 ^c	1.50	4.00	0.93
13. Crustaceans	202.35	73.00 ^c	2.75	10.00	0.99
14. Worms & Molluscs	647.24	119.00 ^c	3.60	8.00	0.96
15. Sessile Animals	1673.58	1673.58 ^d	0.80	9.00	0.85
16. Zooplankton	40.00	39.00 ^c	65.00	165.00	0.96
17. Decomposers & Microfauna	51.78	-	134.00	270.00	0.95
18. Phytoplankton	30.00	25.00 ^f	70.00	-	0.92
19. Benthic Producers	2115.00	2115.83 ^g	13.25	-	0.31
20. Detritus	3400.00	-	-	-	0.47

Sources:

^a Abundances and mean sizes from Bohnsack *et al.* (1987). L-W relationships from Bohnsack and Harper (1988) with additional data provided by J. Bohnsack (pers. comm.; Appendix 1).

^b Polovina (1984).

^c Glynn (1973).

^d Sum of corals (Lewis 1981), sponges (Opitz 1993) and tunicate/bryozoans (Opitz 1993).

^e Porter and Porter (1977).

^f Based on value from Opitz (1993; 1996).

^g Sum of estimates of sand and symbiotic algae (Odum and Odum 1955), seagrasses (Tomasko and Lapointe 1991) and reef macroalgae (Glynn 1973; Carpenter 1985; 1986; 1988; Hughes *et al.* 1987; Klumpp *et al.* 1987; Berner 1990; McClanahan 1995).

period of highest biomass and primary production, and as a result, total system throughput is highest during this time as well. Winter shows the opposite features with lowest biomass, production and throughput. As mentioned above, spring and fall were modeled as transitional periods between two extremes. Therefore, all rates are intermediate and similar to those of the general annual model described above. Table 4 lists the summary statistics by model for all important ecosystem characteristics (see Appendices 6 and 7 for additional details on seasonal models).

With the seasonal input parameters, gross primary production is 2.8 times higher in summer than in winter, whereas respiration rates are only 1.4 times as high. The system appears to be highly productive in the summer with a net primary production value of over 19000 t · km⁻² · year⁻¹ (5.2 gC · m⁻² · day⁻¹) and a P/R of 1.7. In winter there is a general loss of production and the system apparently becomes heterotrophic, with a P/R of 0.9. The system remains heterotrophic only during winter, as P/R values for

Table 4. Summary statistics computed by ECOPATH for all models.

Property (units)	Model				
	Annual Mean	Summer	Fall	Winter	Spring
Sum of all Consumption (t·km ⁻² ·year ⁻¹)	55514	69825	55874	43037	55874
Sum of all Respiratory Flows (t·km ⁻² ·year ⁻¹)	22767	26456	22708	19318	22708
Sum of all flows into Detritus (t·km ⁻² ·year ⁻¹)	64337	84391	69872	49252	63931
Total System Throughput (t·km ⁻² ·year ⁻¹)	142618	180671	148455	111607	142514
Sum of all Production (t·km ⁻² ·year ⁻¹)	45778	66747	45534	27867	45534
Calculated Net Primary Production (t·km ⁻² ·year ⁻¹)	30124	45898	29608	16529	29608
Total P/R	1.32	1.74	1.30	0.86	1.30
Net System Production (t·km ⁻² ·year ⁻¹)	7357	19442	6901	-2789	6901
Total P/B (year ⁻¹)	4.99	7.21	4.94	2.94	4.94
Total B/Total Throughput (year ⁻¹)	0.042	0.035	0.040	0.050	0.042
Total Biomass (Excluding Detritus) (t·km ⁻²)	6037	6362	5991	5623	5991
System Omnivory Index	0.237	0.236	0.269	0.281	0.269
Finn's Cycling Index (%)	15.1	17.4	16.7	13.8	16.5
Mean Transfer Efficiency of All Flows (%)	13.5	12.9	11.6	14.3	12.1
Proportion of Total Flow from Detritus	0.75	0.70	0.76	0.82	0.78

spring and fall were roughly equivalent to those of the annual model (1.3).

The system omnivory indices are lowest in the summer, intermediate in the spring and fall, and highest in winter. Thus, heterogeneity of diet appears to be a function of season, if the changes in diet compositions required to balance the models reflect reality. The proportion of total flow which originates from the detritus group increases from a low of 70% in summer to a high of 82% in winter, reflecting the higher role given to detritus as a winter food source. In addition, the importance of detritus is apparent in Figure 7, where increases in detritus biomass positively affect nearly all groups. This effect is evident in all seasons. The only group negatively affected by increased detritus biomass is the phytoplankton, probably due to the increased biomass of grazers that results from an increase of detritus. Transfer efficiencies from one trophic level to the next (ratio between flow transferred to the next trophic level and the throughput at that trophic level, see Christensen and Pauly 1992a) are generally higher for all flows in winter than in other seasons (mean 14.3 % in winter, 12.9% in summer, 12.1% in spring and 11.6% in fall). The amount of detritus recycling within the system (Finn's cycling index) is highest in summer (17.4%) and lowest in winter (13.8%).

5. Discussion

5.1 Value of the ECOPATH Modeling Approach

One of the values of ecosystem models, such as presented here, lies not only in the results, but also in the process of model construction itself. This is because it is necessary to examine all aspects of the ecosystem which could potentially affect its structure and function. In doing so, the modeler gains a broad understanding of the work that has been done in a variety of ecological disciplines as they apply to the system being analyzed. Christensen and Pauly (1993a) list some of the benefits, other than the model outputs proper, which are inherent in this type of modeling exercise: review and standardization of all data regarding the particular system, identification of information gaps, identification of estimates that are not compatible with the system's functioning and interaction of the modeler with other scientific specialties and/or specialists. The modeling process allows the modeler to critically view the data that he/she uses. It is, therefore, imperative that the data be viewed synthetically in a whole ecosystem context, as opposed to the individual component analyses from which they were derived.

The ECOPATH modeling approach has been applied to a wide variety of aquatic and marine ecosystems (see Christensen and Pauly 1995). Thus, similar ecosystems which have been modeled using ECOPATH can be directly compared for similarities or differences in their structures and functions, and patterns may emerge which may allow generalizations to be made regarding their structures and functions. Identifications of differences between similar systems can also be important, especially if the reasons behind those differences relate to human activities.

The management of reef fisheries may also benefit from ecosystem models. It has been recognized that there is a need to understand the interactions between target and other species (Christensen and Pauly 1995) in order to be able to manage ecosystems, instead of specific stocks. Also, an ecosystem approach to modeling can help shed light on the trophodynamic processes governing reef fish production, of which relatively little is known (Polunin 1996; see also Walters *et al.* 1997).

5.2 Incorporating Uncertainty into the Models

The approach used in this thesis of modifying, until mass-balance is achieved, those input values perceived as least reliable (see Section 3.2), is subjective and hence, ultimately insufficient to provide a sound basis for the modeling of ecosystems, especially if management interventions are to be based on ECOPATH/EcoSim models. In the meantime, however, a formal approach has been proposed by Walters (1996), and incorporated into a recent release of ECOPATH, which reformulates the problem of uncertainty of ECOPATH input parameters in a Bayesian context.

Thus, instead of single values to be subsequently modified, inputs (biomass, P/B, Q/B, EE and diet compositions) are entered as prior distributions (uniform, triangular or uniform). These distributions

are then sampled using a Monte-Carlo procedure, thus generating a large number of ECOPATH models from random selections of parameters. Of these, most will be thermodynamically impossible (i.e., $EE > 1$; $GE = (P/B)/(Q/B) > 0.5$, etc.), and thus rejected. The other, acceptable models, not only generate distributions of estimates (for the parameter of the master equations that was left as unknown), but also posterior distributions of the input variables, i.e., distributions of the inputs associated with possible models. These posterior distributions are usually much narrower than the prior distributions, and hence, represent real knowledge acquired by achieving mass-balance in a system.

Adding distributions about the inputs used to construct the Looe Key models presented here is straightforward and is anticipated prior to their formal publication. This will allow verifying whether, indeed, some of the approximations used in the course of the construction of the models presented here were, in fact, justified.

5.3 General Annual Model

5.3.1 *Functioning of the Ecosystem*

The flow diagram in Figure 8 represents the major pathways of energy within the Looe Key ecosystem. The size of each box is proportional to the logarithm of its group's biomass. The y-axis represents the mean trophic level of the groups and reflects the relative proportion of prey items in their diet compositions. The network of flows in the system is complex and many species feed at more than one trophic level (system omnivory index = 0.237). Thus, there appears to be a great deal of interdependency between all groups within the system (Figure 7). The high EE values (Table 3) indicate that for most groups, the bulk of the production is consumed within the system.

The calculated gross primary production (around $30000 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1} = 8.25 \text{ gC} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), respiration ($22800 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1} = 6.24 \text{ gC} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and net primary production ($7357 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1} = 2.02 \text{ gC} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) values agree well with those from other coral reef areas (see reviews by Lewis 1981; Kinsey 1985; Hatcher 1990). These high rates are possible probably because of the degree of detritus recycling (Finn's cycling index = 15.1%; Table 4) which occurs at Looe Key, making the system more efficient. Thus, the Looe Key ecosystem is a net producer with a P/R of 1.3. Roughly 1/3 of the mortality of the benthic producer group is accounted for by grazing and the other 2/3 is deposited as detritus, largely in the deeper sediment-dominated substratum described in Chapter 3, from where it may be exported. Polunin and Klumpp (1992) suggested that much of the production of algal turf in the reef flat territories of some grazing fishes on the GBR may be lost to export from the zone as dissolved or particulate matter, i.e., as 'detritus.' Depending on the prevailing tides and currents, this will be deposited shoreward of the reef, in seagrass beds or seaward of the reef, in the deeper sediment deposits. Some of the excess production may also be exported as drift vegetation. This probably occurs primarily

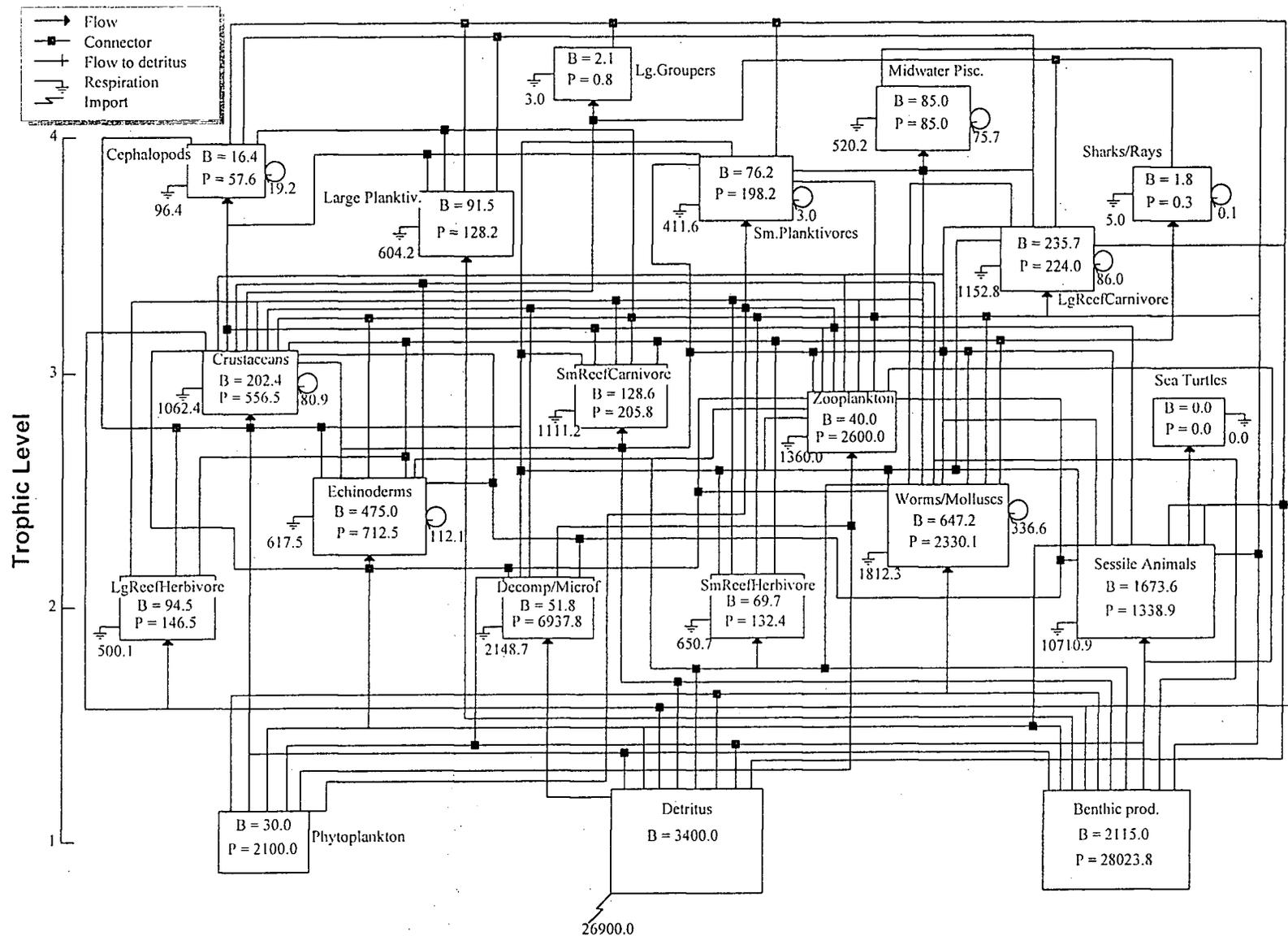


Figure 8. Flow diagram of the Looe Key National Marine Sanctuary ecosystem annual model. Consumption by a group is indicated by arrows entering a box from below, and flows leaving a box from the top represent consumption by other groups on that box. The surface of the boxes is roughly proportional to the logarithm of the biomass of the group they represent, and all are arranged by their trophic level, as calculated by ECOPATH.

for seagrasses and macroalgae species not associated with the reef itself, but with the surrounding habitats within the sanctuary. Kilar and Norris (1988) found that the majority of aquatic vegetation found in the drift around a reef in Panamá had been transported from adjacent systems.

Secondary production is dominated by detritus, from which 75% of all flows originate (Table 4). Many groups feed on detritus within the system as evidenced by the large number of flows from the detritus box in Figure 8. Polunin (1996) noted that much of the fish productivity in coral reef systems is apparently derived from detritus, but that little is known about the way that energy is transferred up the food web. Since the bulk of the detritus is derived from the benthic producers in the model, and these are low in nitrogen and phosphorus (Polunin 1996), the quality of detrital material as a food source is generally poor. Most organisms which have detritus as a component in their diet compositions, tend to avoid it (as reflected in their negative electivity indices, Chapter 3; Appendix 4) and probably only consume it when other, preferred foods are unavailable (as was required here to balance the model; see below). However, the food intake values output by the model for groups which consume detritus but do not show a preference for it, are high. This implies that a large proportion of their production can be derived from this material, despite its lack of nutrients. Sessile organisms and decomposers/microfauna are the only two groups which show a preference for detrital material. These groups are themselves heavily preyed upon within the system and contribute relatively large proportions to the food intake of their predators, especially invertebrates. Thus, much secondary is achieved through microbial links (Sorokin 1990), or directly through consumption of sessile organisms.

The trophic structure of the Looe Key National Marine Sanctuary ecosystem can be seen in Table 5 where the relative importance of each group at each discrete trophic level is presented. Trophic levels for the producer groups and detritus are assigned a definitional value of 1 in ECOPATH, while the trophic levels of consumer groups are derived as the weighted average of the trophic levels of their prey + 1 (Christensen and Pauly 1992a). The important groups at trophic level II are the sessile animals and the decomposer/microfauna group, both of which feed heavily on detritus. The flow at trophic level III is dominated by the zooplankton followed by the worms and molluscs, crustaceans and large reef carnivores. The two planktivorous fish groups and large reef carnivores dominate trophic level IV, while midwater piscivores dominate at the largely notional trophic level V.

The highest order carnivores in the system are the large groupers, but they contribute little to the total system flows. The midwater piscivores, however, contribute substantially to the flow at trophic levels III, IV and V and are thus important predators in the system. The relatively low trophic levels of the carnivorous fish groups reflects their varied diet, which is probably due to the large number of species they contain [note that a flow may occur at, e.g., trophic level V, while its consumer is at trophic level IV].

The high EE values for most species groups indicate that the majority of biomass production is

Table 5. Absolute flows ($t \cdot km^{-2} \cdot year^{-1}$) by trophic level (I - V). The flows of groups are arranged by discrete trophic level (TL). Total flow ($t \cdot km^{-2} \cdot year^{-1}$) and total biomass ($t \cdot km^{-2}$; excluding detritus) for each trophic level are also presented.

TL	Group	I	II	III	IV	V
4.3	Lg. Groupers	-	-	0.9	2.4	1.2
4.1	Midwater Piscivores	-	-	308	198	235
3.9	Cephalopods	-	-	85	79	27
3.8	Sm. Planktivores	-	1.5	158	601	1.8
3.8	Sharks & Rays	-	0.1	3.3	2.0	1.0
3.7	Lg. Planktivores	-	9.2	324	572	10
3.5	Lg. Reef Carnivores	-	159	888	531	130
3.0	Crustaceans	-	658	967	370	23
3.0	Sm. Reef Carnivores	-	672	541	391	38
2.8	Zooplankton	-	1320	5280	-	-
2.8	Sea Turtles	-	0.0	0.0	0.0	0.0
2.4	Echinoderms	-	1345	502	42	10
2.4	Worms & Molluscs	-	3810	1286	64	17
2.1	Sessile Animals	-	14400	362	301	-
2.0	Sm. Reef Herbivores	-	2595	5.9	9.7	0.1
2.0	Lg. Reef Herbivores	-	2142	11	1.3	0.6
2.0	Decomposers/Microf.	-	13979	-	-	-
1.0	Phytoplankton	2100	-	-	-	-
1.0	Benthic Producers	28024	-	-	-	-
1.0	Detritus	30080	-	-	-	-
Total flow by trophic level		60203	41091	10721	3165	495
Total biomass by trophic level		2145	2777	711	341	59

used within the Looe Key ecosystem. Sea turtles are not consumed within the system and thus have an ecotrophic efficiency of 0 (Table 3). For the groups with high EE's, the mortality coefficients are dominated by predation, while 'other mortality' (i.e., senescence, disease, etc.) is low. The opposite is true of the groups that have low EE values, and most of their biomass ends up as detritus and/or is consumed outside the system.

The trophic effects that the high degree of predation and the varied diets of most of the groups within the system have on other groups are both direct and indirect (Figure 7). Direct effects include predator-prey relationships and competition for food, while indirect effects include an increase or decrease of a group's biomass via negative or positive impacts on the group's predators. For example, an increase in the biomass of sessile animals directly decreases zooplankton, decomposers/microfauna and detritus biomass via predation, but increases the biomass of another of their prey items, phytoplankton, due to higher removal of their main predator, zooplankton. As in other ecosystems, e.g., the North Sea (Christensen 1995a) or the Virgin Islands (Opitz 1993), the fish groups generally have negative impacts on each other due to predation and competition. Invertebrate groups have mostly positive impacts on other groups within the system which reflects their importance as prey.

5.3.2 Maturity of the System

Ecosystem maturity can be quantified using several of Odum's (1969) attributes (Table 6) from the information output by an ECOPATH model. Here, I describe the maturity of Looe Key in relation to four other coral reef models by comparing 6 of Odum's 24 attributes (P/R, net system production, total biomass/total throughput, total biomass, system omnivory index and Finn's cycling index).

The six values which correlate to Odum's attributes are presented for each coral reef ecosystem in Table 7. Total system P/R for Looe Key is approximately 1.3. Mature systems will tend to have P/R values close to 1 (Odum 1969). Here, Looe Key ranks 3rd when compared to the other reefs. The highest net primary production occurs at Looe Key, while the lowest occurs in the heterotrophic fringing reefs of Moorea. Looe Key thus ranks 4th in terms of net primary productivity.

Table 6. Trends evident in the successional development of ecosystems (from Odum 1969). * indicates attributes discussed in this paper.

Ecosystem Attributes	Developmental Stages	Mature Stages
<i>Community Energetics</i>		
*Gross Production / Community Respiration (P/R)	Greater or less than 1	Approaches 1
Gross Production / Standing Crop/Biomass (P/B)	High	Low
*Biomass Supported / Unit Energy Flow (B/E)	Low	High
*Net Community Production	High	Low
*Food Chains	Linear, mostly grazing	Weblike, mostly detritus
<i>Community Structure</i>		
*Total Organic Matter	Small	Large
Inorganic Nutrients	Extrabiotic	Intrabiotic
Species Diversity – Variety Component	Low	High
Species Diversity – Equitability Component	Low	High
Biochemical Diversity	Low	High
Stratification & Spatial Heterogeneity	Poorly Organized	Well Organized
<i>Life History</i>		
Niche Specialization	Broad	Narrow
Size of Organism	Small	Large
Life Cycles	Short, Simple	Long, Complex
<i>Nutrient Cycling</i>		
Mineral Cycles	Open	Closed
Nutrient Exchange Rate, with Environment	Rapid	Slow
*Role of Detritus in Nutrient Regeneration	Unimportant	Important
<i>Selection Pressure</i>		
Growth Form	For Rapid Growth ('r')	For Feedback Control ('K')
Production	Quantity	Quality
<i>Overall Homeostasis</i>		
Internal Symbiosis	Undeveloped	Developed
Nutrient Conservation	Poor	Good
Stability (resistance to external perturbations)	Poor	Good
Entropy	High	Low
Information	Low	High

Total biomass (which excludes detritus) is greatest at Looe Key, a feature characteristic of mature systems, and is more than two times as large as the Moorea reefs and over 34 times as large as that found at French Frigate Shoals. The total biomass that can be supported within a system can be expressed by the biomass/throughput ratio. This ratio can be expected to increase as an ecosystem matures (Odum 1971). The highest value comes from French Frigate Shoals, the reef system with the smallest biomass. Looe Key ranks 3rd.

The system omnivory index is a measure of the extent to which the ecosystem exhibits weblike features (Christensen and Pauly 1992a). The larger the value, the more trophic levels consumers utilize within the system. Thus, Looe Key appears to have the most weblike attributes, followed by the other Caribbean/Atlantic system, the USVI. The organisms in these systems are not specialized to the extent that they appear to be in the Pacific systems, although this may be an artifact of the number of groups used in each model. Both the Looe Key and USVI models used fewer boxes than the Moorea models, and thus aggregated many species. However, when the number of boxes in the two Moorea models was reduced to 20 via the aggregation routine in ECOPATH, the system omnivory indices decreased, thus confirming that the Pacific reef systems for which models have been constructed contain organisms which are more specialized relative to the two Caribbean/Atlantic systems. Interestingly, the model with the fewest groups (thus the most aggregation; FFS) had the lowest omnivory index. Finn's cycling index is calculated as the percentage of detritus that is recycled over that which passes through the system (Christensen and Pauly 1992a). The recycling of materials within a system is hypothesized to increase with increasing maturity (Odum 1969; Christensen and Pauly in press) and with system resilience (Vasconcellos *et al.* in press). For this measure, Looe Key ranks 4th. It is interesting to note that a higher recycling is evident in the fringing reefs of Moorea; a system which is highly dependent on outside resources due to its negative net production.

From the comparisons presented above, no clear trends emerge as to the overall ranking of Looe Key relative to other coral reefs in terms of maturity. For two out of the six attributes analyzed, the

Table 7. Model outputs from five coral reef ecosystems presented for comparison in relation to Odum's attributes in Table 6. * represents the values best associated with 'maturity.'

Reef System	Number of Model Boxes	Net System Production (t · km ⁻² · year ⁻¹)	P/R	Total Biomass (t · km ⁻²)	Total Biomass/Total Throughput (year ⁻¹)	Omnivory Index (-)	Finn's Cycling Index (%)
Looe Key ^a	20	7357	1.3	6037*	0.042	0.237*	15.1
Virgin Islands ^b	21	157*	1.0*	3903	0.049	0.227	16.0
FFS ^c	16	413	1.5	175	0.058*	0.128	5.4
Moorea Fringing ^d	43	-29644	0.4	2806	0.018	0.169	27.4
Moorea Barrier ^d	46	1736	1.1	2421	0.015	0.169	55.9*

^a) This study.

^b) United States Virgin Islands (Opitz 1991; 1993).

^c) French Frigate Shoals (FFS; Polovina (1984).

^d) Moorea Fringing and Barrier reefs (Arias-González 1993).

system appears the most mature, but for the others, it appears to fall right in the middle. For four out of the six attributes, the Caribbean region appears to contain more mature reefs. However, there are still too few systems in the form of ECOPATH models in the Caribbean and Pacific regions to make any generalizations. Perhaps there is a real difference, but more likely, the differences in the numbers presently available are due to the variations in the methods and assumptions used to construct the models themselves.

5.3.3 *Comparison with Other Coral Reef Ecosystems*

Of the models discussed above, the fringing reef of Moorea differs most from Looe Key in both structure and function. This system apparently receives heavy input from outside and accumulates detritus. Arias-González (1993) described the reef as having over half of its surface covered with detrital materials. The system is large in terms of energy flow, with a throughput of over $160000 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. However, while gross primary production ($17789 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$) is about half as that calculated for Looe Key, total system respiration is more than twice as high ($47433 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$). Thus the Moorea fringing reef system is a net consumer as opposed to the Looe Key system (and others, see Table 7). The Moorea fringing reef appears to be highly dependent upon the secondary production of detritus, with 86% of its flows originating there. This in itself does not differentiate the fringing reef of Moorea from Looe Key, and other systems, but the transfer efficiencies are much lower than those found at Looe. This indicates that, relative to Looe Key, a greater proportion of the production at each discrete trophic level is lost. However, the degree of detritus recycling in the Moorea fringing reef system is higher than that calculated for Looe Key (Table 7), which means that detritus is more efficiently recycled in this system.

The Moorea barrier reef system described by Arias-González (1993), like the fringing reef described above, is also larger in terms of energy flow than Looe Key, with a total throughput of almost $166000 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. However, gross production is much lower than, and respiration is similar to that of Looe Key. The system is a net producer, but has a P/R value closer to 1 than Looe Key. This indicates that the Moorea barrier reef system utilizes its primary production more efficiently than does Looe Key. Secondary production is also based on detritus, where 83% of all flows originate. This value is slightly higher than the 75% calculated for Looe Key. Like the fringing reef, the Moorea barrier reef has lower transfer efficiencies than Looe Key. The degree of detritus recycling (56%) in the Moorea barrier reef system is the highest yet calculated for a coral reef ecosystem.

The French Frigate Shoals coral reef system is much smaller than Looe Key in many ways. Total throughput ($3017 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$) is almost 50 times smaller than at Looe Key. Gross primary production and respiration are 25 times and 29 times as small, respectively. The system appears to be a net producer with a P/R value of 1.5, a value higher than in Looe Key. The French Frigate Shoals system is far less dependent on detritus (14% of all flows originate there) than Looe Key and the other systems discussed

above, which results from its very low (5.4%) degree of detritus recycling. The low degree of detritus recycling is clearly related to the low observed production and respiration rates of the French Frigate Shoals system. Opitz (1996) suspected that the low production and respiration rates were due to the reefs being located at a high latitude, but both Looe Key, at a similar latitude, and the Houtman Abrolhos reefs (Smith 1981), at an even higher latitude, do not show reduced production rates compared to other coral reef systems. Despite its almost total dependence on primary production, transfer efficiencies at French Frigate Shoals are lower than that found at Looe Key, a system highly dependent on the secondary production of detritus. This may result in the small total system biomass value calculated for the French Frigate Shoals system, as there is less production to support it, and the production available to it is not used efficiently.

The Virgin Islands coral reef ecosystem appears to be the most similar to the Looe Key system, although many of its biomass estimates are not as high. However, much of the similarity is probably the result of the similar database used to construct the models. At $80456 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, total throughput was roughly $60000 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ less than that of Looe Key. Both gross primary production ($19969 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$) and respiration ($19812 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$) were smaller than the calculated values for Looe Key. The P/R ratio was lower and closer to one for the Virgin Islands ecosystem, which indicates a more efficient use of system production than that found at Looe Key. The dependency of the system on the secondary production of detritus was less (66% of all flows) than that of Looe Key, but the degree of recycling was slightly higher (16%). Trophic transfer efficiencies were similar between the two systems and were generally higher than those calculated for all other coral reef models. Opitz (1996) noted that the transfer efficiencies between trophic levels I to II and II to III were high compared to those between other trophic levels and hypothesized that there are 'shortcuts' for recycling between these levels which account for the majority of throughput through the system. She reasoned that because the herbivorous fishes in her model had low EE's and their mortality (P/B) was higher than other similar sized fishes, a large proportion of their production was left to accumulate in the detritus. The nutrients from their decomposition are then available for benthic autotrophs to use. These autotrophs are then consumed by the herbivorous fishes, thus completing the cycle. Although similar transfer efficiencies were found at Looe Key between these trophic levels, the EE's of the herbivorous fish groups was near 1, indicating little excess production of biomass. Thus, the same sort of cycling may be going on at Looe Key as is in the Virgin Islands, but not to as great an extent. The feces of herbivorous fishes also contribute to the recycling of nutrients by increasing the amount available for benthic production. The contribution of feces to the available nutrient pool is probably far more important than the decomposition of the fishes' bodies as its availability is more consistent and frequent. For example, Polunin (1988) and Klumpp and Polunin (1989) found that herbivorous fishes released large quantities of nutrients over their algal territories which may increase the production available for subsequent cropping. The high biomass of

herbivorous fishes in the Looe Key system suggests that this mechanism may be partly responsible for the large productivity calculated and the increased transfer efficiencies at the herbivore-associated trophic levels.

5.4 Seasonal Models

There exist relatively large seasonal changes in the structure and functioning of the Looe Key National Marine Sanctuary ecosystem, especially at the lower trophic levels. In terms of flow, the system is much larger during the warmer summer months than during the cooler winter. Perhaps the most important thing to be noticed is that the system is a net producer in the summer ($P/R = 1.7$) and a net consumer in the winter ($P/R = 0.9$). This phenomenon has been observed in other reef systems whose production has been measured during the two seasons (One Tree Reef; Kinsey and Domm 1974; Kinsey 1977, Houtman Abrolhos; Smith 1981). Primary production in the Looe Key system is about 2.8 times higher in the summer than in winter, a value slightly higher than the one estimated in Figure 5. However, this value agrees with Kinsey (1985), who noted a range of 1.7 - 2.5 times more production in summer than in winter (see Table 1).

During the summer, a larger proportion of the biomass than in winter is supported through direct links to the primary producers. The total system biomass is somewhat smaller during the winter, but is more dependent on detritus accumulated during the more productive seasons. Still, the overall degree of recycling within the system is higher during summer than in winter. This may be linked to higher rates of herbivory in summer and the short cycles referred to above.

The value used as an estimate of grazing rate change in the model (1.8 times, from Polunin and Klumpp 1992, which was derived from a study at a lower latitude than Looe Key) may, however, reflect a smaller change than the one which actually takes place at Looe Key. A recent study has shown that on reefs in the Florida Keys, grazing rates may vary by as much as 6.3 times from winter to summer (Schmitt in prep.). This greater fluctuation in grazing intensity would enhance the effects on ecosystem flow discussed above, with an even greater dependence on detritus in winter and increased throughput from primary producers during summer.

Phytoplankton becomes 7 times more abundant in summer and zooplankton 3 times more abundant (Bsharah 1957), and thus is an overly abundant food source for planktivores during this season. Plankton becomes scarce during the winter and organisms which depend on it for food must change their diet or risk starvation. These relationships are reflected in the different EE values for the plankton groups which are substantially lower in summer than in winter. The absence of plankton in the winter was compensated for by increasing the amount of detritus in the diets of planktivores. This was the most straight forward method for balancing the winter model, as initial runs yielded EE values greater than 1 for the plankton groups. Food preferences (i.e., Ivlev's indices, see above; Appendix 4) for the groups

were not altered during this process. The increased amount of detrital material in the diets of planktivorous groups implies an even greater dependence on detritus in the system as it is consumed higher in the trophic web during winter than in any other season.

The values for primary production are intermediate in the spring and fall. As stated earlier, these seasons were parameterized to represent transitional times between summer and winter extremes. Their P/R ratios are positive, and a smaller proportion of the flows within the ecosystem originate from the secondary production of detritus, although the value is greater than that of the winter. The system becomes increasingly dependent upon detritus in the fall and primary production in the spring, as the system goes through its seasonal production cycle.

The biomasses of most functional groups change slightly over the seasonal cycle (Appendix 7), mainly as a function of temperature-varying mortality and consumption rates. For the fish groups, these changes mimic the effect of seasonal recruitment cycles (see Chapter 2): recruitment episodes occur during the spring and summer months in the Florida Keys, and abundances of fishes monitored on artificial reefs increased during this period and subsequently declined throughout the remainder of the year (Bohnsack *et al.* 1994). It has been shown that fish populations at Looe Key show increasing abundances during the spring up to annual peaks during the summer months (Gorham and Alevizon 1989). Changes in biomass associated with these pulses of settlement vary less than changes in abundance (Bohnsack *et al.* 1994). The seasonal fluctuations in biomass calculated from the models are relatively small and thus in good agreement with the admittedly scanty field evidence, as is the steady increase in biomass possibly associated with recruitment during the spring which is accounted for in ECOPATH by the biomass accumulation term.

In conclusion, it appears that a marked seasonality in ecosystem structure and function occurs at Looe Key, and within reef habitats in the Florida Keys in general. These changes were modeled here as a function of seasonal changes in temperature and fluctuations in food supply on the reef. Primary productivity is higher during the warmer months of the year and the detritus produced during these times apparently sustains the system through the period of heterotrophy in winter. This winter reliance on detritus is reflected in the greater heterogeneity of the diets of many groups evidenced by the increased system omnivory index during winter in comparison to the other seasons (Table 4). Thus, the secondary production of the detritus is carried through the trophic levels, through detritivory, and subsequently through predation on detritivores.

Biomass fluctuations are relatively small for groups trophically higher in the food web (<7%). These top predators have high longevities and hence their populations, when no fishing pressure exists, is relatively stable since their mortality rates are low. The low P/B and Q/B values allow for only small changes in biomass to occur when the temperature changes from season to season, and thus keeps biomass fluctuations relatively small. The increases, along with being associated to the temperature-

dependent P/B changes, may also be associated with recruitment episodes, which could potentially increase abundances of juveniles, and their subsequent growth during the summer maximums of system productivity and temperature, although this hypothesis was not modeled. The declines which occur throughout the fall and winter may reflect steady rates of mortality enacting on system components that have no additional sources of input (i.e., recruitment pulses). Since the biomass of the system is lower in winter, a lower throughput is required to sustain the system as apparent in the smaller ratio of total system biomass/total system throughput (Table 4).

5.5 Dynamic Simulations

5.5.1 *EcoSim as a Tool*

A dynamic subroutine, called EcoSim, has been recently developed which re-expresses the linear equations of ECOPATH as differential equations (Walters *et al.* 1997). This allows the trophic relationships defined in the mass balance approach of ECOPATH to be simulated over time when perturbations are introduced to the system. Thus, changes in the biomasses of groups within the system chosen, and thus changes in the structure and functioning of the ecosystem, can be followed over time. EcoSim works through user-specified changes in fishing mortality subjected on groups in the system and simulates the subsequent changes that are incurred over a given period. Thus, EcoSim can be used by managers to analyze fishery policy changes for any group defined by ECOPATH and their biological effects on the rest of the ecosystem through changes in equilibrium biomasses (Walters *et al.* 1997). EcoSim has been shown to be a useful tool for analyzing 'top-down' and 'bottom-up' effects (Mackinson *et al.* in press) and system stability (Vasconcellos *et al.* in press) when various schemes of fishing pressure were introduced to upwelling systems.

One ecosystem effect will be simulated in the Looe Key National Marine Sanctuary ecosystem here, i.e., the impact of an increase of fishing mortality (F) from the baseline of zero to an arbitrary value of 0.4 year^{-1} for large groupers, midwater piscivores, and large reef carnivores. The objective of this simulation is to assess changes in Looe Key ecosystem structure which could potentially occur when spearfishing pressure is exerted on the large predators in the system. Spearfishers target the larger predatory fishes due to their greater food and sport value (Bohnsack 1982).

5.5.2 *Response of Ecosystem to Spearfishing*

Figure 9 shows the response of the Looe Key ecosystem when the large predators are subjected to a constant fishing mortality of 0.4 year^{-1} following 10 years of simulation at baseline levels. The relative biomass of each group can be seen to change during the first years after spearfishing is introduced. With spearfishing, the large groupers are fished out almost immediately and do not recover

over the subsequent 80 - 90 years. Thus, the groupers are especially sensitive to perturbations affecting their biomass and mortality relative to the other groups. Large reef carnivores quickly reach a new equilibrium level after an initial drastic decrease. This biomass level is roughly half of what the system sustained before spearfishing was initiated. The midwater piscivores are the least effected group with only a small drop in biomass, followed by a small increase to a new equilibrium level. It is interesting to note that even when groupers are not fished at all, but spearfishing pressure exists for the other two groups, grouper biomass still crashes due to decreased availability of food fishes. This suggests that this group is extremely sensitive to perturbations to the system.

The lower equilibrium biomasses of these predators and the collapse of groupers in the presence of spearfishing has mixed direct and indirect effects on the biomasses of the other groups in the system. Small positive effects can be seen for worms and molluscs, cephalopods, echinoderms, phytoplankton, decomposers/microfauna, sessile animals, small herbivorous fishes, large and small planktivorous fishes and sharks and rays. Larger increases occur for small carnivorous and large herbivorous fishes. Small negative impacts occur for zooplankton, benthic producers and sessile animals.

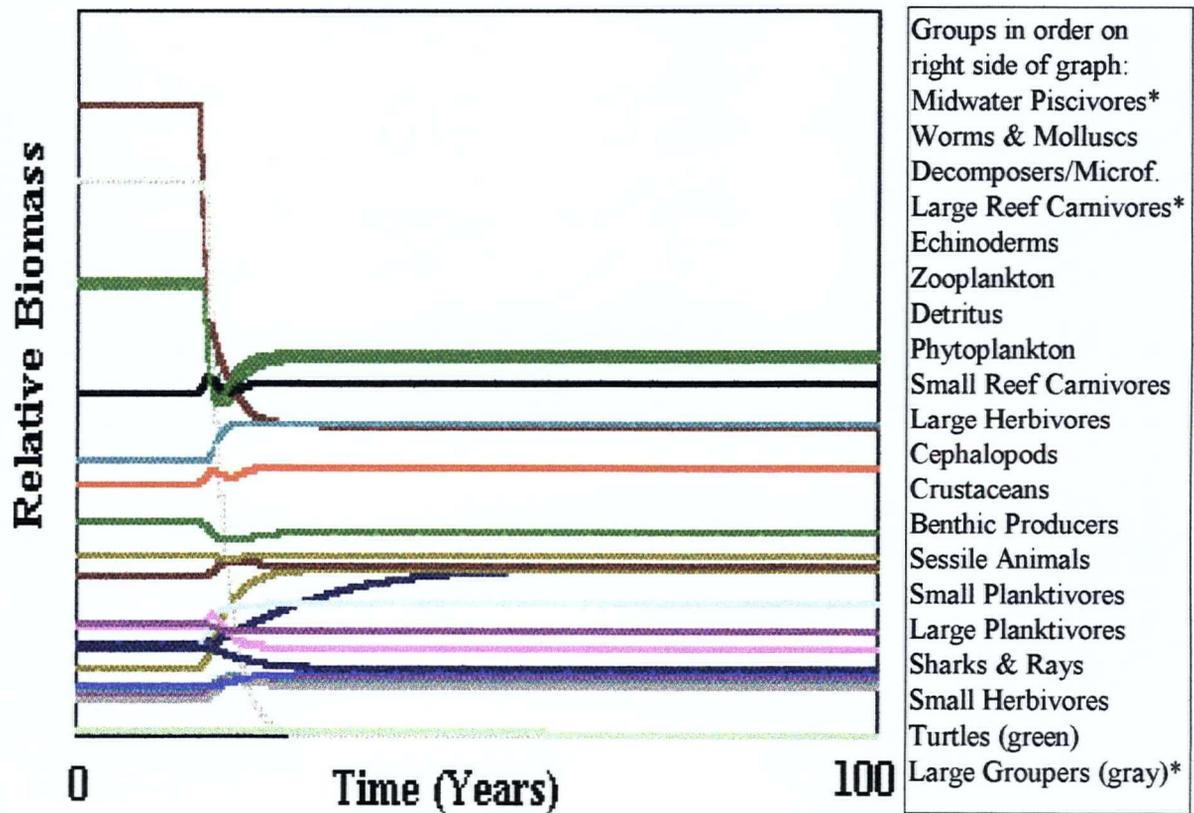


Figure 9. Response of ecosystem functional groups to the introduction of spearfishing (at $t = 10$ years) on the large predators (marked with a *). A fishing mortality of 0.4 year^{-1} was used (see text).

The larger relative increases in small carnivorous and large herbivorous fish biomass suggests that these groups were originally constrained by the larger predators. Once the latter are reduced, there is an ecological release and the former increase. These increases probably result in the subsequent declines in the benthic producers and sessile animals shown in Figure 9. The magnitude of other invertebrate group increases is probably restrained by the rise in small carnivore abundance. The small decrease in zooplankton abundance probably results from the small increases in the planktivorous fish groups. It is also likely to cause the small increase in the biomass of phytoplankton. The biomass of crustaceans remains relatively constant over time suggesting that the decreased predation pressure from a reduction in large carnivore biomass is balanced by increases in their other predators (see also Fig. 7).

The overall results of the simulation suggests that system biomass may very well remain constant, but that the majority of the fish biomass will consist of large herbivores and small carnivores. Bohnsack (1982) compared Looe Key, when spearfishing was legal to two other protected reefs where spearfishing was illegal. He found that Looe Key had smaller piscivore and more abundant small carnivore (especially Haemulidae) populations than the other protected reefs. Large lutjanids and haemulids were conspicuously absent from Looe Key, while present in significantly higher abundances at the two control reefs. These fishes were replaced at Looe by smaller haemulids (notably *H. aurolineatum*) and labrids which obtained significantly higher abundances there than at the other reefs. One small serranid increased in abundance at the fished reef, which was probably the result of reduced predation pressure by large piscivores (Bohnsack 1982). Despite the differences in the abundances of larger species, similarity indices suggested that community structure among the three reefs was generally the same (Bohnsack 1982).

These results are similar to the results obtained using EcoSim. The Looe Key ecosystem, and other reefs along the Florida Reef Tract, apparently react by a shift in biomass to small carnivores and larger herbivores, although the large herbivores were apparently also targeted by the spearfishery that existed at Looe Key, as evidenced in the reduced abundances of some large scarids in Bohnsack (1982). The relatively small decrease of midwater piscivores shown in Figure 9 is probably due to the replacement of some of the targeted species by non-target species such as *Sphyraena barracuda* (Bohnsack 1982). The change in the distribution of biomass and the relatively small changes which occurred at the lower trophic levels, suggest that the level of various fish populations on Florida reefs are controlled by predation though their overall biomass is not.

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Appendix 1. Additional length-weight relationship parameters provided as a supplement to the report by Bohnsack and Harper (1988) by J. Bohnsack of the National Marine Fisheries Service, Miami, Florida to the author. Regression formula: $\log \text{ weight (gms)} = \log a + b \log \text{ length (mm)}$. TL = total length; FL = fork length; DW = disk width.

Species	Length Type	log a	b
<i>Acanthemblemaria aspera</i>	TL	-5.0750	2.9625
<i>A. chaplini</i>	TL	-4.8221	3.0780
<i>Aetobatus narinari</i>	DW	-5.5182	2.6724
<i>Alectis ciliaris</i>	FL	-4.4953	2.9085
<i>Atherinomorus stipes</i>	FL	-4.8641	2.9600
<i>Bothus ocellatus</i>	TL	-5.1974	3.1894
<i>Calamus</i> species	FL	-4.1688	2.8009
<i>Canthigaster rostrata</i>	TL	-5.8424	3.6378
<i>Caranx latus</i>	FL	-4.0201	2.7344
<i>Centropyge argi</i>	TL	-4.3950	2.8994
<i>Chilomycterus antennatus</i>	TL	-4.7512	3.1244
<i>Chromis cyaneus</i>	FL	-4.8921	3.1519
<i>C. enchrysurus</i>	FL	-4.8921	3.1519
<i>C. flavicauda</i>	FL	-4.8921	3.1519
<i>C. multilineatus</i>	FL	-4.8921	3.1519
<i>C. scotti</i>	FL	-4.8921	3.1519
<i>Clepticus parrae</i>	FL	-4.9130	3.0430
<i>Coryphopterus dicrus</i>	TL	-4.8489	2.9674
<i>C. eidolon</i>	TL	-4.8489	2.9674
<i>C. personatus</i>	TL	-4.8489	2.9674
<i>Dactylopterus volitans</i>	FL	-4.9430	3.0285
<i>Decapterus macarellus</i>	FL	-4.8641	2.9600
<i>D. punctatus</i>	FL	-4.8641	2.9600
<i>Diodon</i> species	TL	-2.5498	2.2763
<i>Diplodus argenteus</i>	FL	-5.2350	3.2504
<i>Doratonotus megalepis</i>	TL	-4.9130	3.0430
<i>Elagatis bipinnulata</i>	FL	-4.8641	2.9600
<i>Epinephelus adscensionis</i>	TL	-5.0680	3.1124
<i>E. fulvus</i>	TL	-4.6508	2.9330
<i>E. niveatus</i>	TL	-7.6108	2.9300
<i>Equetus punctatus</i>	TL	-5.2620	3.2017
<i>E. umbrosus</i>	TL	-5.2620	3.2017
<i>Euthynnus alletteratus</i>	FL	-4.9211	3.0350
<i>Fistularia tabacaria</i>	TL	-5.2686	2.8657
<i>Gobiosoma evelynae</i>	TL	-5.2341	3.1370
<i>G. macrodon</i>	TL	-5.2341	3.1370
<i>Gymnothorax saxicola</i>	TL	-6.1561	3.1577
<i>Haemulon</i> sp. (early juvenile)	FL	-5.2562	3.2692
<i>Halichoeres pictus</i>	TL	-4.8117	2.9391
<i>H. poeyi</i>	TL	-4.8117	2.9391
<i>Harengula jaguana</i>	FL	-5.2800	3.2800
<i>Hemipteronotus martinicensis</i>	TL	-4.8221	3.0780
<i>H. novacula</i>	TL	-3.5613	2.2430
<i>H. splendens</i>	TL	-5.0012	2.9995
<i>Hemiemblemaria simulus</i>	TL	-4.8221	3.0780
<i>Holocentrus vexillarius</i>	FL	-3.6218	2.5596

Appendix 1 continued

Species	Length Type	log a	b
<i>Hypoatherina harringtonensis</i>	FL	-5.2800	3.2800
<i>Hypoplectrus chlorurus</i>	FL	-5.2894	2.8553
<i>H. gemma</i>	FL	-4.8858	3.0571
<i>H. guttavarius</i>	FL	-5.2894	2.8553
<i>H. indigo</i>	FL	-5.2894	2.8553
<i>H. nigricans</i>	FL	-5.2894	2.8553
<i>H. puella</i>	FL	-5.2894	2.8553
<i>H. unicolor</i>	FL	-5.2894	2.8553
<i>Inermia vittata</i>	FL	-4.8641	2.9600
<i>Ioglossus calliurus</i>	TL	-4.8865	2.9162
<i>I. helenae</i>	TL	-4.8865	2.9162
<i>Jenkinsia species</i>	FL	-5.2800	3.2800
<i>Liopropoma eukrines</i>	TL	-4.8862	3.0475
<i>Malacanthus plumieri</i>	FL	-4.1981	2.6290
<i>Malacoctenus aurolineatus</i>	TL	-4.8489	2.9674
<i>M. gilli</i>	TL	-4.8489	2.9674
<i>M. versicolor</i>	TL	-4.8489	2.9674
<i>Melichthys niger</i>	FL	-4.5359	2.9352
<i>Microgobius carri</i>	TL	-4.8865	2.9162
<i>Monacanthus tuckeri</i>	TL	-3.9200	2.6178
<i>Mycteroperca interstitialis</i>	FL	-4.9169	3.0305
<i>M. phenax</i>	FL	-4.9169	3.0305
<i>M. venenosa</i>	FL	-4.9169	3.0305
<i>Nicholsina usta</i>	TL	-5.7587	3.4291
<i>Ogcocephalus nasutus</i>	FL	-4.9854	3.0073
<i>Opistognathus aurifrons</i>	TL	-5.0210	2.9895
<i>Paraclinus marmoratus</i>	TL	-4.8221	3.0780
<i>Pomacentrus diencaeus</i>	FL	-4.2782	2.8569
<i>Rhinobatos lentiginosus</i>	TL	-5.1910	2.9703
<i>Rypticus saponaceus</i>	TL	-5.3550	3.2370
<i>Scartella cristata</i>	TL	-3.8680	2.3791
<i>Scarus vetula</i>	TL	-5.0162	3.1109
<i>Scomberomorus regalis</i>	FL	-5.0538	2.9731
<i>Serranus tabacarius</i>	FL	-4.8862	3.0475
<i>S. tortugarum</i>	FL	-4.8862	3.0475
<i>Sparisoma radians</i>	FL	-5.7587	3.4291
<i>Sphyrna lewini</i>	TL	-5.9300	3.2300
<i>Trachinotus falcatus</i>	FL	-4.4953	2.9085
<i>Tylosurus crocodilus</i>	FL	-3.3362	2.3555

Appendix 2. Composition of fish boxes. Species were determined from Bohnsack *et al.* (1987) and aggregated according to Opitz (1993; 1996).

ECOPATH Box	Family	Common Name	Species
Sharks & Rays	Orectolobidae	Nurse Shark	<i>Ginglymostoma cirratum</i>
	Dasyatidae	Southern Stingray	<i>Dasyatis americana</i>
		Yellow Stingray	<i>Urolophus jamaicensis</i>
	Myliobatidae	Spotted Eagle Ray	<i>Aetobatus narinari</i>
Midwater Piscivores	Carangidae	Yellow Jack	<i>Caranx bartholomaei</i>
		Blue Runner	<i>C. crysos</i>
		Bar Jack	<i>C. ruber</i>
		Greater Amberjack	<i>Seriola dumerili</i>
	Elopidae	Tarpon	<i>Megalops atlanticus</i>
	Scombridae	King Mackerel	<i>Scomberomorus cavalla</i>
		Spanish Mackerel	<i>S. maculatus</i>
		Cero	<i>S. regalis</i>
	Sphyraenidae	Great Barracuda	<i>Sphyraena barracuda</i>
	Large Groupers	Serranidae	Jewfish
Black Grouper			<i>Mycteroperca bonaci</i>
Large Carnivores	Aulostomidae	Trumpetfish	<i>Aulostomus maculatus</i>
	Balistidae	Scrawled Filefish	<i>Aluterus scriptus</i>
		Gray Triggerfish	<i>Balistes capriscus</i>
		Queen Triggerfish	<i>B. vetula</i>
		Ocean Triggerfish	<i>Canthidermis sufflamen</i>
		Redfin Needlefish	<i>Strongylura notata</i>
	Belonidae	Timucu	<i>S. timucu</i>
		Houndfish	<i>Tylosurus crocodilus</i>
	Carangidae	African Pompano	<i>Alectis ciliaris</i>
		Permit	<i>Trachinotus falcatus</i>
	Diodontidae	Porcupinefish	<i>Diodon hystrix</i>
		Balloonfish	<i>D. holocanthus</i>
	Echeneidae	Sharksucker	<i>Echeneis naucrates</i>

Appendix 2 continued

ECOPATH Box	Family	Common Name	Species	
	Ephippidae	Atlantic Spadefish	<i>Chaetodipterus faber</i>	
	Gerreidae	Yellowfin Mojarra	<i>Gerres cinereus</i>	
	Grammistidae	Greater Soapfish	<i>Rypticus saponaceus</i>	
	Haemulidae	Black Margate	<i>Anisotremus surinamenis</i>	
		Porkfish	<i>A. virginicus</i>	
		Margate	<i>Haemulon album</i>	
		Tomtate	<i>H. aurolineatum</i>	
		Caesar Grunt	<i>H. carbonarium</i>	
		Smallmouth Grunt	<i>H. chrysargyreum</i>	
		French Grunt	<i>H. flavolineatum</i>	
		Spanish Grunt	<i>H. macrostomum</i>	
		Cottonwick	<i>H. melanurum</i>	
		Sailors Choice	<i>H. parrai</i>	
		White Grunt	<i>H. plumieri</i>	
		Bluestriped Grunt	<i>H. sciurus</i>	
		Holocentridae	Squirrelfish	<i>Holocentrus ascensionis</i>
			Longspine Squirrelfish	<i>H. rufus</i>
		Labridae	Dusky Squirrelfish	<i>H. vexillarius</i>
			Spanish Hogfish	<i>Bodianus rufus</i>
	Puddingwife		<i>Halichoeres radiatus</i>	
	Lutjanidae	Hogfish	<i>Lachnolaimus maximus</i>	
		Mutton Snapper	<i>Lutjanus analis</i>	
		Schoolmaster	<i>Lutjanus apodus</i>	
		Gray Snapper	<i>L. griseus</i>	
		Dog Snapper	<i>L. jocu</i>	
		Mahogany Snapper	<i>L. mahogoni</i>	
		Lane Snapper	<i>L. synagris</i>	
	Malacanthidae	Yellowtail Snapper	<i>Ocyurus chrysurus</i>	
		Sand Tilefish	<i>Malacanthus plumieri</i>	
	Mullidae	Yellow Goatfish	<i>Mulloidichthys martinicus</i>	
		Spotted Goatfish	<i>Pseudupeneus maculatus</i>	
	Muraenidae	Viper Moray	<i>Enchelycore nigricans</i>	

Appendix 2 continued

ECOPATH Box	Family	Common Name	Species	
Small Carnivores	Ostaciidae	Green Moray	<i>Gymnothorax funebris</i>	
		Spotted Moray	<i>Gymnothorax moringa</i>	
		Goldentail Moray	<i>Muraena miliaris</i>	
		Honeycomb Cowfish	<i>Lactophrys polygonia</i>	
		Scrawled Cowfish	<i>L. quadricornis</i>	
		Pomacanthidae	Blue Angelfish	<i>Holacanthus bermudensis</i>
			Rock Beauty	<i>H. tricolor</i>
			Queen Angelfish	<i>H. ciliaris</i>
			Gray Angelfish	<i>Pomacanthus arcuatus</i>
		Priacanthidae	French Angelfish	<i>P. paru</i>
	Glasseye Snapper		<i>Priacanthus cruentatus</i>	
	Sciaenidae	High-hat	<i>Equetus acuminatus</i>	
		Jackknife-fish	<i>E. lanceolatus</i>	
		Spotted Drum	<i>E. punctatus</i>	
	Scorpaenidae	Reef Croaker	<i>Odontoscion dentex</i>	
		Spotted Scorpionfish	<i>Scorpaena plumieri</i>	
	Serranidae	Rock Hind	<i>Epinephelus adscensionis</i>	
		Graysby	<i>E. cruentatus</i>	
		Coney	<i>E. fulvus</i>	
		Red Hind	<i>E. guttatus</i>	
		Red Grouper	<i>E. morio</i>	
		Sparidae	Nassau Grouper	<i>E. striatus</i>
			Jolthead Porgy	<i>Calamus bajonado</i>
			Saucereye Porgy	<i>C. calamus</i>
			Sheepshead Porgy	<i>C. penna</i>
		Synodontidae	Red Porgy	<i>Pagrus pagrus</i>
	Sand Diver		<i>Synodus intermedius</i>	
Balistidae	Slender Filefish	<i>Monocanthus tuckeri</i>		
	Callionymidae	Lancer Dragonet	<i>Callionymus bairdi</i>	
		Chaetodontidae	Foureye Butterflyfish	<i>Chaetodon capistratus</i>
	Spotfish Butterflyfish		<i>C. ocellatus</i>	

Appendix 2 continued

ECOPATH Box	Family	Common Name	Species
		Reef Butterflyfish	<i>Chaetodon sedentarius</i>
		Banded Butterflyfish	<i>C. striatus</i>
	Cirrhitidae	Redspotted Hawkfish	<i>Amblycirrhitus pinos</i>
	Clinidae	Wrasse Blenny	<i>Hemiemblemaria simulus</i>
		Dusky Blenny	<i>Malacoctenus gilli</i>
		Rosy Blenny	<i>M. macropus</i>
		Saddled Blenny	<i>M. triangulatus</i>
		Barfin Blenny	<i>M. versicolor</i>
		Blackfin Blenny	<i>Paraclinus nigripinnis</i>
	Gobiidae	Tiger Goby	<i>Gobiosoma macrodon</i>
		Neon Goby	<i>G. oceanops</i>
	Holocentridae	Reef Squirrelfish	<i>Holocentrus coruscus</i>
	Labridae	Spotfin Hogfish	<i>Bodianus pulchellus</i>
		Slippery Dick	<i>Halichoeres bivattatus</i>
		Yellowhead Wrasse	<i>H. garnoti</i>
		Clown Wrasse	<i>H. maculipinna</i>
		Blackear Wrasse	<i>H. poeyi</i>
		Pearly Razorfish	<i>Hemipteronotus novacula</i>
		Green Razorfish	<i>H. splendens</i>
		Bluehead	<i>Thalassoma bifasciatum</i>
	Ostaciidae	Spotted Trunkfish	<i>Lactophrys bicaudalis</i>
		Smooth Trunkfish	<i>L. triqueter</i>
	Serranidae	Sand Perch	<i>Diplectrum formosum</i>
		Blue Hamlet	<i>Hypoplectrus gemma</i>
		Black Hamlet	<i>H. nigricans</i>
		Barred Hamlet	<i>H. puella</i>
		Butter Hamlet	<i>H. unicolor</i>
		Peppermint Bass	<i>Lioproma rubre</i>
		Lantern Bass	<i>Serranus baldwini</i>
		Tobaccofish	<i>S. tabacarius</i>
		Harlequin Bass	<i>S. tigrinus</i>
		Chalk Bass	<i>S. tortugarum</i>
	Tetradontidae	Sharpnose Puffer	<i>Canthigaster rostrata</i>

Appendix 2 continued

ECOPATH Box	Family	Common Name	Species
		Bandtail Puffer	<i>Sphoeroides spengleri</i>
Large Planktivores	Carangidae	Mackeral Scad Round Scad	<i>Decapterus macarellus</i> <i>D. punctatus</i>
	Holocentridae	Blackbar Soldierfish	<i>Myripristis jacobus</i>
	Inermiidae	Boga	<i>Inermia vittata</i>
	Labridae	Creole Wrasse	<i>Clepticus parrai</i>
	Pomacentridae	Sergeant Major Blue Chromis Brown Chromis	<i>Abudefduf saxatilis</i> <i>Chromis cyaneus</i> <i>C. multilineatus</i>
	Serranidae	Creole-fish	<i>Paranthias furcifer</i>
Small Planktivores	Apogonidae	Barred Cardinalfish Flamefish Twospot Cardinalfish Sawcheck Cardinalfish	<i>Apogon binotatus</i> <i>A. maculatus</i> <i>A. pseudomaculatus</i> <i>A. quadrisquamatus</i>
	Atherinidae	Hardhead Silverside	<i>Atherinomorus stipes</i>
	Clinidae	Papillose Blenny	<i>Acanthemblemaria chaplini</i>
	Clupeidae	Dwarf Herring	<i>Jenkinsia lamprotaenia</i>
	Gobiidae	Masked Goby Blue Goby Seminole Goby	<i>Coryphopterus personatus</i> <i>Ioglossus calliurus</i> <i>Microgobius carri</i>
	Labridae	Rainbow Wrasse	<i>Halichoeres pictus</i>
	Opistognathidae	Yellowhead Jawfish	<i>Opistognathus aurifrons</i>
	Pempheridae	Glassy Sweeper	<i>Pempheris schomburgki</i>
	Pomacentridae	Sunshinefish Purple Reefish Bicolor Damselfish	<i>Chromis insolatus</i> <i>C. scotti</i> <i>Pomacentrus partitius</i>
Large Herbivores	Balistidae	Orange Filefish Whitespotted Filefish	<i>Aluterus schoepfi</i> <i>Cantherhines macrocerus</i>
	Kyphosidae	Bermuda Chub	<i>Kyphosus sectatrix</i>
	Scaridae	Midnight Parrotfish	<i>Scarus coelestinus</i>

Appendix 2 continued

ECOPATH Box	Family	Common Name	Species
		Blue Parrotfish	<i>S. coeruleus</i>
		Striped Parrotfish	<i>S. croicensis</i>
		Rainbow Parrotfish	<i>S. guacamaia</i>
		Princess Parrotfish	<i>S. taeniopterus</i>
		Queen Parrotfish	<i>S. vetula</i>
		Redband Parrotfish	<i>Sparisoma aurofrenatum</i>
		Redtail Parrotfish	<i>S. chrysopterus</i>
		Redfin Parrotfish	<i>S. rubripinne</i>
		Stoplight Parrotfish	<i>S. viride</i>
Small Herbivores			
	Acanthuridae	Ocean Surgeonfish	<i>Acanthurus bahianus</i>
		Doctorfish	<i>A. chirurgus</i>
		Blue Tang	<i>A. coeruleus</i>
	Balistidae	Orangespotted Filefish	<i>Cantherhines pullus</i>
	Blenniidae	Redlip Blenny	<i>Ophioblennius atlanticus</i>
		Molly Miller	<i>Scartella cristatus</i>
	Gobiidae	Colon Goby	<i>Coryphopterus dicrus</i>
		Bridled Goby	<i>C. glaucofraenum</i>
		Goldspot Goby	<i>Gnatholepis thompsoni</i>
	Pomacentridae	Yellowtail Damselfish	<i>Microspathodon chrysurus</i>
		Longfin Damselfish	<i>Pomacentrus dieneaeus</i>
		Dusky Damselfish	<i>P. fuscus</i>
		Beaugregory	<i>P. leucostictus</i>
		Threespot Damselfish	<i>P. planifrons</i>
		Cocoa Damselfish	<i>P. variabilis</i>
	Scaridae	Bluelip Parrotfish	<i>Cryptotomus roseus</i>
		Greenblotch Parrotfish	<i>Sparisoma atomarium</i>
		Bucktooth Parrotfish	<i>S. radians</i>

Appendix 3. Locations, details and sources of data used to construct Figure 5 (Chapter 3). The temperature ranges presented are based on the difference between highest and lowest monthly averages. GPP is the gross primary production measured in $\text{gC} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ of the reef or section of reef studied.

Reef Location	Reef Type	Temp.Range (°C)	Summer/Winter Ratio of GPP	Source(s)
North Kapaa Reef, HI	Fringing Reef	1.5	1.1	Kohn and Helfrich (1957)
Lizard Island, GBR	Reef Flat	2.5	2.4	Kinsey (1977; 1979)
Kaneohe Bay, HI	Fringing Reef	3.2	2.0	Clausen and Roth (1975); Kinsey (1979)
French Frigate Shoals, HI	Reef Flat	3.8	2.0	Atkinson and Grigg (1984)
French Frigate Shoals, HI	Lagoon Habitats (excluding patch reefs)	3.8	1.1	Atkinson and Grigg (1984)
French Frigate Shoals, HI	Lagoon Patch Reefs	3.8	2.7	Atkinson and Grigg (1984)
Houtman Abrolhos, Aust.	Whole Reef	3.9	1.7	Crossland (1981); Smith (1981)
Davies Reef, GBR	Reef Slope (10 m) Algal Community	5.0	1.5	Klumpp and McKinnon (1989)
Davies Reef, GBR	Reef Flat Algal Community	5.8	1.6	Klumpp and McKinnon (1989)
One Tree Reef, GBR	Lagoon Patch Reef	7.0	2.4	Kinsey and Domm (1974)
One Tree Reef, GBR	Reef Flat	9.5	2.5	Kinsey (1977)

Appendix 4. Ivlev's electivity indices for all models calculated by ECOPATH II version 2.22. The index is defined by values between -1 and 1 such that positive values indicate a preference for a particular prey item and 1 corresponds to exclusive feeding on that prey. Negative values indicate a general aversion to a prey item and -1 indicates total avoidance. Values close to 0 represent non-selective feeding on a prey group. A.A. = annual average model; Sum. = summer model; Win. = winter model; Spr. = spring model.

Predator	Prey	Ivlev's Electivity Index				
		A.A.	Sum.	Win.	Spr.	Fall
Sharks and Rays	Sharks and Rays	0.944	0.945	0.942	0.943	0.943
	Large Planktivores	0.245	0.246	0.245	0.243	0.243
	Large Reef Carnivores	-0.592	-0.595	-0.588	-0.593	-0.593
	Small Planktivores	0.329	0.327	0.333	0.327	0.327
	Small Reef Carnivores	0.579	0.576	0.585	0.578	0.578
	Large Groupers	0.973	0.973	0.973	0.973	0.973
	Small Reef Herbivores	0.748	0.749	0.747	0.747	0.747
	Large Reef Herbivores	0.437	0.433	0.445	0.436	0.436
	Cephalopods	0.938	0.937	0.939	0.938	0.938
	Echinoderms	-0.579	-0.572	-0.586	-0.581	-0.581
	Crustaceans	0.775	0.771	0.782	0.775	0.775
	Worms & Molluscs	0.482	0.473	0.496	0.482	0.482
	Sessile Animals	-0.924	-0.922	-0.925	-0.924	-0.924
	Detritus	-0.945	-0.944	-0.946	-0.945	-0.945
	Midwater Piscivores	Midwater Piscivores	0.753	0.757	0.748	0.703
Large Planktivores		0.791	0.792	0.791	0.775	0.775
Large Reef Carnivores		0.538	0.535	0.543	0.508	0.508
Small Planktivores		0.845	0.844	0.846	0.834	0.834
Small Reef Carnivores		0.649	0.646	0.653	0.648	0.648
Small Reef Herbivores		0.857	0.858	0.857	0.847	0.847
Large Reef Herbivores		0.729	0.727	0.734	0.703	0.703
Cephalopods		0.737	0.733	0.743	0.737	0.737
Crustaceans		0.088	0.077	0.104	0.087	0.087
Worms & Molluscs		-0.267	-0.278	-0.250	-0.268	-0.268
Large Planktivores	Zooplankton	0.502	0.345	0.710	0.862	0.862
	Crustaceans	0.088	0.077	0.104	0.087	0.087
	Worms & Molluscs	-0.035	-0.047	-0.017	-0.036	-0.036
	Sessile Animals	-0.368	-0.360	-0.378	-0.372	-0.372
	Zooplankton	0.982	0.973	0.978	0.956	0.956
	Decomposers/Microfauna	-	-	-	0.862	0.862
	Benthic Producers	-0.945	-0.943	-0.946	-0.944	-0.944
Large Reef Carnivores	Detritus	-	-	-0.315	-0.308	-0.308
	Midwater Piscivores	-0.867	-0.865	-0.870	-0.866	-0.866
	Large Planktivores	-0.583	-0.582	-0.582	-0.584	-0.584
	Large Reef Carnivores	0.123	0.119	0.130	-0.133	-0.133
	Small Planktivores	0.408	0.406	0.412	0.406	0.406
	Small Reef Carnivores	0.533	0.530	0.539	0.401	0.401
	Small Reef Herbivores	-0.181	-0.179	-0.182	-0.184	-0.184
	Cephalopods	0.572	0.566	0.580	0.571	0.571
	Echinoderms	0.208	0.217	0.197	0.204	0.204
	Crustaceans	0.498	0.490	0.510	0.457	0.457
	Worms & Molluscs	0.510	0.501	0.523	0.473	0.473
	Sessile Animals	-0.597	-0.590	-0.604	-0.513	-0.513
	Zooplankton	0.895	0.850	0.844	0.780	0.780

Appendix 4 continued

Predator	Prey	Ivlev's Electivity Index					
		A.A.	Sum.	Win.	Spr.	Fall	
Small Planktivores	Decomposers/Microfauna	-	-	-	-0.288	-0.288	
	Benthic Producers	-0.602	-0.596	-0.693	-0.684	-0.684	
	Detritus	-	-	-0.699	-0.600	-0.600	
	Small Planktivores	-0.519	-0.520	-0.515	-0.520	-0.520	
	Crustaceans	-0.473	-0.481	-0.460	-0.473	-0.473	
	Sessile Animals	-0.958	-0.957	-0.959	-0.958	-0.958	
	Zooplankton	0.986	0.980	0.978	0.956	0.956	
Small Reef Carnivores	Decomposers/Microfauna	-0.622	-0.714	0.935	0.902	0.902	
	Phytoplankton	-0.426	-0.620	0.223	-0.429	-0.429	
	Detritus	-	-	-0.070	-0.063	-0.063	
	Large Reef Carnivores	-0.696	-0.698	-0.692	-0.697	-0.697	
	Small Planktivores	-0.727	-0.728	-0.724	-0.727	-0.727	
	Echinoderms	-0.293	-0.284	-0.303	-0.297	-0.297	
	Crustaceans	0.409	0.400	0.423	0.409	0.409	
	Worms & Molluscs	0.345	0.334	0.361	0.301	0.031	
	Sessile Animals	-0.548	-0.541	-0.555	-0.550	-0.550	
	Zooplankton	0.920	0.885	0.919	0.846	0.846	
	Decomposers/Microfauna	-	-	0.863	0.797	0.797	
Large Groupers	Benthic Producers	-0.237	-0.228	-0.248	-0.232	-0.232	
	Detritus	-0.494	-0.486	-0.502	-0.458	-0.458	
	Sharks and Rays	0.944	0.945	0.942	0.943	0.943	
	Large Reef Carnivores	0.875	0.875	0.877	0.875	0.875	
	Crustaceans	0.846	0.843	0.851	0.846	0.846	
	Small Reef Herbivores	Echinoderms	-0.975	-0.974	-0.975	-0.975	-0.975
Worms & Molluscs		-0.982	-0.982	-0.981	-0.982	-0.982	
Zooplankton		-0.247	-0.418	0.083	-0.251	-0.251	
Benthic Producers		0.442	0.484	0.468	0.481	0.481	
Detritus		-0.979	-0.979	-0.979	-0.979	-0.979	
Large Reef Herbivores	Crustaceans	-0.942	-0.943	-0.940	-0.942	-0.942	
	Sessile Animals	-0.965	-0.964	-0.965	-0.965	-0.965	
	Benthic Producers	0.442	0.450	0.433	0.447	0.447	
	Detritus	-0.730	-0.725	-0.735	-0.732	-0.732	
Sea Turtles	Echinoderms	-0.326	-0.317	-0.336	-0.329	-0.329	
	Crustaceans	0.577	0.570	0.588	0.576	0.576	
	Worms & Molluscs	-0.409	-0.419	-0.393	-0.409	-0.409	
	Sessile Animals	0.181	0.191	0.171	0.178	0.178	
	Benthic Producers	0.054	0.063	0.043	0.059	0.059	
Cephalopods	Large Planktivores	0.622	0.623	0.622	0.620	0.620	
	Large Reef Carnivores	-0.323	-0.326	-0.317	-0.324	-0.324	
	Small Planktivores	0.675	0.673	0.677	0.084	0.084	
	Small Reef Carnivores	-0.620	-0.623	-0.615	-0.621	-0.621	
	Cephalopods	0.947	0.946	0.948	0.934	0.934	
	Crustaceans	0.577	0.570	0.588	0.576	0.576	
	Worms & Molluscs	0.593	0.585	0.605	0.608	0.608	
	Zooplankton	0.936	0.907	0.967	0.948	0.948	
	Echinoderms	Echinoderms	-0.143	-0.133	-0.154	-0.147	-0.147
		Crustaceans	-0.836	-0.839	-0.831	-0.836	-0.836
Worms & Molluscs		-0.347	-0.357	-0.331	-0.347	-0.347	

Appendix 4 continued

Predator	Prey	Ivlev's Electivity Index					
		A.A.	Sum.	Win.	Spr.	Fall	
Crustaceans	Sessile Animals	-0.169	-0.160	-0.180	-0.173	-0.173	
	Zooplankton	-0.377	-0.529	-0.061	-0.380	-0.380	
	Decomposers/Microfauna	0.439	0.295	0.593	0.435	0.435	
	Phytoplankton	-0.247	-0.480	-	-	-	
	Benthic Producers	0.225	0.234	0.215	0.230	0.230	
	Detritus	-0.681	-0.675	-0.682	-0.678	-0.678	
	Large Reef Carnivores	-0.773	-0.774	-0.770	-0.774	-0.774	
	Small Planktivores	-0.433	-0.434	-0.429	-0.434	-0.434	
	Small Reef Carnivores	-0.828	-0.830	-0.826	-0.829	-0.829	
	Small Reef Herbivores	-0.841	-0.840	-0.841	-0.841	-0.841	
	Large Reef Herbivores	0.343	0.338	0.351	-0.134	-0.134	
	Cephalopods	-0.153	-0.161	-0.141	-0.154	-0.154	
	Echinoderms	0.246	0.255	0.236	0.242	0.242	
	Crustaceans	0.088	0.077	0.104	-0.541	-0.541	
	Worms & Molluscs	Worms & Molluscs	0.498	0.489	0.512	0.415	0.415
Sessile Animals		-0.776	-0.772	-0.780	-0.777	-0.777	
Zooplankton		0.827	0.756	0.908	0.862	0.862	
Decomposers/Microfauna		0.707	0.614	0.793	0.699	0.699	
Phytoplankton		0.003	-0.261	-	-	-	
Benthic Producers		-0.273	-0.264	-0.283	-0.268	-0.268	
Detritus		-0.691	-0.686	-0.687	-0.485	-0.485	
Echinoderms		-0.950	-0.949	-0.951	-0.951	-0.951	
Crustaceans		-0.540	-0.548	-0.529	-0.541	-0.541	
Worms & Molluscs		-0.245	-0.256	-0.228	-0.246	-0.246	
Sessile Animals		-0.649	-0.643	-0.655	-0.651	-0.651	
Zooplankton		-0.050	-0.238	0.278	-0.053	-0.053	
Decomposers/Microfauna		0.904	0.868	0.946	0.917	0.917	
Phytoplankton		0.888	0.816	0.775	0.333	0.333	
Sessile Animals		Benthic Producers	-0.324	-0.315	-0.333	-0.319	-0.319
	Detritus	-0.140	-0.130	-0.113	-0.106	-0.106	
	Zooplankton	0.581	0.439	0.761	0.578	0.578	
	Decomposers/Microfauna	0.378	0.227	0.527	0.355	0.355	
	Phytoplankton	0.378	0.127	0.595	-0.001	-0.001	
	Benthic Producers	-0.613	-0.607	-0.620	-0.610	-0.610	
	Detritus	0.209	0.218	0.202	0.209	0.209	
	Zooplankton	Decomposers/Microfauna	0.979	0.971	0.986	0.976	0.976
		Phytoplankton	0.952	0.918	0.964	0.866	0.866
		Detritus	-	-	-0.655	-0.539	-0.539
Decomposers/Microfauna	Detritus	0.279	0.288	0.269	0.276	0.276	

TROPIC DYNAMICS OF A FLORIDA KEYS CORAL REEF ECOSYSTEM

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ABSTRACT

A trophic model of the Looe Key National Marine Sanctuary, Florida, U.S.A. (=30 km²) was constructed, using the ECOPATH II approach for construction of mass-balance ecosystem models, the results of local biomass surveys by J. Bohnsack and collaborators and a structure adapted from an earlier ECOPATH II model, by S. Opitz, of a Virgin Island coral reef. Flows of energy and other relationships between the 20 functional groups in the system were examined (9 fish groups, 11 non-fish groups), then compared with those in five other coral reef ecosystem models. The Looe Key reef has the best recycling of detritus and is hence the most "mature" of the coral reef systems so far studied. Improvements of the model will consider seasonal changes of biomass and other system variables, and uncertainty in parameter inputs, using a semi-Bayesian approach. The impact of various management measures can then be simulated, using a new dynamic subroutine (EcoSim) of ECOPATH.

INTRODUCTION

It has long been appreciated that "nearly all [species] either prey on or serve as prey for others. [...and] that each organic being is either directly or indirectly related in the most important manner to other organic beings..." (Darwin 1872). Translating this observation into an operational research program has not been easy for ecologists, particularly for those working on coral reefs, whose very high diversity of species, with consequent diversity of trophic and other interactions, may seem to defy the reductionist assumptions required for quantitative modelling (Pauly and Christensen 1994). However, two modelling approaches have emerged and successfully applied to coral reef systems: 1) simulation models (McClanahan 1995) and 2) mass-balance models (Polovina 1984; Christensen and Pauly 1992). Moreover, the latter approach, which is generally straightforward to implement, has recently been shown to facilitate the parameterization of simulation models (Walters et al. submitted), thus opening up an avenue for the routine application of simulation modelling to complex ecosystems such as coral reefs.

We present here an application of the mass-balance approach to reefs in the Looe Key National Marine Sanctuary, as a prelude to a study of its response to management interventions, using the simulation module (EcoSim) of the ECOPATH software.

MATERIALS AND METHODS

Looe Key reef is located approximately 13 km off of Big Pine Key, Florida, U.S.A. The sanctuary proper comprises an area of approximately 30 km² (Bohnsack et al. 1987) and includes the reef itself, and surrounding coral, sand and seagrass habitats (Wheaton and Jaap

1983). The sanctuary is a popular location for diving and snorkeling and is subjected to heavy use throughout the year. Although hook-and-line fishing is allowed within the sanctuary boundaries, the harvest is very small and was not considered in the version of the model presented here.

Although many studies have been conducted on the various components of Florida reef ecosystems, no comprehensive ecosystem models have been constructed so far. Looe Key was chosen as a representative reef for the Florida Reef Tract, which runs from Miami southwest to the Dry Tortugas, both because of the research conducted in and around it and because the first author is familiar with it from diving visits.

The mass-balance approach implemented in the ECOPATH software (we used its newly released version 3.0; Christensen and Pauly 1996) relies on the master equation

$$B_i * (P/B)_i * (EE)_i = (Catch)_i + \sum_j B_j * (Q/B)_j * DC_{ji} \quad \dots(1)$$

where B is the mean biomass of functional group i during the period under consideration, P/B_i is its production/biomass ratio, EE_i its ecotrophic efficiency (ie., the fraction of its production consumed within the system), Q/B_i its food consumption per unit biomass and DC_{ji} the fraction of prey i consumed by predator j.

The data required to parameterize the model were obtained from the published literature on Florida reefs where possible, but also on the greater Caribbean Sea and other areas, due to substantial gaps in the published Florida database. Following Opitz (1993), species groups were aggregated into 20 boxes representing functional groups, ie., 9 fish and 11 non-fish groups. The fish groups' definition and biomasses were based on a visual census study by Bohnsack et al. (1987) that estimated the abundances of the 188 species occurring within the sanctuary boundaries. Non-fish taxa input values were from a diverse array of sources, documented in Opitz (1991, 1993). The data were converted into the common currency (t wet weight km⁻² year⁻¹) before entry into ECOPATH, using conversion factors in Atkinson and Grigg (1984) and in the contributions in Christensen and Pauly (1993).

The system of equation (1) allows one entry per group to be left unknown, to be estimated through the mass-balance requirement. The unknowns here were the EE values, or the biomasses (the majority of the latter in cases where visual survey estimates were unavailable); P/B and Q/B values were estimated using the empirical relationships of Pauly (1980) and Palomares and Pauly (1989).

The biomasses estimated after successive runs of ECOPATH were accepted only when they generated thermodynamically acceptable values of EE (51). The diet matrix (not shown) can be inferred from Fig. 1.

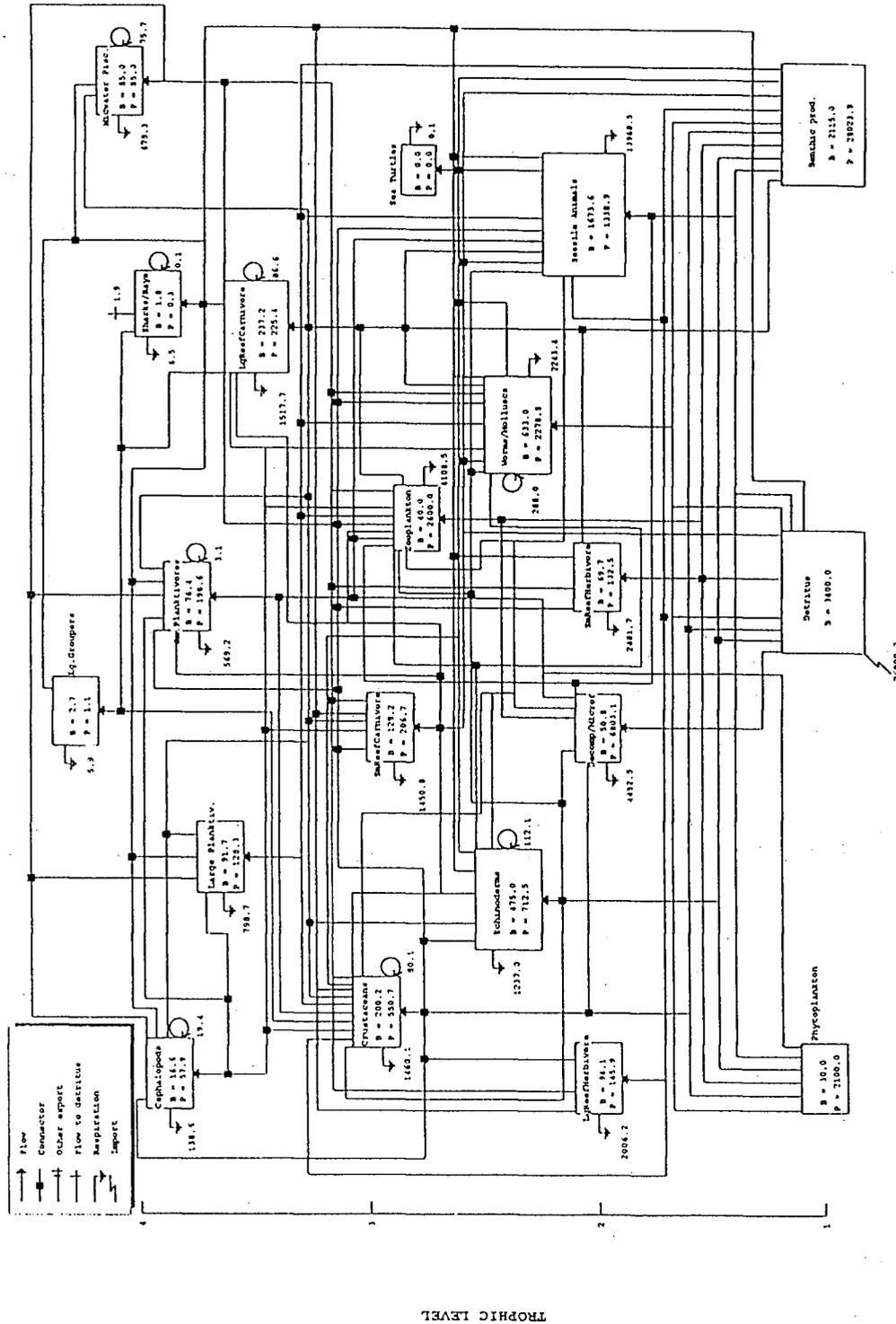


Fig. 1: Trophic flow diagram of the Looe Key National Marine Sanctuary ecosystem. Flows are in $t \cdot km^{-2}$. Backflows to the detritus and other lesser flows are not shown. The area of the boxes is proportional to the logarithm (B; in $t \cdot km^{-2}$) of the biomass of the groups they represent. The boxes are arranged by trophic level on the y-axis. Consumption flows entering a box do so at the bottom while those which represent predation on a box exit from the top and sides.

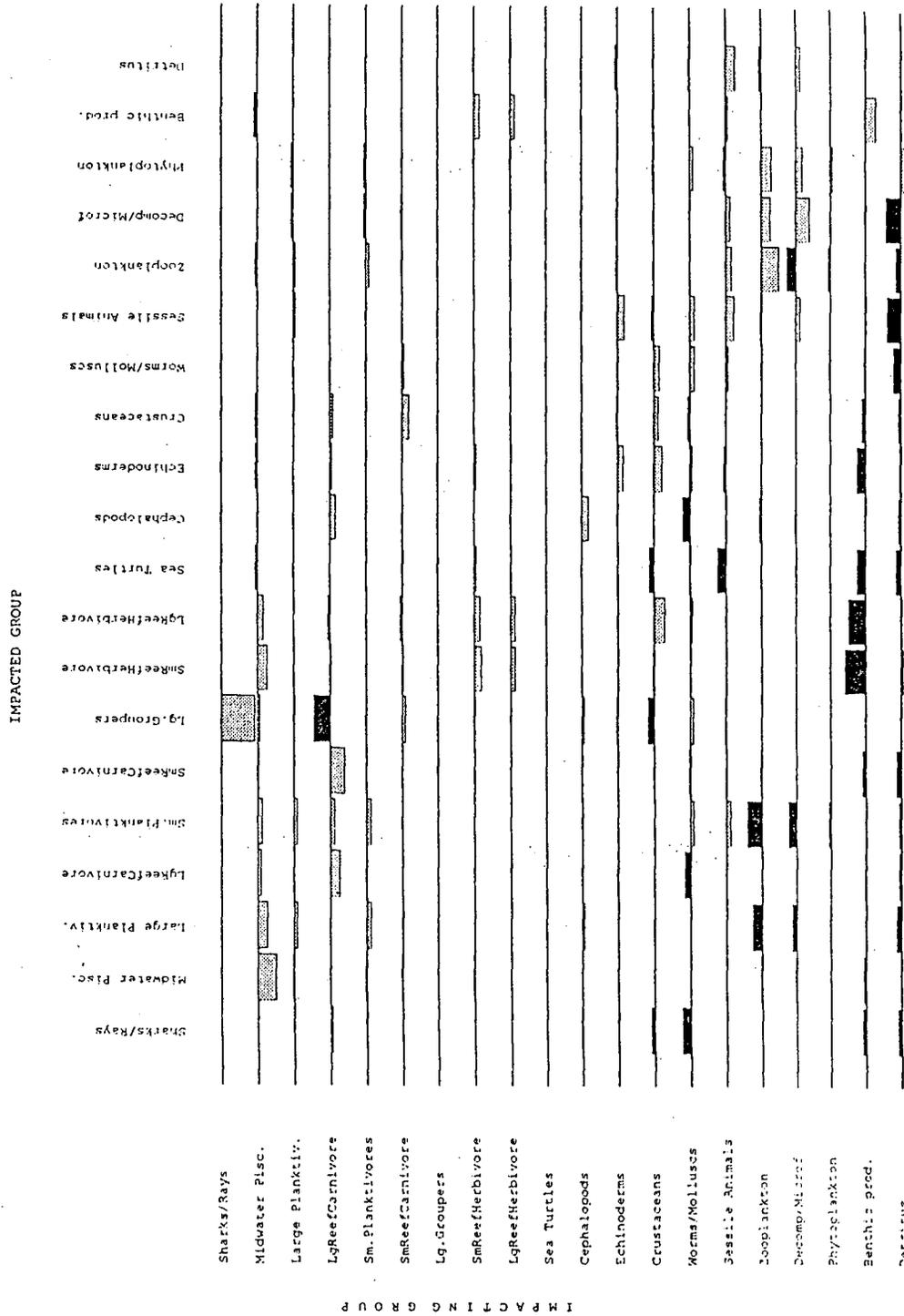


Fig. 2: Mixed trophic impacts in the Looe Key ecosystem. Positive impacts reflect relative increases in biomass while the converse is true of negative impacts. Note the high number of impacts, both positive and negative, which occur at the lower trophic levels. The histograms are reflective of the interdependencies of all groups within the ecosystem.

Table 1: Inputs and outputs (in parentheses) of the Looe Key National Marine Sanctuary ECOPATH model.

Group	B (t km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE
1. Sharks & Rays	1.75	0.18	4.90	(0.47)
2. Midwater Piscivores	85.00	1.00	8.90	(0.92)
3. Large Planktivores	(91.67)	1.40	10.00	0.92
4. Large Reef Carnivores	(237.24)	0.95	7.30	0.95
5. Small Planktivores	(76.38)	2.60	10.00	0.98
6. Small Reef Carnivores	(129.17)	1.60	12.80	0.98
7. Large Groupers	(2.68)	0.40	2.30	0.20
8. Small Reef Herbivores	(69.74)	1.90	37.45	0.98
9. Large Reef Herbivores	(94.14)	1.55	22.80	0.96
10. Sea Turtles	0.02	0.15	3.50	(0.00)
11. Cephalopods	(16.55)	3.50	11.70	0.95
12. Echinoderms	475.00	1.50	4.00	(0.93)
13. Crustaceans	(200.25)	2.75	10.00	0.99
14. Worms & Molluscs	(633.00)	3.60	7.00	0.96
15. Sessile Animals	1673.58	0.80	9.00	(0.82)
16. Zooplankton	40.00	65.00	165.00	(0.96)
17. Decomposers & Microfauna	(50.77)	134.00	215.00	0.95
18. Phytoplankton	30.00	70.00	-	(0.89)
19. Benthic Producers	2115.00	13.25	-	(0.31)
20. Detritus	3400.00	-	-	(0.84)

RESULTS AND DISCUSSION

Several of the input parameters required strong adjustments to achieve mass-balance. In particular, the biomass of several groups of small fishes had to be increased, and nearly doubled in one case. This is not surprising, as the stationary visual sampling technique used for Looe Key fishes (see Bohnsack and Bannerot 1986; Bohnsack et al. 1987) provides only conservative minimum estimates of relative abundance (J. Bohnsack pers. comm.). Opitz (1991) also had to increase her initial estimates of biomass for small, cryptic species, for the same reason.

Fig. 1. presents a flow diagram of the Looe Key ecosystem and illustrates its high number of trophic links and the resulting complex network flows: a characteristic of coral reef systems. Most species groups feed at more than one trophic level, leading to the numerous indirect interactions illustrated in Fig. 2, where the relative impact that each group has on the others is represented.

Overall, the Looe Key ecosystem is characterized by high ecotrophic efficiency and high biomass values. This is achieved by a high degree of detritus recycling (13.1%), the highest value so far calculated for any coral reef system (Fig. 3). This, jointly with a high productivity/respiration ratio (Fig 3), defines Looe Key Reef as an ecosystem that is highly mature, according to the concept of Odum (1969) reinterpreted by Pauly and Christensen (in press) and Christensen and Pauly (submitted).

It is planned to refine this model by considering seasonal changes in the parameters of equation (1) (especially P/B, Q/B), as mediated by temperature changes (summer-winter difference at Looe Key = 10°C), and any observed seasonal changes in biomass, diet composition or other biological characteristics. Additionally, we will use the model in Fig. 1 as the basis for a simulation model, wherein the parameters of the system of linear equations in (1) define a system of differential equations that can be integrated over time (Walters et al. submitted).

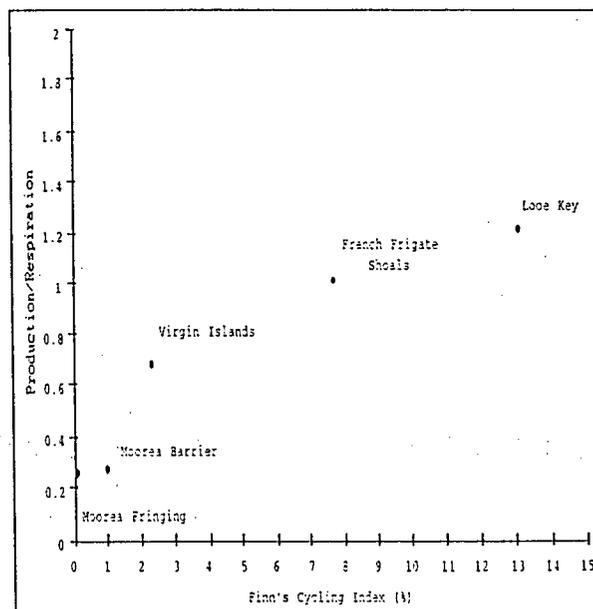


Fig. 3: Relationship between two indices usually increasing with increasing ecosystem maturity: Total system primary production/respiration ratio vs Finn's cycling index, expressing the % of total detritus flow that is recycled (U.S. Virgin Islands: Opitz 1993; Moorea Fringing and Barrier Reefs: Arias-Gonzalez 1993; French Frigate Shoals: Polovina 1984; Looe Key: this study).

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Appendix 6. Diet compositions of the component groups in the Looe Key National Marine Sanctuary ECOPATH models. Numbers represent the proportion of each group's diet that other groups contribute.

6a. Annual Average.

Prey	Predator																
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.
1. Sharks/Rays	0.010	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-
2. Midwater Piscivores	-	0.100	-	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Large Planktivores	0.025	0.130	-	0.004	-	-	-	-	-	-	0.065	-	-	-	-	-	-
4. Large Reef Carnivores	0.010	0.130	-	0.050	-	0.007	0.588	-	-	-	0.020	-	0.005	-	-	-	-
5. Small Planktivores	0.025	0.150	-	0.030	0.004	0.002	-	-	-	-	0.065	-	0.005	-	-	-	-
6. Small Reef Carnivores	0.080	0.100	-	0.070	-	-	-	-	-	-	0.005	-	0.002	-	-	-	-
7. Large Groupers	0.025	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8. Small Reef Herbivores	0.080	0.150	-	0.008	-	-	-	-	-	-	-	-	0.001	-	-	-	-
9. Large Reef Herbivores	0.040	0.100	-	-	-	-	-	-	-	-	-	-	0.032	-	-	-	-
10. Sea Turtles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. Cephalopods	0.085	0.018	-	0.010	-	-	-	-	-	-	0.100	-	0.002	-	-	-	-
12. Echinoderms	0.021	-	-	0.120	-	0.043	-	0.001	-	0.040	-	0.059	0.130	0.002	-	-	-
13. Crustaceans	0.265	0.040	0.040	0.100	0.012	0.080	0.402	-	0.001	0.125	0.125	0.003	0.040	0.010	-	-	-
14. Worms & Molluscs	0.307	0.062	0.100	0.330	-	0.220	-	0.001	-	0.045	0.420	0.052	0.320	0.065	-	-	-
15. Sessile Animals	0.011	-	0.128	0.070	0.006	0.081	-	-	0.005	0.400	-	0.197	0.035	0.059	-	-	-
16. Zooplankton	-	0.020	0.722	0.120	0.974	0.160	-	0.004	-	-	0.200	0.003	0.070	0.006	0.025	-	-
17. Decomposers/Microf.	-	-	-	-	0.002	-	-	-	-	-	-	0.022	0.050	0.170	0.019	0.800	-
18. Phytoplankton	-	-	-	-	0.002	-	-	-	-	-	-	0.003	0.005	0.084	0.011	0.200	-
19. Benthic Producers	-	-	0.010	0.087	-	0.216	-	0.988	0.906	0.390	-	0.554	0.200	0.179	0.084	-	-
20. Detritus	0.016	-	-	-	-	0.191	-	0.006	0.088	-	-	0.107	0.103	0.425	0.861	-	1.000
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Appendix 6 continued

6b. Summer.

Prey	Predator																
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.
1. Sharks/Rays	0.010	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-
2. Midwater Piscivores	-	0.100	-	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Large Planktivores	0.025	0.130	-	0.004	-	-	-	-	-	-	0.065	-	-	-	-	-	-
4. Large Reef Carnivores	0.010	0.130	-	0.050	-	0.007	0.588	-	-	-	0.020	-	0.005	-	-	-	-
5. Small Planktivores	0.025	0.150	-	0.030	0.004	0.002	-	-	-	-	0.065	-	0.005	-	-	-	-
6. Small Reef Carnivores	0.080	0.100	-	0.070	-	-	-	-	-	-	0.005	-	0.002	-	-	-	-
7. Large Groupers	0.025	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8. Small Reef Herbivores	0.080	0.150	-	0.008	-	-	-	-	-	-	-	-	0.001	-	-	-	-
9. Large Reef Herbivores	0.040	0.100	-	-	-	-	-	-	-	-	-	-	0.032	-	-	-	-
10. Sea Turtles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. Cephalopods	0.085	0.018	-	0.010	-	-	-	-	-	-	0.100	-	0.002	-	-	-	-
12. Echinoderms	0.021	-	-	0.120	-	0.043	-	0.001	-	0.040	-	0.059	0.130	0.002	-	-	-
13. Crustaceans	0.265	0.040	0.040	0.100	0.012	0.080	0.402	-	0.001	0.125	0.125	0.003	0.040	0.010	-	-	-
14. Worms & Molluscs	0.307	0.062	0.100	0.330	-	0.220	-	0.001	-	0.045	0.420	0.052	0.320	0.065	-	-	-
15. Sessile Animals	0.011	-	0.128	0.070	0.006	0.081	-	-	0.005	0.400	-	0.197	0.035	0.059	-	-	-
16. Zooplankton	-	0.020	0.722	0.120	0.974	0.160	-	0.004	-	-	0.200	0.003	0.070	0.006	0.025	-	-
17. Decomposers/Microf.	-	-	-	-	0.002	-	-	-	-	-	-	0.022	0.050	0.170	0.019	0.800	-
18. Phytoplankton	-	-	-	-	0.002	-	-	-	-	-	-	0.003	0.005	0.084	0.011	0.200	-
19. Benthic Producers	-	-	0.010	0.087	-	0.216	-	0.988	0.906	0.390	-	0.554	0.200	0.179	0.084	-	-
20. Detritus	0.016	-	-	-	-	0.191	-	0.006	0.088	-	-	0.107	0.103	0.425	0.861	-	1.000
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Appendix 6 continued

6c. Winter.

Prey	Predator																
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.
1. Sharks/Rays	0.010	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-
2. Midwater Piscivores	-	0.100	-	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Large Planktivores	0.025	0.130	-	0.004	-	-	-	-	-	-	0.065	-	-	-	-	-	-
4. Large Reef Carnivores	0.010	0.130	-	0.050	-	0.007	0.588	-	-	-	0.020	-	0.005	-	-	-	-
5. Small Planktivores	0.025	0.150	-	0.030	0.004	0.002	-	-	-	-	0.065	-	0.005	-	-	-	-
6. Small Reef Carnivores	0.080	0.100	-	0.070	-	-	-	-	-	-	0.005	-	0.002	-	-	-	-
7. Large Groupers	0.025	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8. Small Reef Herbivores	0.080	0.150	-	0.008	-	-	-	-	-	-	-	-	0.001	-	-	-	-
9. Large Reef Herbivores	0.040	0.100	-	-	-	-	-	-	-	-	-	-	0.032	-	-	-	-
10. Sea Turtles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. Cephalopods	0.085	0.018	-	0.010	-	-	-	-	-	-	0.100	-	0.002	-	-	-	-
12. Echinoderms	0.021	-	-	0.120	-	0.043	-	0.001	-	0.040	-	0.059	0.130	0.002	-	-	-
13. Crustaceans	0.265	0.040	0.040	0.100	0.012	0.080	0.402	-	0.001	0.125	0.125	0.003	0.040	0.010	-	-	-
14. Worms & Molluscs	0.307	0.062	0.100	0.330	-	0.220	-	0.001	-	0.045	0.420	0.052	0.320	0.065	-	-	-
15. Sessile Animals	0.011	-	0.128	0.070	0.006	0.081	-	-	0.005	0.400	-	0.197	0.035	0.059	-	-	-
16. Zooplankton	-	0.020	0.300	0.040	0.300	0.080	-	0.004	-	-	0.200	0.003	0.070	0.006	0.025	-	-
17. Decomposers/Microf.	-	-	0.122	-	0.176	0.080	-	-	-	-	-	0.023	0.051	0.210	0.019	0.810	-
18. Phytoplankton	-	-	-	-	0.002	-	-	-	-	-	-	-	-	0.010	0.005	0.070	-
19. Benthic Producers	-	-	0.010	0.065	-	0.216	-	0.988	0.906	0.390	-	0.554	0.200	0.179	0.084	-	-
20. Detritus	0.016	-	0.300	0.102	0.500	0.191	-	0.006	0.088	-	-	0.109	0.107	0.459	0.867	0.120	1.000
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Appendix 6 continued

6d. Spring.

Prey	Predator																
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.
1. Sharks/Rays	0.010	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-
2. Midwater Piscivores	-	0.080	-	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Large Planktivores	0.025	0.120	-	0.004	-	-	-	-	-	-	0.065	-	-	-	-	-	-
4. Large Reef Carnivores	0.010	0.120	-	0.030	-	0.007	0.588	-	-	-	0.020	-	0.005	-	-	-	-
5. Small Planktivores	0.025	0.140	-	0.030	0.004	0.002	-	-	-	-	0.015	-	0.005	-	-	-	-
6. Small Reef Carnivores	0.080	0.100	-	0.050	-	-	-	-	-	-	0.005	-	0.002	-	-	-	-
7. Large Groupers	0.025	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8. Small Reef Herbivores	0.080	0.140	-	0.008	-	-	-	-	-	-	-	-	0.001	-	-	-	-
9. Large Reef Herbivores	0.040	0.090	-	-	-	-	-	-	-	-	-	-	0.012	-	-	-	-
10. Sea Turtles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. Cephalopods	0.085	0.018	-	0.010	-	-	-	-	-	-	0.080	-	0.002	-	-	-	-
12. Echinoderms	0.021	-	-	0.120	-	0.043	-	0.001	-	0.040	-	0.059	0.130	0.002	-	-	-
13. Crustaceans	0.265	0.040	0.040	0.090	0.012	0.080	0.402	-	0.001	0.125	0.125	0.003	0.010	0.010	-	-	-
14. Worms & Molluscs	0.307	0.062	0.100	0.300	-	0.200	-	0.001	-	0.045	0.440	0.052	0.260	0.065	-	-	-
15. Sessile Animals	0.011	-	0.128	0.090	0.006	0.081	-	-	0.005	0.400	-	0.197	0.035	0.059	-	-	-
16. Zooplankton	-	0.090	0.300	0.055	0.300	0.080	-	0.004	-	-	0.250	0.003	0.090	0.006	0.025	-	-
17. Decomposers/Microf.	-	-	0.122	0.005	0.176	0.080	-	-	-	-	-	0.023	0.051	0.210	0.019	0.760	-
18. Phytoplankton	-	-	-	-	0.002	-	-	-	-	-	-	-	-	0.010	0.005	0.070	-
19. Benthic Producers	-	-	0.010	0.065	-	0.216	-	0.988	0.906	0.390	-	0.554	0.200	0.179	0.084	-	-
20. Detritus	0.016	-	0.300	0.142	0.500	0.211	-	0.006	0.088	-	-	0.109	0.197	0.459	0.867	0.170	1.000
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Appendix 6 continued

6e. Fall.

Prey	Predator																
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.
1. Sharks/Rays	0.010	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-
2. Midwater Piscivores	-	0.080	-	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Large Planktivores	0.025	0.120	-	0.004	-	-	-	-	-	-	0.065	-	-	-	-	-	-
4. Large Reef Carnivores	0.010	0.120	-	0.030	-	0.007	0.588	-	-	-	0.020	-	0.005	-	-	-	-
5. Small Planktivores	0.025	0.140	-	0.030	0.004	0.002	-	-	-	-	0.015	-	0.005	-	-	-	-
6. Small Reef Carnivores	0.080	0.100	-	0.050	-	-	-	-	-	-	0.005	-	0.002	-	-	-	-
7. Large Groupers	0.025	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8. Small Reef Herbivores	0.080	0.140	-	0.008	-	-	-	-	-	-	-	-	0.001	-	-	-	-
9. Large Reef Herbivores	0.040	0.090	-	-	-	-	-	-	-	-	-	-	0.012	-	-	-	-
10. Sea Turtles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. Cephalopods	0.085	0.018	-	0.010	-	-	-	-	-	-	0.080	-	0.002	-	-	-	-
12. Echinoderms	0.021	-	-	0.120	-	0.043	-	0.001	-	0.040	-	0.059	0.130	0.002	-	-	-
13. Crustaceans	0.265	0.040	0.040	0.090	0.012	0.080	0.402	-	0.001	0.125	0.125	0.003	0.010	0.010	-	-	-
14. Worms & Molluscs	0.307	0.062	0.100	0.300	-	0.200	-	0.001	-	0.045	0.440	0.052	0.260	0.065	-	-	-
15. Sessile Animals	0.011	-	0.128	0.090	0.006	0.081	-	-	0.005	0.400	-	0.197	0.035	0.059	-	-	-
16. Zooplankton	-	0.090	0.300	0.055	0.300	0.080	-	0.004	-	-	0.250	0.003	0.090	0.006	0.025	-	-
17. Decomposers/Microf.	-	-	0.122	0.005	0.176	0.080	-	-	-	-	-	0.023	0.051	0.210	0.019	0.760	-
18. Phytoplankton	-	-	-	-	0.002	-	-	-	-	-	-	-	-	0.010	0.005	0.070	-
19. Benthic Producers	-	-	0.010	0.065	-	0.216	-	0.988	0.906	0.390	-	0.554	0.200	0.179	0.084	-	-
20. Detritus	0.016	-	0.300	0.142	0.500	0.211	-	0.006	0.088	-	-	0.109	0.197	0.459	0.867	0.170	1.000
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Appendix 7. Inputs and outputs (in bold) of the Looe Key National Marine Sanctuary seasonal ECOPATH models.

7a. Summer.

Group	B (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE
1. Sharks & Rays	1.75	0.19	4.00	0.37
2. Midwater Piscivores	85.00	1.04	9.36	0.92
3. Large Planktivores	93.11	1.46	10.52	0.92
4. Large Reef Carnivores	242.12	0.99	7.68	0.95
5. Small Planktivores	78.08	2.70	10.52	0.98
6. Small Reef Carnivores	132.33	1.70	13.47	0.98
7. Large Groupers	2.10	0.42	2.42	0.20
8. Small Reef Herbivores	70.76	1.98	48.15	0.98
9. Large Reef Herbivores	97.48	1.61	29.31	0.96
10. Sea Turtles	0.02	0.16	3.68	0.00
11. Cephalopods	17.04	3.64	12.31	0.95
12. Echinoderms	475.00	1.56	4.21	0.97
13. Crustaceans	210.85	2.86	10.52	0.99
14. Worms & Molluscs	676.14	3.74	8.42	0.96
15. Sessile Animals	1673.58	0.83	9.47	0.88
16. Zooplankton	60.00	67.60	173.58	0.66
17. Decomposers & Microfauna	73.71	139.36	284.04	0.95
18. Phytoplankton	52.50	93.33	-	0.56
19. Benthic Producers	2320.60	17.67	-	0.25
20. Detritus	3400.00	-	-	0.45

7b. Winter.

Group	B (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE
1. Sharks & Rays	1.75	0.17	3.57	0.36
2. Midwater Piscivores	85.00	0.96	8.37	0.90
3. Large Planktivores	89.47	1.34	9.40	0.92
4. Large Reef Carnivores	227.53	0.91	6.86	0.95
5. Small Planktivores	73.82	2.48	9.40	0.98
6. Small Reef Carnivores	123.79	1.53	12.03	0.98
7. Large Groupers	2.05	0.38	2.16	0.20
8. Small Reef Herbivores	68.28	1.82	26.75	0.98
9. Large Reef Herbivores	90.78	1.48	16.29	0.96
10. Sea Turtles	0.02	0.14	3.29	0.00
11. Cephalopods	15.68	3.34	11.00	0.95
12. Echinoderms	475.00	1.43	3.76	0.88
13. Crustaceans	191.54	2.63	9.40	0.99
14. Worms & Molluscs	610.41	3.44	7.52	0.96
15. Sessile Animals	1673.58	0.76	8.46	0.81
16. Zooplankton	20.00	62.08	155.10	0.98
17. Decomposers & Microfauna	34.73	127.97	253.80	0.95
18. Phytoplankton	7.50	46.67	-	0.96
19. Benthic Producers	1831.60	8.83	-	0.43
20. Detritus	3400.00	-	-	0.51

Appendix 7 continued

7c. Spring.

Group	B (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE
1. Sharks & Rays	1.75	0.18	3.79	0.36
2. Midwater Piscivores	83.50	1.00	8.87	0.88
3. Large Planktivores	91.29	1.40	9.96	0.96
4. Large Reef Carnivores	234.83	0.98	7.27	0.99
5. Small Planktivores	75.95	2.59	9.96	0.97
6. Small Reef Carnivores	128.06	1.60	12.75	0.97
7. Large Groupers	2.07	0.40	2.29	0.48
8. Small Reef Herbivores	69.52	1.90	37.45	0.98
9. Large Reef Herbivores	94.13	1.55	22.80	0.81
10. Sea Turtles	0.02	0.15	3.49	0.00
11. Cephalopods	16.36	3.49	11.65	0.98
12. Echinoderms	475.00	1.50	3.98	0.93
13. Crustaceans	201.20	2.74	9.96	0.98
14. Worms & Molluscs	643.28	3.59	7.97	0.99
15. Sessile Animals	1673.58	0.80	8.96	0.87
16. Zooplankton	40.00	64.84	164.34	0.62
17. Decomposers & Microfauna	54.21	133.67	268.92	0.97
18. Phytoplankton	30.00	70.00	-	0.37
19. Benthic Producers	2076.10	13.25	-	0.38
20. Detritus	3400.00	-	-	0.52

7d. Fall.

Group	B (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE
1. Sharks & Rays	1.75	0.18	3.79	0.36
2. Midwater Piscivores	83.50	1.00	8.87	0.59
3. Large Planktivores	91.29	1.40	9.96	0.74
4. Large Reef Carnivores	234.83	0.98	7.27	0.48
5. Small Planktivores	75.95	2.59	9.96	0.80
6. Small Reef Carnivores	128.06	1.60	12.75	0.64
7. Large Groupers	2.07	0.40	2.29	0.00
8. Small Reef Herbivores	69.52	1.90	37.45	0.83
9. Large Reef Herbivores	94.13	1.55	22.80	0.44
10. Sea Turtles	0.02	0.15	3.49	0.00
11. Cephalopods	16.36	3.49	11.65	0.78
12. Echinoderms	475.00	1.50	3.98	0.93
13. Crustaceans	201.20	2.74	9.96	0.70
14. Worms & Molluscs	643.28	3.59	7.97	0.76
15. Sessile Animals	1673.58	0.80	8.96	0.87
16. Zooplankton	40.00	64.84	164.34	0.49
17. Decomposers & Microfauna	54.21	133.67	268.92	0.93
18. Phytoplankton	30.00	70.00	-	0.19
19. Benthic Producers	2076.10	13.25	-	0.24
20. Detritus	3400.00	-	-	0.47