
Trophic interactions in the coastal ecosystem of Sri Lanka: An ECOPATH preliminary approach

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Abstract:

This study attempts to assemble and summarize existing information in order to build a general representation of the trophic interactions within the shallow coastal ecosystem of Sri Lanka. A multispecific ecosystem-based approach on trophic relationships and their possible variations was performed using ECOPATH. Thirty-nine functional groups were considered representing all trophic levels in the food web.

Time-dynamic simulation was carried out using the ECOSIM routine to evaluate the impact of the 1998 El Niño event on key functional groups. Results show that the time needed for any impacted functional group to recover to its initial abundance increased with the trophic level. Two time-series data sets derived from commercial catch and effort statistics were used for validation of ECOSIM results. The El Niño simulation results validated by the time-series data confirmed the ability of the proposed multispecies model to describe the sudden environmental changes.

Possible impacts due to increase of fishing effort were also simulated by separately considering frequently used fishing gears. The analysis revealed that small-mesh gillnet fishery operates independently from the other existing developing fisheries in the same area and can be managed accordingly.

Fishing-effort simulations suggest that the increase of fishing intensity by small-mesh gillnets would contribute to the decline of small pelagic catch. This was also found to influence the overall catch. The present level of exploitation of small pelagic fishery resources does not seem sustainable.

Keywords: trophic modelling; ECOPATH; ECOSIM; trophic level; feeding relationships; fisheries management; Indian Ocean; Sri Lanka

1. Introduction

An ecosystem-based approach to fisheries is essential for the management of exploited species and for their long term sustainability (ICES, 2000; Garcia and Cochrane, 2005). Species in an ecosystem interact biologically and are interconnected through the food webs (Pascual and Dunne, 2006). Earlier practice of treating fish stocks as independent from one another when implementing management policies is being progressively replaced by this approach (Christensen and Pauly, 1993; ICES, 2000; Garcia and Cochrane, 2005). An obvious limitation of single from multispecies fisheries management is that it does not consider a global evaluation of changes in ecosystem structure and functions related to species interactions (Mace, 2001; Pikitch et al., 2004). In the ecosystem-based fisheries management, several factors affecting resource sustainability can be integrated. Interspecies interactions within an ecosystem, impacts of the massive climatic and environmental changes and the fishing impacts are just some of the critical factors that should be integrated in the formulation of management strategies (Browman et al., 2004; Pikitch et al., 2004). Worldwide, the capacity of coastal and marine ecosystems to produce fish to serve human interest is highly degraded by over fishing, trawling and loss of nursery areas (Pauly et al., 1998; McGlade et al., 2002). In Sri Lanka, exploitation of marine resources occurs all around the coast but is mainly confined

61 to the narrow continental shelf, which rarely exceeds 40 km and averages around 22 km in width. The
62 total area of the shelf is about 30 000 km², which is around 6% of the total area of the Exclusive
63 Economic Zone (EEZ) of Sri Lanka. Coastal fishery from the seas off Sri Lanka (except in the northern
64 and eastern areas) is a proliferating activity, which targets particularly small pelagic species. This is
65 basically due to the remarkable productivity and high accessibility of this zone and based on the
66 recent government incentive to develop the coastal fishery sub-sector to alleviate the increasing level
67 of unemployment. Fishing intensity had rapidly increased due to the motorization of boats and the
68 introduction of synthetic materials for gillnet webbing after the 1950s (Dayaratne and Sivakumaran,
69 1994). The fisheries sector has become adversely affected by the influx of displaced personnel due to
70 the civil war in the North and East of the island. Unemployed people were forced to consider fishing as
71 an occupation and resulted to the war-torn northern and the eastern parts of the island. Disputes were
72 further aggravated during the 1990s due to the successful experimental purse seining initially
73 practised for capturing live bait for the pole-and-line fishery.

74

75 Biodiversity of the coastal ecosystem of Sri Lanka is very rich and includes various fish populations
76 (De Bruin et al., 1995), similarly to most other tropical marine ecosystems (Burke et al., 2001; Rocha
77 et al., 2005). However, individual contribution of most species to the total catch is very small. The
78 coastal fish production is mainly dominated by clupeids and other small pelagic species which are
79 exploited by small mesh gillnets (Dayaratne and Sivakumaran, 1994).

80

81 The complex food web of this coastal ecosystem and its functioning are basically unknown. Although
82 the biology and population dynamics of some key coastal species have been studied individually,
83 providing estimations of population parameters, mortality, stock size and recruitment (Dayaratne,
84 1998; Karunasinghe and Wijeyaratne, 1998; Sanders et al., 2000, Jayawardane et al., 2002), these
85 studies in themselves provide insufficient information to plan sustainable resource management for
86 this ecosystem. Moreover, no attempt has been made to understand the population dynamics at an
87 ecosystem level through trophic links.

88

89 The ECOPATH approach was designed exactly for the above purpose (Christensen and Pauly, 1993).

90 The advantage of this kind of model is that it provides an overview of the ecosystem's trophic state

91 using few data requirements. Once constructed, the model can be updated and used to assess
92 biomass response as a function of change, i.e. exploitation, climate change or degradation
93 (Christensen et al., 2005).

94

95 Massive climatic and environmental changes due to natural phenomena such as El Niño are
96 frequently reported from many parts of the world (Kim and Kang, 2000; Pulwarty and Melis, 2001;
97 Cubillos and Arcos, 2002; Rodríguez-Graña and Castro, 2003; Tam et al., 2006). Some of them have
98 affected the different functional groups of marine ecosystems (Miller and Fluharty, 1992; Souter et al.,
99 2000; Cubillos and Arcos, 2002; Tam et al., 2006). The ability to understand how climate will change
100 from one year to the next will lead to better management of fisheries. The resource fluctuations
101 induced by climate variability however make complex the fisheries management. Regardless, fish
102 populations collapse due to the inability of the fishing industry to recover from over exploitation
103 (Forrester, 1997; <http://www.csa.com/discoveryguides/archives/elnino.php>). Fishery managements
104 have to respond for minimizing those negative impacts by taking appropriate measures in resources
105 exploitation.

106

107 The 1998 El Niño event which occurred in the Indian Ocean resulted to an elevation of sea surface
108 temperature. Many coral reefs in the region have been affected with an extensive coral bleaching and
109 subsequent mortality (Le Blanc, 1999). As a result, between 50 and 90% of the corals in the shallow
110 seas off Sri Lanka were destroyed (Rajasuriya and Karunarathne, 2000). The biophysical and socio-
111 economic impacts on the coral reef associated fish population and dependents, particularly focusing
112 on vulnerable groups of the coastal human population, are now being studied. However, only few
113 studies have addressed the impact of the El Niño Southern Oscillation (ENSO) phenomenon on the
114 coastal fish communities. Le Blanc (1999) addressed the impact of this phenomenon on tuna fisheries.

115

116 The objectives of the present study were to assemble, integrate and summarize available information
117 to develop a comprehensive picture the Sri Lankan coastal ecosystem trophic structure and living
118 resources exploitation in the fisheries. The recent developments of the ECOPATH mass-balance
119 approach (Christensen and Pauly, 1992) were used as a modelling tool to develop a multispecific,
120 trophic model for the ecosystem considered. Time-dynamic analyses using the ECOSIM routine

121 (Christensen et al., 2005) were also considered to evaluate possible impacts of increase in fishing
122 effort and the severe El Niño event of 1998 on key functional groups of the ecosystem.

123

124 **2. Materials and Methods**

125

126 *2.1. The ECOPATH model and software*

127

128 *2.1.1. Mass balance modelling*

129 The ECOPATH software (Polovina, 1984; Christensen and Pauly, 1993; 1996; Pauly et al., 2000;
130 Christensen et al., 2005; Pauly et al., 2000) was used to perform a mass-balance model. ECOPATH
131 production equation for any group ‘*i*’ can be written as:

132

$$133 \quad P_i = Y_i + B_i \cdot M2_i + P_i (1-EE_i) \quad (1)$$

134

135 where P_i is its total production of *i*, Y_i its yield or catch in weight, B_i the biomass, $M2_i$ is its total
136 predation, E_i the net migration (emigration – immigration), while $P_i (1-EE_i)$ is the ‘other mortality’. EE_i is
137 the “ecotrophic efficiency”, i.e., the proportion of the production of *i* that is exported or consumed by
138 the predators in the system.

139 The above equation can be re-expressed as:

140

$$141 \quad B_i \cdot (P/B)_i \cdot EE_i = Y_i + \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji} \quad (2)$$

142

143 Where $(P/B)_i$ is the production/biomass ratio usually assumed to be equal to total mortality Z defined in
144 fisheries sciences (Allen, 1971; Lévêque et al., 1977), $(Q/B)_j$ is the consumption/biomass ratio, and DC_{ji}
145 is the fraction of prey *i* in the average diet of predator *j*.

146

147 When the values for the parameters of the model are provided, ECOPATH estimates the missing
148 parameter for each group in the model e.g. the mean annual biomass, the annual biomass production,
149 the annual biomass consumption or ecotrophic efficiency for each of the groups in the ecosystem.

150

151 2.1.2. *Time-dynamic simulation (ECOSIM)*

152 Once an ECOPATH model is built, it can be used directly for simulation modelling using ECOSIM.
153 ECOPATH mass balance results are used here as input data for this trophodynamic simulation
154 modeling (Walters et al., 1997). The basic biomass dynamic differential equation in ECOSIM is given
155 by:

156
157
$$dB_i/dt = f(B) - M_0B_i - F_iB_i - \sum_{j=1}^n c_{ij}(B_i, B_j) \quad (3)$$

158
159 Where dB_i/dt represents the growth rate of group i in terms of its biomass, $f(B)$ is a function of B_i if i
160 represents primary production. In other words, M_0 is for unaccounted mortality, F_i is fishing mortality
161 rate and $c_{ij}(B_i, B_j)$ is the function for predicting the amount of i consumed by a predator j . ECOSIM
162 solves the set of equations numerically.

163

164 2.2. *Model construction*

165

166 2.2.1. *Boundaries for the proposed ECOPATH model*

167 The proposed ecosystem model represents a part of the shallow coastal ecosystem of Sri Lanka in
168 year 2000 from Chilaw up to Trincomalee (Fig.1). For the purpose of this analysis, the coastal zone
169 has been defined to include the intertidal and subtidal areas on and above the continental shelf to
170 about 20 km from the main shoreline (total area of around 14 000 km²). Average Sea Surface
171 Temperature (SST) is 28°C.

172

173 2.2.2. *Identification of functional groups*

174 Fifty-eight fish species frequently reported in the fisheries data for the year 2000 were re-grouped into
175 29 fish functional groups (Table 1). Functional groups were categorized/grouped based on similarities
176 in habitat, maximum body size, feeding habits, physiological behaviour and ecological distribution in
177 order to obtain and keep homogeneous characteristics among the species within a group (Yodzis and
178 Winemiller, 1999). For each group, whenever possible, a representative species was selected based
179 on its importance in the fisheries and information availability. Shrimps, crabs and cephalopods which
180 appear in the fisheries statistics were also incorporated. In addition, the following food sources for fish

181 were considered: bivalves, annelids, other benthic invertebrates, zooplankton, phytoplankton,
182 phytobenthos and detritus.

183

184 As a general rule for every group, demographical parameters, diet composition, food consumption,
185 habitat and other information were obtained from the existing literature, with preference to local and
186 regional data. In the absence of this information, data from similar ecosystems were considered.

187 Fishbase (www.fishbase.org) (Fröese and Pauly, 2006) has also been utilized to bridge gaps
188 whenever possible. For non-fish groups, data sources are summarized in table 2.

189

190 2.2.3. *Actual catch*

191 Annual yield (Table 3) was estimated from the National Aquatic Resources Research and
192 Development Agency of Sri Lanka (NARA) fish landings survey data and from fish landing estimates
193 of the Ministry of Fisheries and Aquatic Resources of Sri Lanka (MFAR). Data from NARA and MFAR
194 were used to estimate monthly catches of most small pelagic species and demersal species,
195 respectively. For each species, annual catch is calculated as:

196 Total annual catch = mean catch in kg per craft × mean number of crafts operated per day × mean
197 number of fishing days per month × 12 months

198 Annual yield for crabs is estimated based on export statistics (NARA, 2001).

199 The total estimated annual catch is 61,500 tons which was mainly captured by two categories of
200 fishing gears: small mesh gillnets (i.e. mesh size 6 - 38 mm) and other gears for the multispecies
201 consideration. Input catch data were standardized by area.

202

203 2.2.4. *Basic parameters of fish*

204

205 2.2.4.1. *The Production/Biomass (P/B) ratio*

206 For this study, we assume that P/B is equal to the total instantaneous mortality, Z , as indicated by
207 Allen (1971). Consequently, for commercially exploited stocks, this was calculated by obtaining the
208 sum of the fishing (F) and natural (M) mortalities. M was calculated using the empirical formula of
209 Pauly (1980).

210

211 2.2.4.2. *Biomass (B)*

212 This is the total mass per functional group expressed as t.km². A variety of techniques have been
213 used to estimate this parameter. Except for halfbeaks and soles, biomass per habitat area was
214 estimated using the relationship:

215

$$216 \quad B = Y/F \quad (4)$$

217

218 where Y is the annual yield and F is the coefficient of the fishing mortality.

219 For halfbeaks and soles, biomass per habitat area was estimated using an EE value of 0.5 for
220 halfbeaks, which do not experience heavy predation, and an EE value of 0.95 for soles, which are
221 heavily predated by certain fish.

222

223 Biomasses for non-fish groups were not available except for shrimps. For shrimps, biomass was
224 estimated from the equation (4) using the data of Jayawardane et al (2002). Phytoplankton biomass
225 for the site considered is estimated at 2.625 t.km² (Table 3). The Bay of Bengal large marine
226 ecosystem (LME) has a class II productivity level, moderately productive (150-300 gC.m⁻².yr⁻¹), based
227 on SeaWiFS global primary productivity. According to Dwivedi (1993), marshes and mangroves
228 contribute to the overall productivity of this LME. Phytoplankton biomass is based on estimations by
229 Pattiaratchi (2002).

230

231 2.2.4.3. *The relative food consumption (Q/B)*

232 For fish groups Q/B ratios were computed using the predictive model of Palomares and Pauly (1998).

233 For other groups, Q/B was estimated from the empirical relationship proposed by Palomares and
234 Pauly (1989). The aspect ratio of the caudal fin (A), indicative of metabolic activity and expressed as
235 the ratio of the square of the height of the caudal fin and its surface area, is obtained mainly from

236 | Fishbase (www.fishbase.org) (Fröese and Pauly, 2006).

237

238 The asymptotic weight (W_{∞}), which is required for both models (Palomares and Pauly, 1989; 1998),
239 was derived from the asymptotic length (L_{∞}). Length-weight ($L-W$) relationships from Dayaratne (1998)
240 were considered for some fish groups such as sardines; herrings; pony fishes and flying fishes,

241 *Hirundichthys coromandelensis*. For other groups, the *L-W* relationships were based from Fishbase
242 (www.fishbase.org) (Fröese and Pauly, 2006).

243

244 2.2.5. *The diet composition of every group*

245 As indicated earlier, trophic interactions were poorly investigated in the coastal ecosystem of Sri
246 Lanka. Only a few previous studies on feeding ecology have been carried out in this area (De Silva
247 and Wijeyaratne, 1977 in Mohsin and Ambak, 1996). Due to the lack of available information on diet
248 composition of groups considered, data were taken from Fishbase (www.fishbase.org) (Fröese and
249 Pauly, 2006) and from the work of Mohsin and Ambak (1996).

250

251 When the diet of the predatory fish was not described, spatial distribution and size-range were used to
252 predict potential prey/s (Pauly 1998; Blaber, 2000). The feeding matrix is provided in annex 1.

253

254 2.3. *Estimating unknown parameters and evaluating the model*

255

256 Basic estimations are independently made of missing parameters of ECOPATH functional groups,
257 including estimations for trophic level (*TL*) and omnivory index (*OI*) of each group. The group-specific
258 omnivory index *OI* is computed as the variance of the *TL*s of each predator's prey groups (Christensen
259 and Pauly, 1993) *OI* varies from 0 to 1, where a value close to 0 indicates high predatory
260 specialization (feeding on one *TL* only) and 1 indicates a maximum feeding versatility on several *TL*s.

261

262 Following Christensen et al. (2000) the pedigree of an ECOPATH input is here understood as a coded
263 statement that categorizes data sources based on their type and the uncertainty associated with them.

264 Based on the options selected for each parameter for each group, a pedigree index *P* can be
265 calculated for the whole ecosystem as the product of all the pedigree parameter specific indices and
266 its scale varies between 0 and 1.

267

268 2.4. *ECOSIM simulations*

269 In order to assess the possibility of over-fishing, simulations using ECOSIM were carried out by
270 increasing by two folds the fishing effort within the next ten years for small-mesh gillnets and other

271 gears, first separately as suggested by Walters et al. (1997), and then together. Here, the vulnerability,
272 a parameter incorporated by Walters et al. (1997) and documented by Christensen et al. (2005) for a
273 proper use of ECOSIM expresses the mechanism of trophic flows control in the ecosystem. It ranges
274 from 0 (bottom up) to 1 (top down) (See Christensen et al., 2000 for more details). For preliminary
275 investigations, an intermediate default value of 0.3 was adopted for all groups as suggested by
276 Christensen et al. (2005). A Vulnerability Index (V) of 0.2 as predators was only assigned to small
277 sized fish species, for zooplankton and benthic organisms, which might be directly influenced by food
278 availability at lower TLs.

279
280 In addition to these exercises, an attempt was made to assess the influence of an El Niño event to
281 depict changes in primary production and fish recruitment the one that occurred in 1998. It affects the
282 ecosystem in two ways: modifications of the recruitment of fish and decrease of the primary
283 production. A decrease of the primary production by 2, which lasted three months (May-June), was
284 simulated. This is a reasonable assumption, which corresponds to what happened in other marine
285 ecosystems during a massive El Niño (<http://www.csa.com/discoveryguides/archives/elniño.php>). For
286 clarity, the evolutionary trends of the biomass of few groups selected in various trophic levels (TL)
287 were summarized. They are Phytoplankton (TL 1), Zooplankton (TL2), Herrings (TL 2.64) Sardines
288 (TL 2.84 i.e. close to 3), Anchovies (TL 2.95 i.e. close to 3), Large tuna (TL 3.86 i.e. close to 4) (see
289 below). For such a simulation, ECOSIM requires the fishing activity to remain constant.

290

291 *2.5. ECOSIM simulation on fishing effort impacts*

292 Two time series derived from commercial catch and effort statistics, obtained before, during and after
293 the El Niño were used for validation of ECOSIM results. Average monthly catch rates of Herring (catch
294 in $\text{kg boat}^{-1} \text{day}^{-1}$) derived from the fisheries statistics collected from west to east of the ecosystem for
295 the Fibber Reinforced Plastic (FRP) boats during the period January 1998 – December 2001 were
296 plotted to observe their trends in abundance. It should be noted that *Amblygaster sirm* (the
297 representative species of the ECOPATH group Herring) is the key target species for this coastal
298 vessel. Moreover, the catch rates for the ECOPATH group of large tunas and king fish obtained from
299 January 1998 to December 2003 for a special category of coastal vessels (day boats, 3.5 tons with
300 inboard engine) from the west part of the ecosystem were also plotted. It should be noted that species

301 represented by the ECOPATH group of large tunas and king fish are considerably exploited by these
302 vessels. Moving average tool of Microsoft Excel software was employed to obtain smooth plots for
303 monthly catch rates. For the validation of ECOSIM results, it was assumed that the catch rates derived
304 from commercial fisheries statistics reflect the species abundance (Bellido et al., 2001; Haputhantri
305 and Jayawardena, 2006).

306

307 **3. Results**

308 An estimated pedigree index of 0.587 conformed to the lower limit of overall quality of an Ecopath
309 model as discussed by Christensen et al. (2005).

310

311 *3.1. Basic estimations*

312 The basic inputs and estimated parameters are presented in Table 3. The estimated total fish biomass
313 was $5.101 \text{ t km}^{-2} \text{ year}^{-1}$. *EEs* computed for phytoplankton and detritus were very low.

314

315 Assuming that zooplankton is distributed homogeneously within the first 50 meters of the water
316 column, $0.041 \text{ g fw.m}^{-3}$, it should be noted that the volumetric density of zooplankton is very low and
317 this value appears to be close to several values available in Christensen and Pauly (1993).

318

319 Higher TLs (more than 3.6) were estimated for tunas and barracudas (Table 3). Important groups for
320 fisheries belong between TL2 and TL3, mainly small-sized species which mostly feed on zooplankton
321 and benthic organisms even as juveniles.

322

323 The data collected and assumptions made and integrated as basic inputs appear reasonable,
324 considering the results obtained for gross efficiency (*GE*) of each group. In particular, *GE* is higher for
325 medium and large tunas than for small ones (Table 3) which is in agreement with differential feeding
326 habits related to maximum size. *P/Q* for sardines is quite high due to an exceptionally high *P/B* value,
327 whereas it is low for large barracudas.

328

329

330 For several groups, the estimated *EE* values were higher than 0.9 (Table 3) meaning that these
331 groups are highly predated and exploited by fisheries. A particular emphasis has to be put on the
332 groups exploited by small mesh gillnets for which possible over fishing might be considered. The
333 assumption of high *EEs* for invertebrate groups appears to be appropriate as they are highly
334 consumed as they constitute a high proportion of the diet composition of several groups (see annex 1)
335 The computed low *EEs* for both phytoplankton and detritus could presumably be attributed to absent
336 of typical primary consumers (except zooplankton) in the ecosystem. For other groups, the *EE* values
337 computed by the model seem to be in an agreement with what is known both in terms of fishing
338 pressure and possibilities of predation.

339

340 The flow diagram of the ECOPATH model is shown in Fig. 2. The ecosystem is phytoplankton-based,
341 as 70.4% of the total food consumption comes from primary producers and only 29.6 % originated
342 from detritus, a feature of relevance in deep water bodies (Christensen and Pauly, 1993). Most
343 primary production was consumed by the benthic organisms and zooplankton groups whereas the
344 dominant flow to detritus (about 80% of the total) came from primary producers (TL1).

345

346 The *OI* of each group is also presented in Table 3. Higher *OI* was estimated for needlefish, sea catfish
347 and other carangids (0.377, 0.367 and 0.332 respectively). High *OIs* reflect large feeding spectrum
348 and distribution in the ecosystem. The *OI* of shrimps and crabs were also exceptionally high. The TL
349 of catch is 2.88 whereas the *GE* of catch is 0.0042.

350

351 3.2. *Fishing effort simulation results*

352 The outputs of the fishing effort simulations describe the situation of the ecosystem at the end of the
353 three distinct exercises in terms of biomass and possible catch (Tables 4 to 6). When the small-mesh
354 gillnets is considered, results show a biomass decline of several targeted species at various extents;
355 for example the catch of sardines would collapse. Catches would increase to various levels for most
356 other groups except yellowstripes, the abundance of which would decrease, most likely due to
357 unavailability of their preys (Table 4).

358

359 Increasing the fishing effort of other gears would, most likely, not have any negative affect to the
360 biomass of small fishes since these are mainly caught by small-mesh gillnets. Catch of some less
361 predated fish groups are less impacted (Table 5). Moreover, the decrease in abundance of principal
362 groups predated by tuna and barracuda increased following the stock collapse of these predators.

363

364 The increase in fishing effort for both fishing activities led to the collapse of the sardine stocks and
365 fishery. Similar trends were observed for the three tuna groups. Herring and other clupeids stocks
366 seem to decrease as a response to increasing fishing pressure. *Thryssa* and *Anchovies* biomass and
367 catch would increase substantially.

368

369 An increase in fishing activity of all combined gears seemed to affect biomass of functional groups
370 captured by the different gears. In terms of catch, small mesh-gillnet fishing seems to contribute
371 largely to the overall decline in catch. Fishing activities by other gears increases the total catch of
372 targeted species to about 31% (Table 5). Finally, if both fishing activities were developed
373 simultaneously to the same extent, this would result to a decline (about 18%) of small-mesh gillnets
374 catches while increasing catches from other gears to about 25% (Table 6).

375

376 3.3. *El Niño simulation results*

377 From El Niño simulation results (Fig. 3), groups belonging to the lower TLs appear to be strongly
378 influenced by phytoplankton abundance variations. The Zooplankton group seems immediately
379 affected whereas other groups would affect with some delay. The delay would increase whereas the
380 magnitude of variations decreases with increasing TL. A minimum lag time of one year was observed
381 for trends to be stabilised. The time needed for any group to get back to its initial abundance
382 increased with the TL. The depletion of large tuna and other predators (not displayed on Fig. 3) might
383 have contributed to the temporary very high abundance of the clupeids, which is simulated one year
384 after the El Niño event.

385

386 3.4. *Model validation results*

387 The plots of the derived monthly mean catch in kg per boat per day (CPUE) for two of the ECOPATH
388 functional groups are shown in the Fig. 4. The figure also indicates the trends in abundance of two

389 groups estimated by the moving average method. The catch rates of Herring had been on a declining
390 trend since the early months of 1999 (Fig. 4a). This was observed until end of 2000. However, this
391 group managed to recover after 2000. The catch rates of other ECOPATH groups (large tuna and
392 kingfish) have considerably been affected from 1999 – 2002 and gradually recovered since 2003 (Fig.
393 4b). Accordingly, the ECOSIM simulation results were in accordance with the actual trends in the
394 abundance of two ECOPATH groups represented by the monthly catch rates.

395

396 **4. Discussion**

397 There are few pitfalls in the ECOPATH/ECOSIM approach. ECOSIM can produce misleading
398 predictions. Erroneous predictions usually result from bad estimates or errors of omission for a few
399 key parameters such as B, P/B and Q/B (Christensen et al., 2005). Moreover, incorrect assessments
400 of predation impacts for prey that are rare in predator diets, underestimates of predation vulnerabilities
401 and temporal variation in species-specific habitat had also been previously noted as some factors that
402 could be influenced for final results.

403

404 The main limitation of the present model is related to the steady-state consideration, as most of the
405 input data referred to different time periods. This ecosystem has experienced environmental
406 fluctuations over the studied period such as the massive El Niño of 1998: Therefore, the steady-state
407 assumption might not reflect environmental conditions closed to the reality. Moreover, the ecosystem
408 is not completely closed and many groups such as larger fishes (tunas) are not restricted to the area.

409

410 As noted above, the major challenge for this multispecies modelling was the lack of studies on the
411 feeding ecology of the functional groups considered. Therefore, further investigation should be carried
412 out on this topic which should be considered as one of the key priority objective in this research area.

413 To improve the quality of the presented model, it would therefore be necessary to improve the quality
414 of the catch landing statistics under the above-mentioned catch monitoring programmes in order to
415 obtain more precise estimations for a multispecies approach.

416 Preparation of the feeding matrix for this ECOPATH model was a difficult task since lack of previous
417 studies on feeding ecology in relation to this ecosystem. Most of the qualitative data provided by
418 outside studies were converted into a quantitative form for preparation of the feeding matrix. As the

419 model consists of many groups (39 groups), the feeding matrix contains some low percentages. In
420 fact, these values are hard to determine from field data. This nature too might substantially influence
421 for the final result.

422 The TL of catch is 2.88 due to the relative importance of intermediate TLs. The *GE* of catch is in
423 agreement with earlier findings for various marine environments (Christensen and Pauly, 1993), but
424 much lower than that observed in the San Miguel Bay, Philippines: 0.016 (Bundy and Pauly, 2001). By
425 contrast, West African ecosystems display much lower values of the *GE* of the catch: less than 0.001
426 (Chavance et al., 2004).

427 The estimated total fish biomass was in fact quite low compared to some tropical littoral marine
428 ecosystems documented in West Africa by (Palomares et al., 2003) in which estimated biomasses
429 vary from 16.1 to 27.2 t km⁻². The fish biomass of 5.1 t km⁻² in the littoral waters of Sri Lanka is similar
430 to what was computed by Christensen (1998).

431

432 For ECOSIM simulations, the choice of the values for the vulnerability parameter is very important
433 since simulations are very sensitive to this parameter. We adopted default values which compromise
434 between top down and bottom up regulations of the food web and might not be too far from the reality.

435 A further increase in the fishing effort of small-mesh gillnet fishery would seriously affect the small
436 pelagic fish populations, mainly sardines, in terms of biomass and catches. Sardines play a vital role
437 contributing to a significant wasp-waist control in the ecosystem. They are key species in the
438 transferring energy from primary and secondary productions to higher TLs.

439

440 Within the ECOSIM simulations, a special attempt was made to understand the possible impacts of a
441 sudden environmental change which could be similar to the massive El Niño event experienced in
442 1998. The ENSO phenomenon takes place every three to seven years and each time substantial
443 impacts to fisheries have been observed (<http://www.csa.com/discoveryguides/archives/elnino.php> ;
444 Le Blanc, 1999; Loukos et al., 2003). This phenomenon has been observed responsible for drastic
445 reduction in the primary production due to the lack cold nutrient-rich water, which becomes limiting
446 (Loukos et al., 2003; Roessing et al., 2004). An increase in sea surface temperature levels can alter

447 ecological behaviours (i.e. migration patterns, increased mortalities, change in spawning season, etc)
448 of some groups living resources and as a consequence lead to change in ecosystem structure. This
449 was already observed in 1997-98 in California where the distribution, abundance and catch of market
450 squid declined (National Assessment Synthesis Team –US Global Change Research Programme,
451 2000; <http://www.usgcrp.gov/usgcrp/Library/nationalassessment/overviewcoastal.htm>) following the
452 ENSO phenomenon. Other unusual co-occurring changes observed were widespread sea lion pup
453 mortality in California, catches of warm-water marlin in the usually frigid waters off the Washington
454 State and poor salmon returns in Bristol Bay, Alaska.

455
456 Roessing et al. (2004) examined the global climate change-related effects like El Niño on tropical
457 fishes by looking at comparatively well-studied tropical coral reef ecosystems and their fish
458 communities. They selected only the coral reef communities since previous physiological studies of
459 other tropical fishes were found to be comparatively few. It concluded that adverse impacts on coral
460 reef (coral bleaching and the loss of reef complexity, etc.) after severe climate-related effects could be
461 the main causes of considerable reduction in terms of abundance and the biodiversity of several
462 invertebrates and fishes. Coral reef communities seem to be among the first groups to show signs of
463 such adverse effects probably due to weak trophic links even if these groups are less exploited in the
464 fisheries (Dulvy et al. 2004). It has also been observed in some cases that increases in temperature
465 could affect immune system function and decrease fecundity in coral reef fishes (Cubillos and Arcos,
466 2002).

467
468 In West Africa, the El Niño effect had completely changed the hydrology of several aquatic
469 ecosystems. Sine Saloum, as an example, had evolved into an inverse hypersaline estuary following
470 this event. Although it did not have considerable detrimental effects on the system's species richness,
471 inhabiting species, mainly true estuarine, were considerably replaced by marine-estuarine species nor
472 in some life-history traits of some fish species (Panfili et al., 2004).

473
474 Recruitment in clupeid fish species is known to be highly seasonal and variable (Karunasinghe and
475 Wijeyaratne, 1998). Low biomass in late 1998 may be due to recruitment failure caused by El Niño.
476 The El Niño effect in 1998 might have appeared with a certain time lag in small pelagic fishes. As

477 sardines and herrings have high turn-over rates (i.e., high P/B ratio), the El Niño effect might have
478 affected the landings within a short time lag.

479

480 Fish populations may need many years to recover after an ENSO phenomenon, as observed from our
481 ECOSIM simulations. This might be due not only to the trophic link re-structuring cumulated with high
482 fishing mortality of fished groups. Understanding such responses from different communities
483 experiencing similar environmental changes seem to be essential to improve management decisions
484 for sustainable utilisation of the fishery resources. But, time lag events could be tested from ECOSIM
485 routine, which allows for the simulation of the ecosystem and therefore, provides a basis for the
486 consideration of it as a dynamic system.

487

488 Time dynamic simulation has been an effective tool in describing the El Niño simulation results and
489 proved useful in depicting ecosystem response to sudden environmental change. However, as noted
490 above, there was some disagreement concerning the recovery time of affected populations between
491 the ECOSIM predictions and the field observations. The delays in the actual recovery time of the
492 affected populations could presumably be attributed to other factors related to significant adaptive
493 response/s in some aggregated groups that may be “masked” due to limited information. Moreover,
494 the catch rates derived from commercial fisheries data may not reflect correctly the abundance of the
495 concerned fish groups.

496

497 Although it is impossible to predict the effects of global warming on the frequency of El Niño events, all
498 indications seem to be that they are becoming stronger, more common, and are no longer
499 disappearing completely. Some climate model experiments suggest an increase in El Niño frequency,
500 linked to a future greenhouse warming (Timmermann et al. 1999). On the other hand, a different
501 physical model leads to strong upwelling in the eastern equatorial Pacific that could weaken the
502 warming there, thereby strengthen equatorial winds, causing more upwelling and a net cooling in the
503 eastern Pacific (Cane et al. 1997).

504

505 The fishing industry of Sri Lanka was severely affected owing to the surprised tsunami disaster in 26th
506 December 2004. Heavy damages were especially reported from the fishing crafts operated in the

507 shallow coastal waters. This was greatly contributed to ease the fishing pressure on the coastal
508 waters. Small pelagic fish landing statistics in 2005 indicated an increase trend in the catch per boat
509 compared to previous years. On the other hand, habitat destruction by the tsunami has affected to
510 reduce the abundance, particularly species associated with coral substrates such as butterflyfish
511 (Chaetodontidae), gobies (Gobiidae) and wrasses (Labridae) (Rajasuriya et al., 2005;
512 <http://www.nara.ac.lk/RAP>). In addition to the above, ground level species of the food web such as
513 phytoplankton and zooplanktons might have considerably affected during the tsunami. This would
514 gradually affect to the higher TLs as previously observed in El Niño simulation.

515

516 The above results furthermore suggest that there is not enough evidence to accept that the current
517 fishing practices of small pelagic species and factors other than fishery (depletion of the stocks due to
518 other reasons) might have produced some severe changes in the fish resources availability resulting
519 in a time limited but apparent over fishing. Therefore, more cautions should be made to keep the
520 present levels or possibly of a lower level of exploitations of small pelagic fishes. Moreover, there are
521 some possibilities to increase the exploitation from other gears and to target large predatory fishes,
522 which are more abundant in deeper waters outside the present ecosystem.

523

524 **5. Conclusion**

525 The ECOPATH model built up to describe the trophic relationships in the coastal ecosystem of Sri
526 Lanka helps to understand the general dynamic of this ecosystem. Moreover, quantitative and
527 qualitative information provided by the model are in agreement with studies for similar ecosystems.
528 This multispecific approach furthermore provides informative explanations of some incidents which
529 took place during the past.

530

531 During a natural event such as El Niño, there is a high risk to affect the marine food web of this
532 ecosystem. Therefore, additional care must be taken into consideration on sudden crashes of the fish
533 populations after such an event. Recovery time of the displaced populations after a sudden
534 environmental change could vary due to several reasons. Continuation of the exploitations furthermore
535 by fishing during such a crucial stage might lead to a total collapse of the resources.

536

537 It was noted that there are few possibilities to increase the current exploitation of large pelagic fishery
538 resources. However, it is advisable to provide subsidies for few fishermen who are currently engaged
539 in coastal small scale gillnet fishery, and to direct them to the exploitation of large pelagic fish and
540 thereby reduce the fishing pressure on small pelagic fishes. Sri Lanka has not yet been able to make
541 effective use of the high value tuna and other resources in the deep sea areas as well as in the high
542 seas due to the non-availability of fishing vessels with the requisite capabilities.

543

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545

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Table 1. Growth and mortality parameters of the selected ECOPATH functional fish groups with the selected representative species in the coastal ecosystem of Sri Lanka.

ECOPATH Group	Representative species	L_{∞} (cm TL)	K (year ⁻¹)	Z (P/B) (year ⁻¹)	M (year ⁻¹)	F (year ⁻¹)
Sea catfish	<i>Arius bilineatus</i>	64.3 ^a	0.15 ^b	0.98 ^c	0.42 ^d	0.56 ^e
Needlefish	<i>Strongylura leiura</i>	73.0 ^a	0.12 ^b	0.50 ^f	0.35 ^d	0.15 ^e
Pomfrets & Torp	<i>Parastromateus niger</i>	39.4 ^a	0.60 ^a	2.50 ^g	1.18 ^d	1.32 ^e
Bigeye scad	<i>Selar crumenophthalmus</i>	34.8 ^h	0.50 ^h	1.60 ^h	1.09 ^d	0.51 ^e
Yellowstripe	<i>Selaroides leptolepis</i>	23.0 ^a	1.15 ^a	4.26 ^j	2.10 ^d	2.16 ^e
Other Carangids	<i>Carangoides malabaricus</i>	29.0 ^a	0.96 ^a	2.00 ^f	1.75 ^d	0.25 ^e
Milk fish	<i>Chanos chanos</i>	47.9 ^j	0.30 ^k	0.81 ^l	0.71 ^e	0.10 ^l
Wolf-herrings	<i>Chirocentrus dorab</i>	117.9 ^a	0.10 ^l	0.35 ^f	0.28 ^d	0.07 ^e
Sardines	<i>Sardinella gibbosa</i>	17.0 ^h	2.20 ^h	10.30 ^h	3.60 ^d	6.70 ^e
Herrings	<i>Amblygaster sirm</i>	24.1 ^h	1.52 ^h	3.65 ^h	2.49 ^d	1.16 ^e
Other Clupeids	<i>Hilsa kelee</i>	21.5 ^a	1.10 ^a	3.09 ⁱ	2.08 ^d	1.01 ^e
Dolphinfishes	<i>Coryphaena hippurus</i>	177.7 ^a	0.05 ^l	0.25 ^f	0.15 ^d	0.10 ^e
Thryssa sp.	<i>Thryssa setirostris</i>	22.8 ^a	1.30 ^b	2.45 ^f	2.29 ^d	0.16 ^e
Anchovies	<i>Stolephorus heterolobus</i>	8.6 ^h	4.02 ^h	7.57 ^h	6.48 ^d	1.09 ^e
Flyingfishes	<i>Hirundichthys oxycephalus</i>	28.5 ^h	1.10 ^h	3.09 ^h	1.93 ^d	1.16 ^e
Halfbeaks	<i>Rhynchorhamphus malabaricus</i>	36.6 ^a	NA	1.92 ^c	0.96 ^d	0.96 ^e
False trevallie	<i>Lactarius lactarius</i>	27.0 ^a	0.63 ^a	1.61 ^l	1.39 ^d	0.25 ^l
Ponyfishes	<i>Leiognathus brevisrostris</i>	13.8 ^a	0.90 ^a	4.40 ^a	2.10 ^d	2.30 ^e
Mugilids	<i>Mugil cephalus</i>	89.7 ^m	0.09 ^m	1.10 ⁿ	0.51 ^d	0.59 ^e
Terapontids	<i>Terapon theraps</i>	34.0 ^a	0.61 ^a	1.39 ^l	1.24 ^d	0.15 ^e
Ribbon fish	<i>Lepturacanthus savala</i>	108.0 ^a	0.75 ^a	1.41 ^f	1.03 ^d	0.38 ^e
Drums	<i>Otolithes ruber</i>	45.9 ^a	0.32 ^a	1.00 ^l	0.78 ^d	0.22 ^e
Indian mackerel	<i>Rastrelliger kanagurta</i>	36.0 ^h	1.70 ^h	3.99 ^h	2.48 ^d	1.51 ^e
Small Tunas	<i>Auxis thazard thazard</i>	63.7 ^o	0.83 ^o	2.84 ⁱ	1.28 ^d	1.56 ^e
Medium Tunas	<i>Katsuwonus pelamis</i>	85.0 ^p	0.44 ^p	2.46 ^c	0.78 ^d	1.68 ^e
Large Tunas & Kingfish	<i>Scomberomorus commerson</i>	146.0 ^h	0.37 ^h	1.49 ⁱ	0.60 ^d	0.89 ^e
Soles	<i>Euryglossa orientalis</i>	33.0 ^a	NA	1.2 ^l	0.97 ^q	0.23 ^e
Large Barracuda	<i>Sphyraena jello</i>	148.0 ^a	0.10 ^a	0.50 ^l	0.25 ^d	0.25 ^e
Small barracuda	<i>Sphyraena obtusata</i>	39.5 ^a	0.62 ^a	3.37 ^c	1.23 ^d	2.14 ^e

- a. Fröese and Pauly (2006);
- b. Estimated value with reference to L_{∞} ;
- c. Computed value indirectly after the computation of Q/B from the predictive model of Palomares and Pauly (1989) (see the text below) by assuming a reasonable value of gross food-conversion efficiency GE (defined by $GE = P/Q$) by referring to the group's diet composition (DC) as suggested by Christensen and Pauly (1993).
- d. Pauly (1980) (temperature for the study area was considered as 28° C);
- e. Estimated value from the relationship $Z = F + M$;
- f. Lévêque et al (1977);
- g. An average of several Z values for fish of the same family mainly Pampus species (Dwiponggo et al., 1986 and Dadzie et al 2003 in press);
- h. Dayaratne (1998);
- i. Moshin and Ambak (1996);
- j. Siriwardena (1986);
- k. A computed value using auximetric grid in fishbase (Fröese and Pauly, 2006);
- l. A suggested value;
- m. Wijeyaratne and Costa (1987);
- n. An average value from two out side studies ((Abarca-Arenas and Valero-Pacheco, 1993 and Chavez et al, 1993);
- o. Sivasubramaniam (1973);
- p. BOBP (1987);
- q. Value computed based on empirical relation of Fröese and Binohlan (2000).

Table 2. Sources of the data (mainly P/B and Q/B) of non fish groups

<i>Group</i>	<i>P/B</i>	<i>Q/B</i>	<i>EE</i>
Shrimps (<i>Penaeus indicus</i>)	Jayawardane (2001)	A value set for P/Q = 0.20	Computed by ECOPATH
<i>Crabs:</i>	Abarca-Arenas and Valero-Pacheco (1993)	Arreguín-Sánchez et al. (1993a)	Value was fixed
Cephalopods	Christensen and Pauly (1993).	Christensen and Pauly (1993).	A fixed value
Molluscs	Chavez et al. (1993)	Vega-Cendejas et al. (1993).	A fixed value based on substantial predation
Annelids/Polychaetes	Arreguín-Sánchez <i>et al.</i> , (1993a, b).	Arreguín-Sánchez <i>et al.</i> (1993a, b).	A fixed value based on substantial predation
Zoobenthos	Chavez et al. (1993).	Chavez et al. (1993).	A fixed value based on substantial fish and shrimp predation
Zooplankton	Irvine and Waya, (1999) Sarvala et al. (1999)	Irvine and Waya, (1999) Sarvala et al., (1999) ; Christensen et al. (2005)	A fixed value based on substantial juvenile fish predation
Phytoplankton	Pattiaratchi (2002).	---	Biomass was available
Phytobenthos	Christensen and Pauly, (1993)	---	A fixed value because of high predation

Table 3. Input values and estimated parameters (in brackets) for the coastal ECOPATH model of Sri Lanka. TL is the trophic level, *B* is Biomass, P/B is production rate, Q/B is the consumption rate, P/Q is production per consumption ratio, *EE* is the ecotrophic efficiency and *OI* is the omnivory index.

ECOPATH Group	TL	Catch (t km ⁻² year ⁻¹)		B (t km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	P/Q	EE	OI
		Gillnets	Other gears						
Large tunas	(3.86)		0.154	0.173	1.49	7.77	(0.19)	(0.67)	(0.206)
Medium tunas	(3.83)		0.013	0.008	2.46	12.29	(0.20)	(0.77)	(0.227)
Small barracudas	(3.80)	0.0035	0.032	0.016	3.37	13.48	(0.25)	(0.81)	(0.205)
Small tunas	(3.78)	0.0009	0.008	0.006	2.84	18.85	(0.15)	(0.93)	(0.223)
Large barracudas	(3.66)		0.105	0.428	0.50	5.49	(0.09)	(0.68)	(0.167)
Wolf-herrings	(3.58)		0.022	0.314	0.35	6.84	(0.05)	(0.94)	(0.209)
Neddlefish	(3.54)	0.0025	0.011	0.085	0.50	8.22	(0.06)	(0.48)	(0.377)
Other carangids	(3.48)		0.220	0.879	2.00	17.43	(0.12)	(0.79)	(0.332)
Pomfrets, Torps	(3.41)	0.006	0.064	0.051	2.50	15.70	(0.16)	(0.90)	(0.286)
False trevallie	(3.38)		0.013	0.054	1.61	15.45	(0.10)	(0.93)	(0.235)
Yellowstripe	(3.29)	0.0158	0.002	0.008	4.26	23.10	(0.18)	(0.96)	(0.170)
Dolphinfishes	(3.27)		0.018	0.180	0.25	3.67	(0.07)	(0.69)	(0.205)
Cephalopods	(3.22)		0.033	(2.750)	3.10	12.00	(0.26)	0.95	(0.143)
Sea cat fish	(3.11)		0.053	0.098	0.98	6.53	(0.15)	(0.64)	(0.367)
Ribbonfish	(3.07)		0.075	0.196	1.41	6.18	(0.23)	(0.50)	(0.238)
Ponyfishes	(3.06)	0.0211	0.032	0.023	4.40	24.12	(0.18)	(0.82)	(0.098)
Soles	(3.06)		0.0184	(0.122)	1.20	11.05	(0.11)	0.95	(0.001)
Indian mackerel	(3.05)		0.062	0.041	3.99	20.88	(0.19)	(0.96)	(0.000)
Terapontids	(2.96)		0.004	0.040	1.39	12.58	(0.11)	(0.84)	(0.105)
Anchovies	(2.95)	0.204	0.068	0.250	7.57	40.69	(0.19)	(0.89)	(0.100)
Drums	(2.95)		0.026	0.120	1.00	8.48	(0.12)	(0.85)	(0.114)
Other Clupeids	(2.88)	0.206	0.0228	0.226	3.09	22.31	(0.14)	(0.95)	(0.198)
Sardines	(2.84)	1.385	0.073	0.218	10.30	34.02	(0.30)	(0.91)	(0.176)
<i>Thrissa</i> spp	(2.74)	0.0724	0.024	0.612	2.45	18.56	(0.13)	(0.93)	(0.233)
Herrings	(2.64)	0.668	0.035	0.606	3.65	23.31	(0.16)	(0.93)	(0.260)
Crabs	(2.64)		0.100	(1.938)	2.50	8.50	(0.29)	0.95	(0.261)
Flying fishes	(2.53)		0.013	0.012	3.09	26.34	(0.12)	(0.89)	(0.277)
Milk fish	(2.49)	0.0011	0.003	0.040	0.81	37.75	(0.02)	(0.54)	(0.275)
Shrimps	(2.32)		0.266	0.102	5.28	26.40	(0.20)	(0.93)	(0.233)
Bigeye scad	(2.20)	0.0329	0.099	0.257	1.60	32.93	(0.05)	(0.74)	(0.210)
Halfbeaks	(2.18)	0.00219	0.007	(0.030)	2.68	53.66	(0.05)	0.50	(0.156)
Mugilids	(2.13)		0.004	0.008	1.10	20.36	(0.05)	(0.67)	(0.117)
Annelids	(2.05)			(0.780)	4.60	25.00	(0.18)	0.95	(0.053)
Zoobenthos	(2.05)			(5.559)	10.00	50.00	(0.20)	0.95	(0.053)
Zooplankton	(2.05)			(2.039)	30.00	150.00	(0.20)	0.95	(0.053)
Molluscs	(2.00)			(3.488)	2.50	9.30	(0.27)	0.95	(0.000)
Phytoplankton	(1.00)			2.625	365.00	-	-	(0.33)	
Phytobenthos	(1.00)			(11.477)	12.50	-	-	0.95	
Detritus	(1.00)			10.0	-	-	-	(0.23)	(0.271)

Table 4. ECOSIM simulation results for the small mesh gillnets (key groups are in bold). OB is the original biomass, FB is the final biomass, OY is the original yield and FY is the final yield.

Group name	OB	FB	FB/OB	OY	FY	FY/OY
Large tunas	0.173	0.167	0.97	0.154	0.149	0.97
Medium tunas	0.008	0.007	0.87	0.013	0.011	0.87
Small barracuda	0.016	0.011	0.68	0.036	0.026	0.73
Small tunas	0.006	0.005	0.85	0.009	0.008	0.91
Large barracuda	0.428	0.392	0.92	0.105	0.096	0.92
Wolf-herings	0.314	0.242	0.77	0.022	0.017	0.77
Neddlefish	0.085	0.075	0.88	0.014	0.014	1.00
Other carangids	0.879	0.911	1.04	0.220	0.228	1.04
Pomfrets, Torps	0.051	0.045	0.89	0.070	0.066	0.95
False trevallie	0.054	0.06	1.12	0.013	0.015	1.12
Yellowstrip	0.008	0.002	0.21	0.018	0.006	0.35
Dolphinfishes	0.18	0.186	1.03	0.018	0.019	1.03
Cephalopods	2.75	2.988	1.09	0.033	0.036	1.09
Sea cat fish	0.098	0.100	1.02	0.053	0.054	1.02
Ribbonfish	0.196	0.22	1.12	0.075	0.084	1.12
Ponyfishes	0.023	0.016	0.71	0.054	0.050	0.92
Soles	0.122	0.129	1.06	0.019	0.020	1.06
Indian mackerel	0.041	0.047	1.16	0.062	0.072	1.16
Terapontids	0.04	0.046	1.16	0.004	0.005	1.16
Anchovies	0.249	0.26	1.05	0.283	0.464	1.64
Drums	0.12	0.125	1.04	0.026	0.027	1.04
Other Clupeids	0.224	0.16	0.72	0.238	0.285	1.2
Sardines	0.209	0.028	0.13	1.473	0.336	0.23
<i>Thrissa</i> spp	0.611	0.632	1.03	0.316	0.386	1.22
Herrings	0.6	0.456	0.76	0.731	0.953	1.3
Crabs	1.938	1.970	1.02	0.100	0.102	1.02
Flying fishes	0.012	0.013	1.10	0.013	0.014	1.10
Milk fish	0.040	0.039	0.99	0.004	0.005	1.19
Shrimps	0.102	0.102	1.00	0.266	0.267	1.00
Bigeye scad	0.257	0.231	0.90	0.134	0.144	1.08
Halfbeaks	0.030	0.030	0.99	0.009	0.011	1.17
Mugilids	0.008	0.010	1.27	0.004	0.005	1.27
Annelids	0.78	0.789	1.01			
Zoobenthos	5.562	5.503	0.99			
Zooplankton	2.044	2.28	1.12			
Molluscs	3.49	3.664	1.05			
Phytoplankton	2.625	2.556	0.97			
Phytobenthos	11.473	11.311	0.99			
Detritus	9.299	9.092	0.98			
Small mesh gillnets				2.696	2.165	0.8
Other gears				1.892	1.807	0.95
Total	45.145	44.904	0.99	4.588	3.972	0.87

Table 5. ECOSIM simulation results for “other gears” (key groups are in bold). OB is the original biomass, FB is the final biomass, OY is the original yield and FY is the final yield.

Group name	OB	FB	FB/O B	OY	FY	FY/OY
Large tunas	0.172	0.049	0.29	0.159	0.082	0.52
Medium tunas	0.008	0.001	0.09	0.013	0.002	0.16
Small barracuda	0.016	0.002	0.1	0.036	0.006	0.18
Small tunas	0.006	0.002	0.31	0.009	0.005	0.53
Large barracuda	0.427	0.301	0.7	0.109	0.138	1.26
Wolf-herings	0.314	0.394	1.26	0.023	0.052	2.25
Neddlefish	0.085	0.064	0.76	0.014	0.017	1.25
Other carangids	0.877	0.900	1.03	0.228	0.420	1.84
Pomfrets, Torps	0.05	0.013	0.25	0.072	0.031	0.43
False trevallie	0.054	0.083	1.55	0.014	0.037	2.78
Yellowstripe	0.008	0.011	1.36	0.018	0.027	1.49
Dolphinfishes	0.180	0.137	0.76	0.019	0.025	1.36
Cephalopods	2.750	2.779	1.01	0.034	0.062	1.81
Sea cat fish	0.098	0.034	0.35	0.055	0.035	0.63
Ribbonfish	0.195	0.135	0.69	0.078	0.096	1.24
Ponyfishes	0.023	0.007	0.29	0.054	0.023	0.43
Soles	0.122	0.116	0.95	0.019	0.033	1.70
Indian mackerel	0.041	0.027	0.67	0.064	0.076	1.20
Terapontids	0.040	0.058	1.45	0.004	0.011	2.61
Anchovies	0.250	0.290	1.16	0.275	0.385	1.40
Drums	0.120	0.146	1.22	0.027	0.059	2.18
Other Clupeids	0.226	0.246	1.09	0.230	0.271	1.18
Sardines	0.218	0.208	0.96	1.460	1.453	1.00
<i>Thrissa spp</i>	0.610	0.680	1.11	0.321	0.578	1.8
Herrings	0.606	0.651	1.07	0.704	0.788	1.12
Crabs	1.937	1.872	0.97	0.104	0.180	1.73
Flying fishes	0.012	0.011	0.95	0.013	0.023	1.71
Milk fish	0.040	0.045	1.11	0.004	0.007	1.77
Shrimps	0.100	0.019	0.19	0.272	0.094	0.34
Bigeye scad	0.256	0.208	0.81	0.135	0.176	1.30
Halfbeaks	0.030	0.040	1.32	0.009	0.020	2.12
Mugilids	0.008	0.003	0.38	0.004	0.003	0.67
Annelids	0.780	0.817	1.05			
Zoobenthos	5.561	5.568	1.00			
Zooplankton	2.042	2.024	0.99			
Molluscs	3.488	3.432	0.98			
Phytoplankton	2.625	2.630	1.00			
Phytobenthos	11.475	11.459	1.00			
Detritus	9.300	9.325	1.00			
Small mesh gillnets				2.620	2.645	1.01
Other gears				1.962	2.572	1.31
Total	45.149	44.787	0.99	4.582	5.217	1.14

Table 6. ECOSIM simulation results for combined gears (key groups are in bold). OB is the original biomass, FB is the final biomass, OY is the original yield and FY is the final yield.

Group name	OB	FB	FB/OB	OY	FY	FY/OY
Large tunas	0.172	0.043	0.25	0.159	0.072	0.45
Medium tunas	0.008	0	0.05	0.013	0.001	0.10
Small barracuda	0.016	0	0.02	0.036	0.002	0.04
Small tunas	0.006	0.001	0.18	0.009	0.003	0.32
Large barracuda	0.427	0.267	0.63	0.109	0.125	1.15
Wolf-herrings	0.314	0.319	1.02	0.023	0.043	1.86
Neddlefish	0.085	0.054	0.64	0.014	0.016	1.17
Other carangids .	0.877	0.926	1.06	0.229	0.442	1.93
Pomfrets, Torps	0.050	0.008	0.17	0.072	0.022	0.30
False trevallie	0.054	0.092	1.71	0.014	0.042	3.13
Yellowstripe	0.008	0.003	0.33	0.018	0.011	0.59
Dolphinfishes	0.180	0.139	0.77	0.019	0.026	1.41
Cephalopods	2.751	3.043	1.11	0.034	0.07	2.02
Sea cat fish	0.098	0.033	0.34	0.055	0.034	0.62
Ribbonfish	0.195	0.152	0.78	0.078	0.111	1.42
Ponyfishes	0.023	0.002	0.08	0.054	0.008	0.14
Soles	0.122	0.125	1.02	0.019	0.036	1.87
Indian mackerels	0.041	0.032	0.79	0.064	0.092	1.44
Terapontids	0.040	0.065	1.63	0.004	0.012	2.99
Anchovies	0.249	0.303	1.22	0.283	0.631	2.23
Drums	0.120	0.152	1.27	0.027	0.063	2.32
Other Clupeids	0.224	0.172	0.76	0.237	0.331	1.40
Sardines	0.211	0.015	0.07	1.470	0.188	0.13
<i>Thrissa spp</i>	0.610	0.698	1.14	0.324	0.679	2.09
Herrings	0.601	0.481	0.80	0.726	1.062	1.46
Crabs	1.938	1.909	0.99	0.104	0.188	1.80
Flying fishes	0.012	0.012	1.05	0.013	0.026	1.92
Milk fish	0.040	0.044	1.11	0.004	0.009	2.02
Shrimps	0.100	0.017	0.17	0.272	0.084	0.31
Bigeye scad	0.256	0.175	0.68	0.137	0.171	1.25
Halfbeaks	0.030	0.039	1.30	0.010	0.023	2.39
Mugilids	0.008	0.004	0.51	0.004	0.004	0.94
Annelids	0.780	0.833	1.07			
Zoobenthos	5.563	5.514	0.99			
Zooplankton	2.044	2.282	1.12			
Molluscs	3.489	3.618	1.04			
Phytoplankton	2.625	2.556	0.97			
Phythobenthos	11.474	11.266	0.98			
Detritus	9.299	9.103	0.98			
Small mesh gillnets			2.675	2.185	0.82	
Other gears				1.961	2.443	1.25
Total	45.137	44.497	0.99	4.636	4.628	1

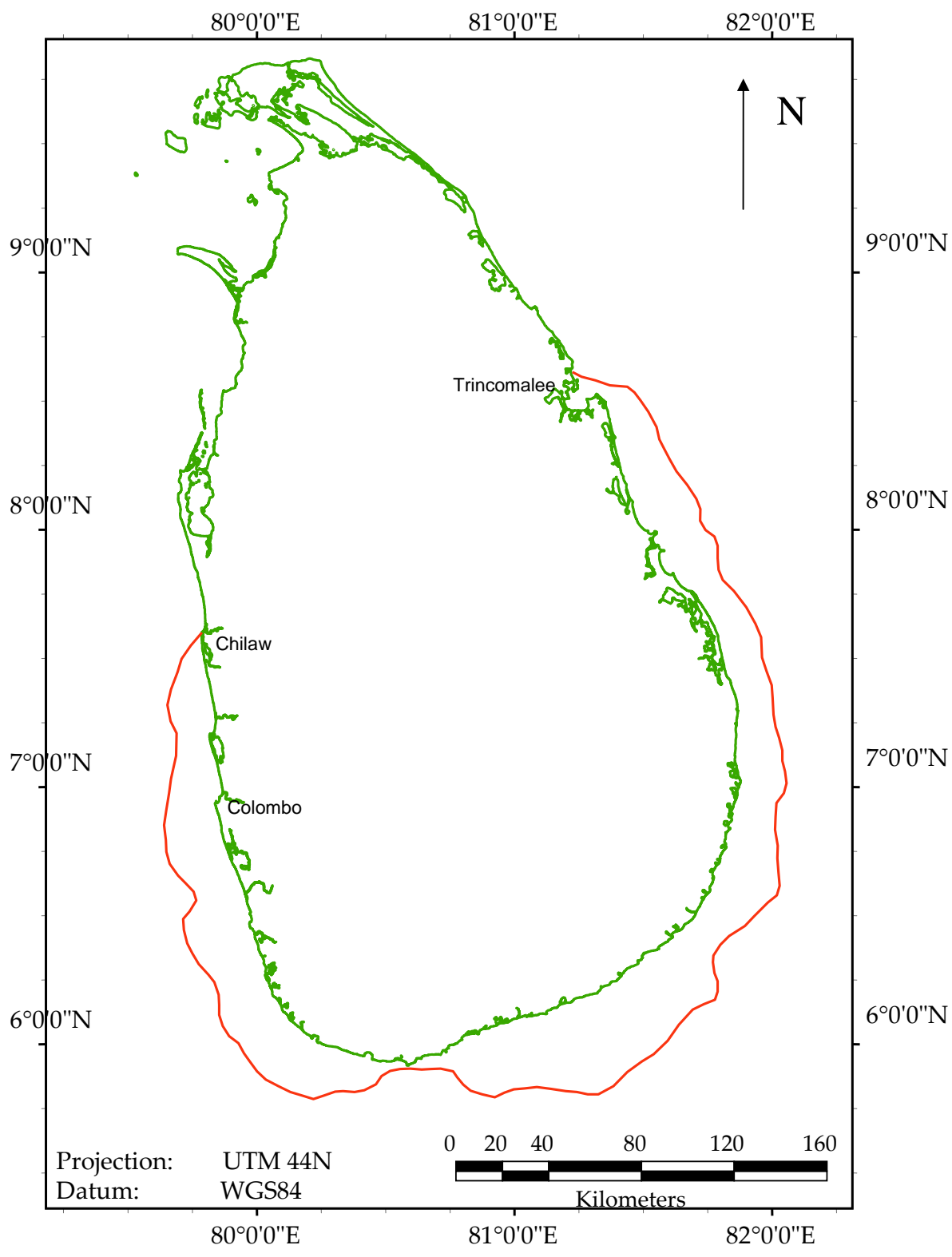
Figure captions

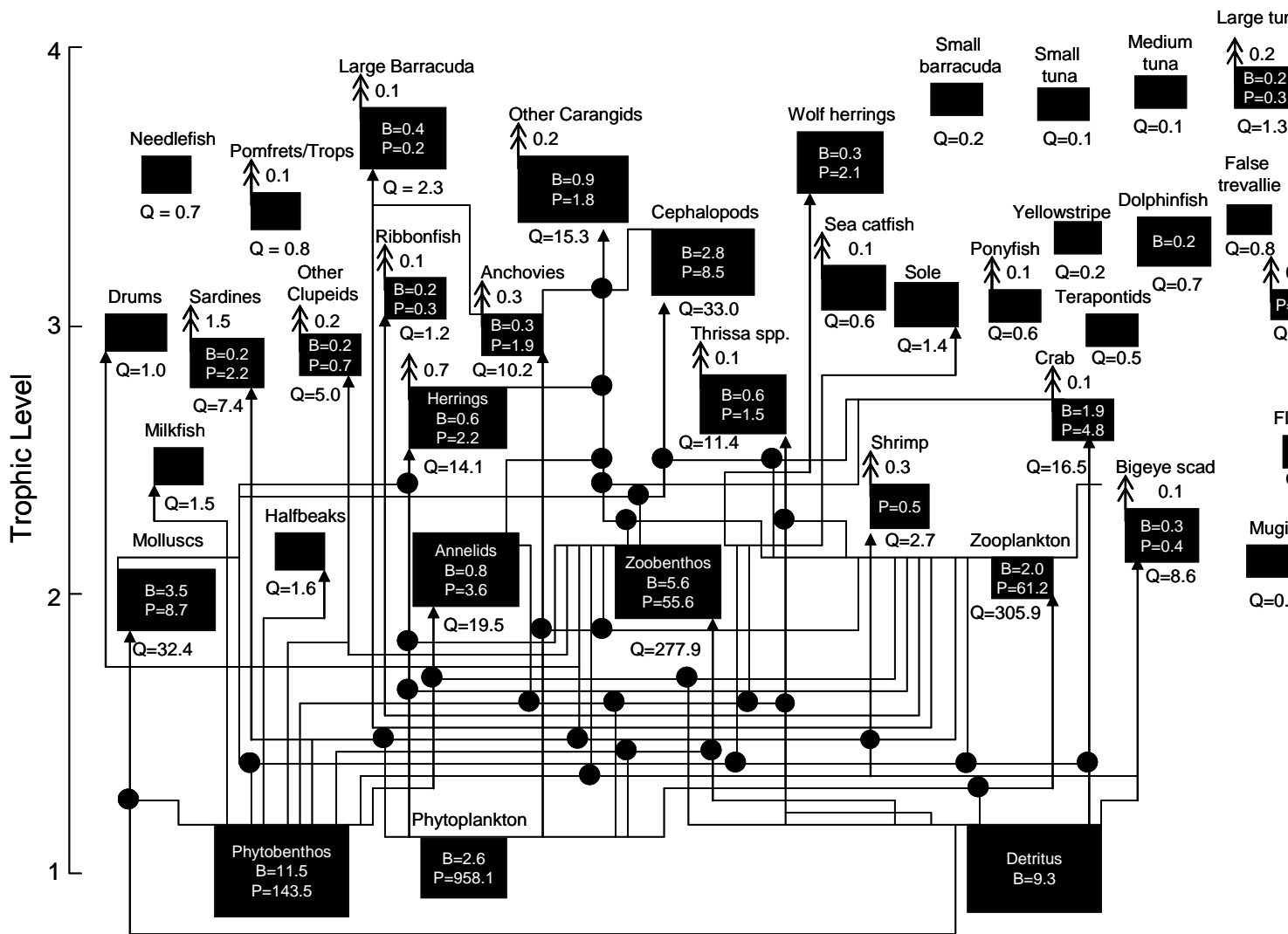
Fig. 1. A map of the studied coastal ecosystem

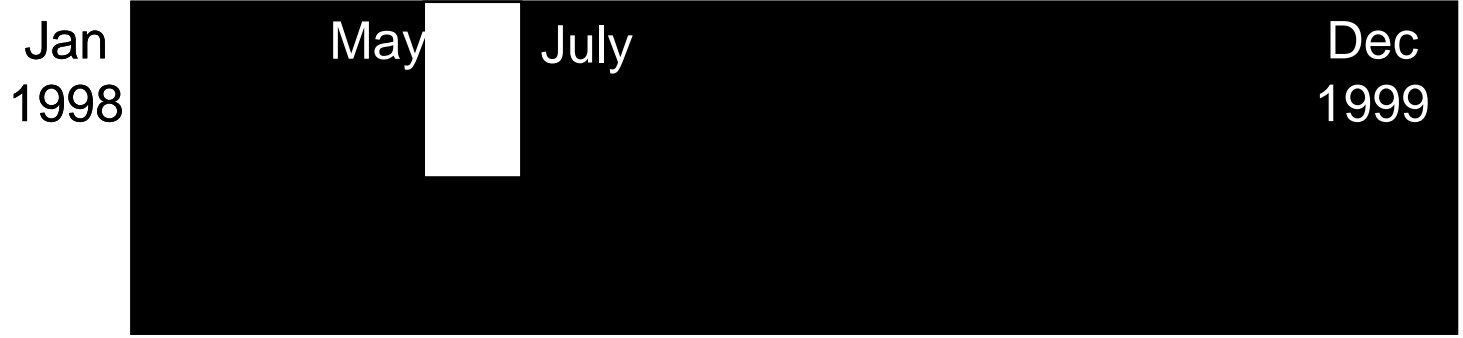
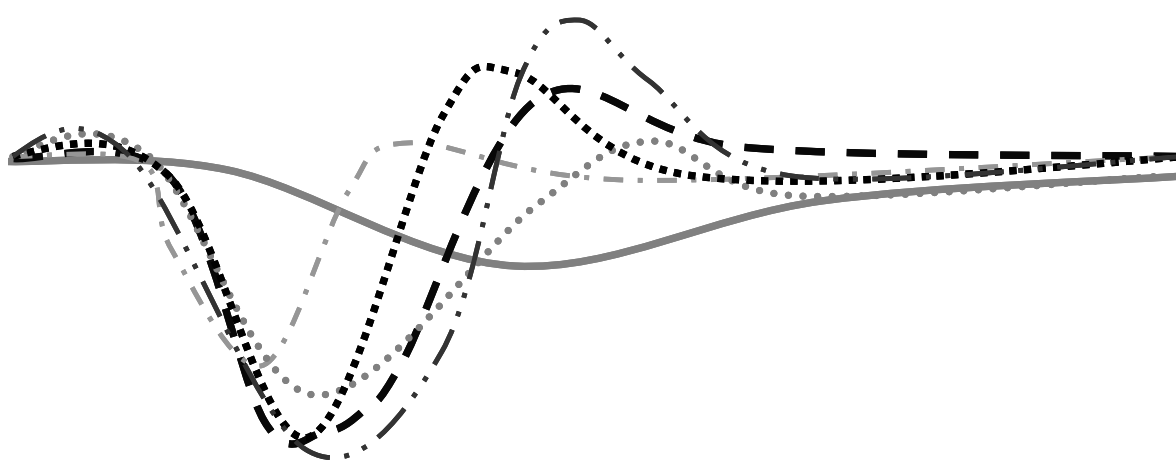
Fig 2. The ECOPATH model for the coastal marine ecosystem of Sri Lanka indicating relative biomass of each group and the major flows connecting them. Less important flows are omitted for clarity sake. The horizontal axis of symmetry of each box is aligned with the trophic level of this box. The value of a trophic level is a fractional because it depends on the diet composition of this group and on the trophic levels of its preys (Christensen and Pauly, 1993). B : Biomass B ($t\ km^{-2}$), P: Production ($t\ km^{-2}\ yr^{-1}$), Q: Food consumption (t/km^2yr^{-1}). Arrows on the top of some box are actual catch. ($t\ km^{-2}yr^{-1}$).

Fig 3. A simulation of the possible effect of an El Niño event (which decreases the primary production by 50% for three months starting in May 1998) on abundance of key groups at various trophic levels. The seasonality in recruitment pattern was not considered.

Fig 4. The derived monthly mean catch rates (CPUE) for two ECOPATH functional groups: (a) Herrings (Period: January 1998 – December 2001) (b) Large tunas and kingfish (Period: January 1998 – December 2003). The trends in the CPUE obtained from the method of the moving average are also shown.







- Phytoplankton
- Zooplankton
- - - - Sardines
- - - - Herrings
- Anchovies
- Large tuna

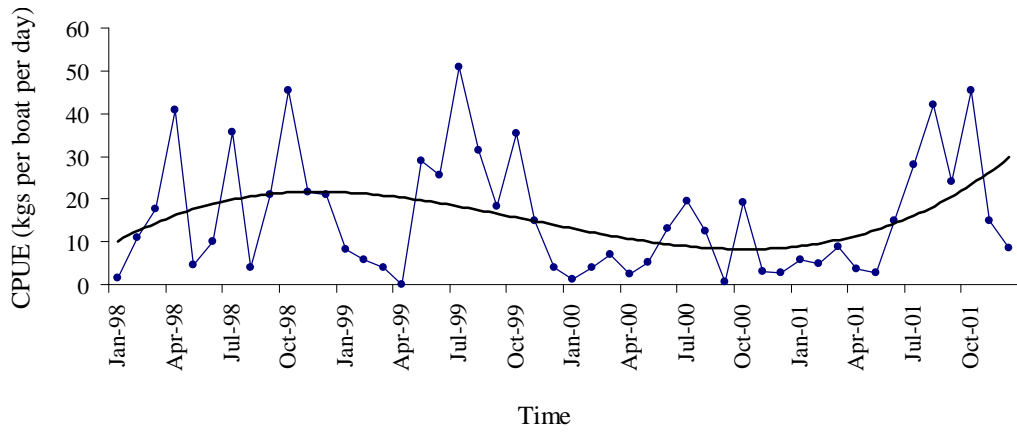


Figure 4 a

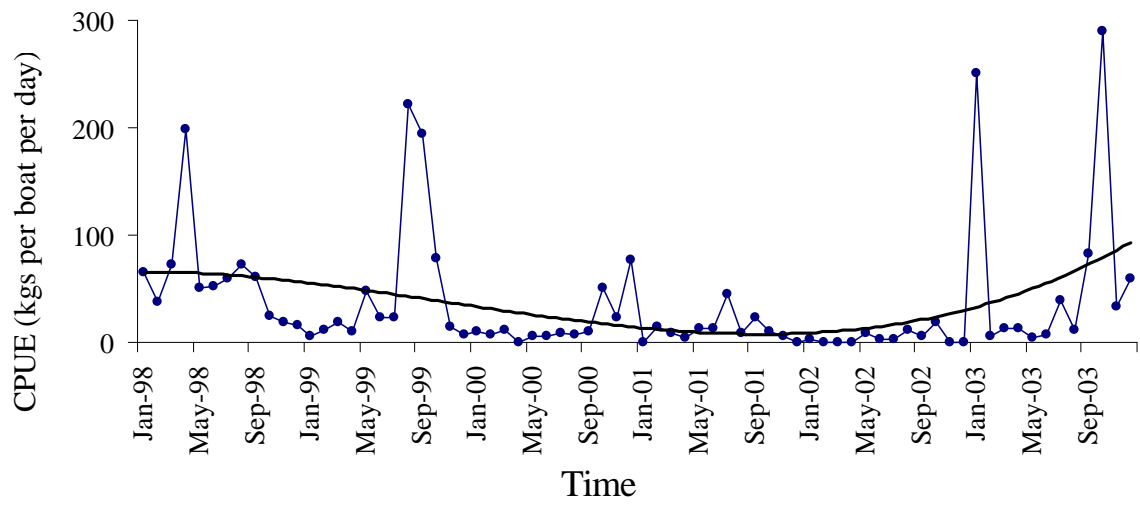


Figure 4 b